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**Lack of conformity to new local dietary preferences in migrating captive chimpanzees**

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24 Conformity to the behavioural preferences of others can have powerful effects on intra-group  
25 behavioural homogeneity in humans, but evidence in animals remains minimal. In this study,  
26 we took advantage of circumstances in which individuals or pairs of captive chimpanzees  
27 (*Pan troglodytes*) were “migrated” between groups, to investigate whether immigrants would  
28 conform to a new dietary population preference experienced in the group they entered, an  
29 effect suggested by recent fieldwork. Such ‘migratory-minority’ chimpanzees were trained to  
30 avoid one of two differently-coloured foods made unpalatable, before ‘migrating’ to, and then  
31 observing, a ‘local-majority’ group consume a different food colour. Both migratory-minority  
32 and local-majority chimpanzees displayed social learning, spending significantly more time  
33 consuming the previously unpalatable, but instead now edible, food, than did control  
34 chimpanzees who did not see immigrants eat this food, nor emigrate themselves. However,  
35 following the migration of migratory-minority chimpanzees, these control individuals and the  
36 local-majority chimpanzees tended to rely primarily upon personal information, consuming  
37 first the food they had earlier learned was palatable before sampling the alternative. Thus,  
38 chimpanzees did not engage in conformity in the context we tested; instead seeing others eat  
39 a previously unpalatable food led to socially learned and adaptive re-exploration of this now-  
40 safe option in both minority and majority participants.

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42 Key Words: conformity, culture, cultural transmission biases, social learning, social learning  
43 strategies

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47 Many of the daily choices faced by animals require decisions about whether to engage in  
48 personal exploration of the environment (asocial learning) or instead to exploit the existing  
49 knowledge of others by learning socially (Kendal, Coolen, & Laland, 2009; Kendal, Coolen,  
50 van Bergen, & Laland, 2005; Laland, 2004). Evolutionary theory predicts that if appropriate  
51 decision making rules can be economically employed, social learning will itself be selective.  
52 Such selectivity may be pursued through heuristics termed social learning strategies (Laland,  
53 2004), or transmission biases (Boyd & Richerson, 1985; Henrich, 2001), which dictate who,  
54 what, when or even how to copy. The identification of such heuristics has proved instructive  
55 in understanding how cultures evolve in humans and other species (Kendal et al., 2015;  
56 Rendell et al., 2011). A variety of social learning strategies have recently been identified in  
57 diverse animal taxa (Kendal et al., 2009; Laland, 2004; Rendell et al., 2011), such as  
58 preferentially copying ‘dominant’ or ‘knowledgeable’ individuals (Kendal et al., 2015). One  
59 particularly powerful social learning strategy is conformist copying of majority behaviour,  
60 shown by mathematical modelling to facilitate intergroup cultural diversity and intragroup  
61 homogeneity (Boyd & Richerson, 1985), especially in spatially variable environments  
62 (Nakahashi, Wakano, & Henrich, 2012). Conformist copying is predicted to be adaptive,  
63 insofar as it can support the rapid uptake and maintenance of local information, by the  
64 copying of traits that are common among individuals already familiar with their environment.  
65 Social psychologists often refer to such effects in terms of two kinds of ‘social norms’. In the  
66 words of one such authority, “In addition to perception of what most other approve (the  
67 injunctive social norm), there is a second social normative type (the descriptive social norm)  
68 that also direct behaviour forcefully. Descriptive social norms refer to one’s perception of  
69 what most others actually do” (Cialdini, 2007. P. 264). It is the latter phenomenon we focus  
70 on here.

71

72 Authors have defined the concept of conformity in other variant ways over the years  
73 (Claidiere & Whiten, 2012; van Leeuwen & Haun, 2014). Originally, social psychologists  
74 emphasised conformity as the subjugation of personal knowledge or behaviour in favour of  
75 an alternative displayed by a majority of others. The classic work of Asch (1956), in which  
76 participants were prepared to express agreement with the clearly incorrect perceptual  
77 judgments of a group of experimental confederates, is an example of this form of conformity.  
78 Human deference to such group responses has since been replicated many times and has been  
79 shown to be sensitive to a number of factors, such as cultural context, audience presence, and  
80 group size (Bond, 2005; Bond & Smith, 1996; see Morgan & Laland, 2012).

81 It is this sense of conformity we address in the present paper concerning our closest  
82 primate relative, the chimpanzee (*Pan troglodytes*). However to avoid confusion, we first  
83 note that some students of cultural evolution have defined conformity in the more specific  
84 sense of a *disproportionate* tendency for individuals to copy a majority, even without  
85 subjugation of known behaviours (Boyd & Richerson, 1985; Whalen & Laland, 2015), a  
86 phenomenon that has been labelled ‘conformist transmission’ (van Leeuwen & Haun, 2014;  
87 Whalen & Laland, 2015). Theoretical simulation studies have suggested that such conformist  
88 transmission may readily evolve in populations of social learners, although strong conformist  
89 tendencies can also be maladaptive in preventing the spread of potentially beneficial  
90 innovations (Henrich & Boyd, 1998; Kandler & Laland, 2013; Wakano & Aoki, 2007).  
91 Recent studies in fish and birds respectively, have suggested that such disproportionate  
92 copying of majorities may occur in non-human animals (e.g., great tit *Parus major*: Aplin et  
93 al., 2015a; nine-spined stickleback *Pungitius pungitius*: Pike & Laland, 2010 ) although this  
94 conclusion has proved controversial (Aplin et al., 2015b; van Leeuwen, Kendal, Tennie, &  
95 Haun, 2015; Whiten & van de Waal, in press).

96           In intermediate levels of environmental change and patterns of spatial heterogeneity,  
97 social learning becomes an adaptive strategy (reviewed in Vale, Carr, Dean, & Kendal, in  
98 press). Conformity may be an important social learning strategy when migrating to a new  
99 area and entering a new group (Boyd & Richerson, 1985), where there is scope for  
100 uncertainty about the optimal ways to behave. ‘Copy when uncertain’ is one of the other  
101 principal social learning strategies highlighted in studies of both humans and non-human  
102 species (Kendal et al., 2009; Kendal et al., 2015; Laland, 2004). Recent evidence consistent  
103 with ‘copy when uncertain’ and/or ‘conformity’ comes from a small but growing set of field  
104 experiments. In one, after four groups of wild vervet monkeys were trained to prefer just one  
105 of two differently coloured corn provisions because one was made severely distasteful, nine  
106 of ten males migrating between groups after the distasteful additive was removed were found  
107 to quickly abandon their earlier learned preference in favour of the other colour if they  
108 entered a group where a majority was eating this (van de Waal, Borgeaud, & Whiten, 2013).  
109 More recently, a similar effect was documented in wild great tits (*Parus major*) that  
110 abandoned an earlier learned preference to peck one side of an artificial foraging device in  
111 favour of the opposite method, if this was shown by a majority of the new community they  
112 entered (Aplin et al., 2015a). There is thus a growing, if still small and controversial,  
113 literature consistent with the existence of this form of conformity to new community  
114 behaviours in the particular circumstance of migrating to a new and unfamiliar social and  
115 physical context (van Leeuwen et al., 2015; Whiten & van de Waal, in press).

116           In the present study of chimpanzees, we focus on conformity as originally defined in  
117 the social psychology literature: adherence to group preferences at the expense of discarding  
118 known or existing personal preferences or behaviours. Specifically, we investigate whether  
119 individuals become flexible in their behavioural options due to the social influences of a  
120 group of conspecifics. Evidence of such a disposition has recently been presented for wild

121 chimpanzees living in neighbouring communities that are each characterised by differing  
122 preferences for nut-cracking hammer materials in different seasons (Luncz, Mundry, &  
123 Boesch, 2012; Luncz & Boesch, 2014). This cannot be easily explained by genetics, given  
124 inter-group transfer and breeding, nor by local environments, since the habitat is similar  
125 across the relevant ranges. However, we note a caveat regarding the role that environment  
126 could play in social transmission via niche construction, if communities' preferred tools  
127 accumulate near nut-bearing trees, thus encouraging their subsequent use. The authors of  
128 these studies have concluded that the differences represent different cultural traditions.  
129 Females display the behavioural profiles that are characteristic of their community, despite  
130 having transferred from other communities, an effect accordingly interpreted as conformity to  
131 local traditions, involving the abandonment of earlier tool preferences (Luncz & Boesch,  
132 2014). This interpretation is supported by tracking of a female migrant that initially displayed  
133 the behavioural profile of her natal community, but over time adopted that of her new  
134 adopted community, and by follow-up studies of changes in tool preferences of a larger  
135 sample of females (Luncz, Wittig, & Boesch, 2015). A possible parallel to this effect in the  
136 vocal domain is the recent tracing of progressive adoption of a local vocalisation dialect at  
137 the expense of their original one by chimpanzees introduced into a new group in a zoo  
138 (Watson et al., 2015a; but see Fisher, Wheeler & Higham, 2015 and Watson et al. 2015b for  
139 further debate). Such results are consistent with an earlier experimental study of the diffusion  
140 of experimentally seeded alternative tool use patterns in different groups of captive  
141 chimpanzees, some of whom discovered the alternative technique, yet re-converged on the  
142 profile of the majority of their group (Whiten, Horner, & de Waal, 2005). However, it is  
143 unclear whether other social learning strategies, such as a tendency to copy particular  
144 individuals or recently observed behaviours, as well as individual learning tendencies, such as  
145 reverting back to a behaviour due to habit formation, may explain such occurrences of

146 behavioural re-convergence (van Leeuwen & Haun, 2013; van Leeuwen & Haun, 2014; van  
147 Leeuwen, Kendal, Tennie & Haun, 2015).

148         Given these emerging findings, in the present study, we experimentally tested for  
149 conformity by exploiting an unusual (perhaps unique) opportunity, in which a statistically viable  
150 sample of individuals or pairs of chimpanzees were to be to new groups in a large US primate  
151 facility, as part of efforts to enhance welfare and social enrichment during the transfer of a  
152 number of chimpanzees to a new facility. Echoing the field experiment of van de Waal et al.  
153 (2013) with wild vervet monkeys, we first exposed chimpanzee subjects to two differently  
154 coloured foods, one of which was made unpalatable, so participants would learn to avoid it.  
155 The group receiving the migrants was taught to prefer the other colour of food. After  
156 allowing time for immigrant chimpanzees to then observe the new, reversed group  
157 preference, we tested whether, like the immigrant males in the vervet study, the immigrants  
158 would conform by changing the food option they chose to ingest.

## 159 METHODS

### 160 *Animals*

161 A total of 60 chimpanzees, housed at the National Center for Chimpanzee Care (NCCC)  
162 Michale E. Keeling Center for Comparative Medicine and Research of the University of  
163 Texas MD Anderson Cancer Center, were included in this study (mean age = 30.7 years,  
164 range 13- 53 years; 32 female).

### 165 *Migratory-Minority Subjects*

166 Eleven chimpanzees (5 female, termed migratory-minority individuals) provided the  
167 migratory subjects for the study. These chimpanzees were migrated into nine new groups all  
168 housed at the same facility. Migration refers to the physical movement of these chimpanzees

169 to new groups that were housed in a different enclosure to the former housing of the  
170 migratory-minority individuals. Migratory-minority individuals moved to their new  
171 enclosures/groups either individually or in pairs (see Table 1). In the wild, females leave  
172 their natal groups to migrate to other groups (Nishida et al., 2003; Pusey, Williams, &  
173 Goodall, 1997), but to provide a reasonable sample size, this study recorded the behaviour of  
174 both migratory males and females. Following these migrations, the average group size was 5  
175 (range 3-10, Table 1).

176

#### 177 *Local-Majority Subjects*

178 Migratory-minority chimpanzees were relocated into nine groups of chimpanzees ( $n = 37$   
179 chimpanzees, 19 female). These groups were termed local-majority individuals to indicate  
180 that they received the migrating chimpanzees, remaining in their enclosure rather than  
181 themselves relocating, and to denote that their group sizes were always greater than the  
182 number of migrating chimpanzees they received (Table 1 outlines the variation in local-  
183 majority group sizes and the number of migrating chimpanzees they received). One local-  
184 majority subject failed to participate in this study.

#### 185 *Control groups*

186 Twelve chimpanzees (8 female) formed our control groups (2 groups consisting of 7 and 5  
187 chimpanzees). Control groups received no migrating individuals. These controls allowed the  
188 assessment of whether chimpanzees, with an induced food preference, may change their food  
189 preferences despite not receiving migrating chimpanzees trained on a different dietary  
190 preference. One control individual failed to participate in the study.

191



192 *Ethical note*

193 Chimpanzees were not moved specifically for the purpose of this study. Instead, we exploited  
194 the fact that in a colony reorganisation, these chimpanzees were to be moved to new groups  
195 to promote enhanced welfare and to sustain large group sizes or to restructure existing  
196 groups. Some chimpanzee movements were designed to also make smaller groups for these  
197 chimpanzees' movement to a new facility. All chimpanzees chose whether or not to  
198 participate in the study. Chimpanzees were not deprived of food or water. Ethical approval  
199 was granted for this study by Institutional Animal Care and Use Committee (IACUC  
200 approval number 0894-RN01) and the University of St Andrews' Animal Welfare and Ethics  
201 Committee.

202 [insert Table 1 around here]

203 *Materials*

204 Two sources of food (toasted oats) were provisioned in two differently coloured (green and  
205 orange) feeders (36" L x 4 W" x 2" H, see supplementary video) located on the outside of the  
206 chimpanzee enclosures. The feeders were positioned flush against the enclosure mesh so that  
207 chimpanzees could reach through the mesh to gain access to the provisioned food. To  
208 distinguish the two food sources, food was also coloured either green or orange (using food  
209 dye) and placed in the corresponding colour feeder. Chimpanzees have been shown to  
210 perceive colours like humans do (Matsuzawa, 1985), so the present study used colour to  
211 distinguish the two food sources. For the purpose of inducing food preferences, one food  
212 source (green or orange, counterbalanced) was made unpalatable by treating it with Foey  
213 Ultra-Bitter Training Aid (see Table 1). Food dye was added to the Foey Ultra-Bitter  
214 Training Aid before spraying the mixture into the food until it was coated. Foey Ultra-Bitter  
215 Training Aid is a bitter liquid used to deter pets from chewing household items.

216 *Procedure*

217 In this study we followed the general procedure of van de Waal and colleagues (2013),  
218 previously applied to wild vervet monkeys (*Chlorocebus aethiops*).

219 *Training Phase*

220 To establish food colour preferences we ran an initial training phase in which all chimpanzees  
221 (migratory-minority, local-majority, control individuals) were provisioned with orange and  
222 green food in two adjacent, differently coloured feeders, one of which (orange or green) was  
223 made unpalatable by spraying it with Fooey Ultra-Bitter Training Aid (Table 1 and  
224 supplementary video). To ascertain whether migratory-minority subjects adopt the food  
225 choice of their new group, different food colour preferences were always induced in resident  
226 local-majorities and the individuals who would be migrating into them (migratory-  
227 minorities). We followed this procedure until both coloured foods were sampled by 80%, or  
228 above, of subjects and until a maximum of one animal per session sampled the unpalatable  
229 food across three consecutive sessions. Each session lasted for 20 minutes, during which the  
230 food sources were refilled when nearly depleted. To re-bait, both food sources were  
231 simultaneously removed from, refilled, and then repositioned within reach of the subjects.  
232 Both food sources were refilled using this procedure when one or both were nearly depleted.  
233 This ensured there was always access to both food sources. This method was employed to  
234 prevent biasing chimpanzees' food selections should only one source remain within their  
235 reach. In situations where two chimpanzees, housed together, were moving to new groups,  
236 they were trained as a pair (see also SM Table 1). For local-majorities, all training was  
237 conducted in a group setting.

238 *Group Stabilization and Observation Phase*

239 Following the migratory-minorities' movements into new groups, and a habituation period  
240 that allowed the newly formed groups time to stabilize, migrants were given the opportunity  
241 to observe the local-majority consume the food colour that these migrants had learned was  
242 unpalatable (observation phase). Habituation periods were determined by the chimpanzee  
243 colony manager and based on behavioural monitoring of the newly formed groups'  
244 interactions. As groups stabilized at different rates and in some cases, chimpanzee  
245 movements were delayed, the interval between the training and observation phase varied  
246 across groups (Mean = 33, range 7-68 days). During the observation phase, the food that  
247 local-majority chimpanzees were trained to discriminate as unpalatable was again treated  
248 with Foey Ultra-Bitter Training Aid. To allow only observation of the local-majority food  
249 preference, migratory-minority individuals voluntarily separated from the local-majority,  
250 while remaining in visual contact through areas of wire mesh of the enclosures. A minimum  
251 of two, 30-minute observation sessions were conducted, during which the attendance levels  
252 of migratory-minority individuals were recorded in situ at 1-minute intervals. Additional  
253 observation sessions were run following subjects' failure to attend to the local majority  
254 consuming food on more than 15 one-minute intervals until this criterion was met. An  
255 individual was recorded as attending to the local-majority if their head was oriented toward  
256 the local majority while they were consuming food. In practice, only a single individual  
257 required an additional observation session. Control groups, which did not receive migrating  
258 chimpanzees, did not participate in an observation phase.

### 259 *Test Phase*

260 In the test phase, conducted the day after the observation phase, chimpanzees, now as a  
261 group, were provisioned with untreated orange and green food for three 30-minute sessions.  
262 This phase allowed an assessment of whether chimpanzees switched their food preferences to  
263 match those of their new companions (previously unpalatable, 'unPal', food) and for controls,

264 whether they stuck with their induced food preference (previously palatable, ‘Pal’, food),  
265 when both foods were palatable. Again, participation was voluntary. All food sampling was  
266 continuously coded, noting the start and end time of the feeding bout and the type of food that  
267 was consumed. This allowed the calculation of the overall consumption times according to  
268 food type. Chimpanzee food selections during three 30-minute test sessions were also coded  
269 by a second researcher and inter-rater reliability was 100%. Due to a limited sample size, data  
270 were analysed using nonparametric, two-sided, statistical tests. The dependent variable was  
271 the proportion of time chimpanzees spent consuming previously unPal food (time spent  
272 consuming previously unPal food (secs)/total time spent consuming previously unPal and Pal  
273 food).

274 Following Kendal et al (2015) dominance rank was assessed by using three chimpanzee  
275 experts’ ratings using a three-point categorical dominance scale ranking each chimpanzee of  
276 each group as either ‘high’, ‘medium’ or ‘low’ dominance. Ratings were given for the newly  
277 formed chimpanzee groups once they had stabilized, and for the controls, ratings were given  
278 for their already stable groups. Inter-rater reliability was high ( $ICC_{2,1} = 0.831$ ,  $P < 0.001$ ; see  
279 section ‘*Group Stabilization and Observation Phase*’ above, for details of how group  
280 stabilization was determined) . As in Kendal et al. (2015), the modal rank was selected for the  
281 few cases of rank disagreements.

## 282 RESULTS

283 The proportion of time spent consuming previously unPal food differed according to subject  
284 group (migratory-minority/local-majority/controls: Kruskal-Wallis test:  $H_2 = 11.10$ ,  $N = 58$ ,  $P$   
285  $= 0.004$ ). Both migratory-minority chimpanzees (median = 0.107) and local-majority  
286 chimpanzees (median = 0.285) spent proportionately more time consuming their previously  
287 unPal food than did controls (median = 0.00; Mann-Whitney U test:  $U = 21.00$ ,  $N_{\text{controls}} = 11$ ,

288  $N_{\text{migratory-minority}} = 11$ ,  $P = 0.008$ ;  $U = 74.00$ ,  $N_{\text{controls}} = 11$ ,  $N_{\text{local-majority}} = 36$ ,  $P = 0.002$ ,  
289 respectively, Figure 1; see also supplementary Tables 2 -5 for individual and group food  
290 preferences), suggesting that chimpanzees in both categories were affected by witnessing  
291 others eating the alternative food. There was no difference in the proportion of time  
292 migratory-minority chimpanzees and local-majority chimpanzees spent consuming their  
293 previously unPal foods (Mann-Whitney U test:  $U = 166.00$ ,  $N_{\text{local-majority}} = 36$ ,  $N_{\text{migratory-minority}}$   
294  $= 11$ ,  $P = 0.420$ ; Bonferroni adjustment applied with alphas set at 0.017). Latencies to first  
295 sample the previously unPal food also did not differ between local-majority (median = 1800s)  
296 and migratory-minority (median = 630s) chimpanzees (Mann-Whitney U test:  $U = 105.00$ ,  
297  $N_{\text{local-majority}} = 29$ ,  $N_{\text{migratory-minority}} = 9$ ,  $P = 0.39$ ).

298 [insert Figure 1 around here]

299

300 There was no difference in the proportion of time local-majority individuals spent consuming  
301 the previously unPal food, nor in their latency to first sample this food, according to  
302 dominance rank (H/M/L proportion of time spent consuming unPal food, Kruskal-Wallis test:  
303  $H_2 = 1.135$ ,  $N = 36$ ,  $P = 0.564$ ; H/M/L latency, Kruskal-Wallis test:  $H_2 = 2.063$ ,  $N = 29$ ,  $P =$   
304  $0.356$ ). This suggests that food switching was not due to competition from more dominant  
305 individuals. Moreover, three of the migratory-minority, ranked 'high', 'medium' and 'low',  
306 displayed overall preferences for the previously unPal food (see supplementary materials).  
307 This suggests that competition did not deter some chimpanzees (of any rank) from consuming  
308 the food preferred by the local-majority.

309 All majority individuals, except one female, that sampled the previously unPal food  
310 during the test phase, did so only after a migrant had already sampled it. Local-majority  
311 individuals sampled the unPal food after observing, on average, just 2 (median) unPal food

312 sampling events (range 0-8 events,  $N = 29$ ; ‘events’ account for observing the same  
313 individual sample the food multiple times), or watching, on average, 1 (median) individual  
314 sample unPal food (range 0-4)). As migratory-minorities were exposed to an observation  
315 phase in which they observed the local-majority consume the food they knew to be unPal, all  
316 migratory-minority subjects, during the test phase, that sampled the unPal food did so only  
317 after observing the local-majority consume it.

318         Although social learning influenced the food sampled by local-majority and  
319 migratory-minority chimpanzees, chimpanzees overall relied preferentially upon personal  
320 information, tending to first consume the known Pal food before sampling the previously  
321 unPal food (49 of 58 chimpanzees, Chi Goodness of Fit test:  $\chi^2_1 = 27.59$ ,  $P < 0.001$ ). The  
322 food that was consumed first (Pal/unPal) did not differ according to subject group (migratory-  
323 minority/local-majority/controls: Fisher’s Exact Test = 3.00,  $P = 0.262$ ). The high prevalence  
324 in first consuming known-Pal food suggests that the variation in the time it took groups to  
325 stabilize (mean = 33, range 7-68 days) did not influence chimpanzees’ first food selections.  
326 Only one of the eleven migratory-minority individuals first sampled the previously unPal  
327 food they had witnessed the residents eat. This female chimpanzee took longer to sample any  
328 of the food (321s) than other migratory-minority individuals (mean = 18s, range 0 – 109s),  
329 and in this sense, appeared more uncertain than others, before making her novel choice.  
330 There appeared to be no sex differences in the food first sampled by migratory-minority  
331 individuals given that all, except this one female, selected the known Pal food first. Overall,  
332 the median proportion of time migratory-minority males spent consuming unPal food was  
333 0.093 (IQR = 0.34) and for migratory-minority females was 0.147 (IQR = 0.79). Migratory-  
334 minority females, on average (median), sampled the previously unPal food after 894s (IQR =  
335 2689.50) and migratory-minority males did so after 276s (median, IQR = 2798.50). The  
336 average time taken to first sample the known Pal was equivalent across sex (female

337 migratory-minority: median = 5.00s, IQR = 1854; male migratory-minority (median = 4.50s,  
338 IQR = 27.25; note that that there are too few participants to perform inferential statistics to  
339 determine possible sex differences).

## 340 DISCUSSION

341 We assessed whether migrating chimpanzees would opt to switch to a conflicting dietary  
342 preference displayed by the resident group they moved to. Both migratory-minority and  
343 local-majority chimpanzees spent proportionately more time consuming their previously  
344 unPal food than control groups that received no migrating chimpanzees. This suggests that  
345 exposure to other animals consuming the alternative food encouraged food exploration  
346 through social learning, despite participants' prior experience of marked unpalatability in this  
347 option. However, we found that instead of conforming, migratory-minority chimpanzees'  
348 initially, and overall, relied upon personal information, preferring to sample the food they  
349 knew to be palatable.

350 Adaptive behaviour requires individuals to be informed by acquiring relevant  
351 information from their surroundings, either by personal exploration (asocial learning),  
352 observing others (social learning), or both (Dall, Giraldeau, Olsson, McNamara, & Stephens,  
353 2005). Simultaneous employment of personal and social learning could lead to better  
354 informed individuals than when concentrating on one information source alone. While our  
355 chimpanzees appeared not to engage in conformity, we did observe bidirectional information  
356 exchange between migratory-minority and local-majority individuals. Indeed, only nine of  
357 the 47 local-majority and migratory-minority chimpanzees failed to sample the food that they  
358 had learned was very unpalatable. Such switching between information sources encouraged  
359 food exploration and maximised the amount of food available to subjects. This capacity to  
360 nimbly switch behavioural responses (socially and asocially learned) has implications for

361 cultural evolution in changing environments, wherein established behaviours can periodically  
362 become redundant (Boyd & Richerson, 1985).

363 Other studies have also recently reported a lack of conformity in captive chimpanzees  
364 (Haun, Rekers, & Tomasello, 2014; van Leeuwen, Cronin, Schütte, Call, & Haun, 2013), a  
365 result with which the current study is consistent. This is despite chimpanzees being shown to  
366 have a disposition to copy a majority, over a minority behaviour when they are task naive  
367 (Haun, Rekers, & Tomasello, 2012) and wild migratory female chimpanzees apparently  
368 transitioning to the behaviour of their new group (Luncz & Boesch, 2014; although see van  
369 Leeuwen & Haun, 2013; van Leeuwen & Haun, 2014; van Leeuwen, Kendal, Tennie &  
370 Haun, 2015).

371 Several different factors might account for the lack of a disposition to conform  
372 reported in this study. First, is a countervailing tendency in chimpanzees for conservative  
373 behaviour; to persevere with a known behaviour despite the availability of a behavioural  
374 alternative that is within participants' capacity to learn, noted in several recent studies (Haun  
375 et al., 2014; Hrubesch, Preuschoft, & van Schaik, 2009; Marshall-Pescini & Whiten, 2008;  
376 although see Manrique, Volter & Call, 2013 and Davis et al. in press, for cases of flexible  
377 behaviour in chimpanzees when past solutions become unavailable or very costly). However,  
378 as local-majority and migratory-minority chimpanzees proceeded to sample both previously  
379 Pal and unPal foods, social information was sufficient to overcome the conservative Pal food  
380 preference documented in control chimpanzees. Given evidence in the literature for the  
381 opposite tendencies of both conservatism and conformity/social learning in chimpanzees, a  
382 key question for future research is identification of the factors that throw the switch between  
383 these opposing dispositions.



384 A further question is whether the conformity documented in wild chimpanzees may  
385 arise from alternative copying strategies such as copying dominant individuals (Kendal et al.,  
386 2015; see van Leeuwen & Haun, 2013; van Leeuwen & Haun, 2014; van Leeuwen, Kendal,  
387 Tennie & Haun, 2015). That local-majority chimpanzees sampled the previously unPal food  
388 following the observation of, on average, only one individual sample this food, indicates that  
389 conformity was not required for flexible behaviour. This is reminiscent of Norway rats  
390 (*Rattus norvegicus*) that switch from food known to be palatable, to sample foods thought to  
391 be toxic or less palatable after interacting with a conspecific that ate the undesirable food  
392 (Galef and Whiskin, 2008). Such findings highlight the need for future migration studies to  
393 include single demonstrator-observer pairs to assess whether behavioural switching requires  
394 social information from one or many individuals.

395 A second possible explanation for our results concerns the costs of alternative options.  
396 Theoretical analyses indicate that reliance upon social information should increase as the  
397 costs associated with acquiring or using personal information increase (Boyd & Richerson,  
398 1985; Feldman, Aoki, & Kumm, 1996). This has been termed the “costly information  
399 hypothesis”, which depicts an evolutionary trade-off between acquiring (or using) accurate,  
400 but costly (personal) information versus less accurate, but cheap (social) information (Boyd  
401 & Richerson, 1985). It is noteworthy that the chimpanzees in the present study acquired  
402 accurate personal information of the Pal food coupled with little cost in its subsequent use.  
403 Conversely, conformity to social information incurred the potential costs of consuming a  
404 food personally known to be distasteful, coupled with competition from the new group if  
405 opting to sample it; the strong conformity effect reported by van de Waal et al. (2013) for  
406 migrating male vervet monkeys occurred most prominently when males could approach the  
407 locally preferred food without a higher-ranked resident present. Such circumstances could  
408 plausibly reduce the incentive for chimpanzees in the present study to conform to the new

409 dietary preference of resident chimpanzees. However, dominance rank did not appear to  
410 predict how much time chimpanzees spent consuming the previously unPal food or when  
411 they first sampled it. Rather, a bias towards personal information may have been reinforced  
412 by a lack of prior exposure in these chimpanzees to potentially noxious foods and general risk  
413 when engaging in individual exploration: the collection and use of personal information may  
414 have very little cost in captive populations. A lack of risk experienced by captive animals,  
415 when presented with novel objects and foods, has been suggested to explain the neophilic  
416 responses of captive animals compared to the neophobic responses for their wild counterparts  
417 (Forss et al., 2015). Thus, it may be more costly for wild populations, which are likely to  
418 have experienced costs for ignoring social information, to ignore the dietary choices of local  
419 individuals.

420           A third possible explanation for the lack of conformity observed relates to  
421 informational uncertainty. Theoretical analyses also suggest that individuals should use social  
422 information when they are uncertain, whether induced by prior information being unreliable,  
423 a lack of prior personal information (Boyd & Richerson, 1988), personal information  
424 becoming outdated (Boyd & Richerson, 1985; Boyd & Richerson, 1988), the accumulated  
425 knowledge of conspecifics being more reliable (Giraldeau, Valone, & Templeton, 2002), or  
426 through environmental variability (Boyd & Richerson, 1985). Environmental heterogeneity in  
427 the present study, introducing uncertainty, may not have been within the right parameters for  
428 chimpanzees to adopt the dietary preference of their group. Modelling studies and theoretical  
429 considerations suggest that social learning pays under intermediate levels of environmental  
430 change, or with moderate levels of spatial heterogeneity, where change is not so rapid as to  
431 require asocial learning, or so slow that adaptive behaviour can evolve through natural  
432 selection (reviewed in Vale et al., in press). In the present study, environmental variability  
433 was introduced by chimpanzees' migrations to a new enclosure with new residents. However,

434 all enclosures at the research site provide rather similar ecological conditions, and migratory-  
435 minority and local-majority chimpanzees were not necessarily unfamiliar to one another in all  
436 cases. Accordingly, environmental variability may not have been sufficient to elicit any  
437 conformist dispositions, compared to that experienced by wild animals migrating to distant  
438 locations and groups.

439         Nevertheless, we did observe social information use in chimpanzees exposed to  
440 conspecifics consuming previously unPal food. Here, personal knowledge of the unPal food  
441 was conflicted by new information, which could explain the chimpanzees sampling of this  
442 previously distasteful food. This may suggest social learning occurred as uncertainty about  
443 the palatability of the two food options increased. Accordingly, it is plausible that the  
444 forgoing of old solutions in favour of group preferred solutions, documented in wild  
445 populations, could occur because of environmental and social uncertainty, as much as from  
446 the number of demonstrators modelling the new behaviour (see van Leeuwen et al., 2015;  
447 Whiten & van de Waal, in press, for discussion).

448         In conclusion, conspecifics foraging on one of two available food sources provided  
449 migratory-minority and local-majority individuals with social information regarding the  
450 quality of resources (Dall et al., 2005). Chimpanzees' resource site selections have been  
451 shown to be influenced by the selections of others when they lack prior personal experience  
452 (Haun et al., 2012; Vale, Flynn, Lambeth, Schapiro, & Kendal, 2014). In contrast to this, our  
453 findings suggest that even persuasive social information (multiple individuals to learn from)  
454 was mostly disregarded by chimpanzees when they possessed conflicting prior personal  
455 information. This reliance on personal information, coupled with the local-majority  
456 chimpanzees' deviation from an established group preference, suggests that chimpanzees did  
457 not engage in conformity in the present context and raises the possibility that matching  
458 majority preferences in other contexts may be driven by alternative non-conformist biases.

459 Nevertheless, our results suggest flexible learning in chimpanzees. Specifically, exposure to  
460 other animals consuming alternative food encouraged food exploration through social  
461 learning. Such flexible use of learning strategies has important implications for chimpanzees'  
462 ability to track potential shifts in circumstances by updating their prior knowledge.

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466 **Author contributions**

467 GLV collected the data and carried out the statistical analyses; GLV and AW drafted the  
468 manuscript with all authors contributing to the final manuscript; the original conception of  
469 the methodology was the work of AW and EW; the original methodology was adapted for  
470 captive chimpanzees by GLV and AW; SD conducted inter-rater reliability, SPL conducted  
471 and monitored all chimpanzee 'migrations' and provided on site logistical support along with  
472 SJS.

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629 **Supplementary materials**

630 **Additional Results**

631 Local-majority groups spent proportionally more time consuming Pal food in T1 (MD =  
632 1.00) than in T3 (MD = 0.61;  $W = -2.07$ ,  $P = 0.038$ ). There were no significant differences in  
633 the proportion of time local-majority groups spent consuming Pal food between T1 and T2  
634 (MD = 0.58;  $W = -1.82$ ,  $P = 0.069$ ) or between T2 and T3 ( $W = -0.889$ ,  $P = 0.374$ ).

635 Comparable analyses were not conducted for migratory-minority chimpanzees due to a small  
636 sample size.

637         Immigrant chimpanzees moved to new groups as a pair or individually (see SM Table  
638 1 and SM Figure 1 for the proportion of time migratory-minority chimpanzees spent  
639 consuming food according to local-majority group sizes). The average proportion of time  
640 spent consuming the previously unPal food, during the test phase, by chimpanzees that  
641 moved as a pair was 0.459 ([MD], IQR = 0.78,  $N = 4$  chimpanzees) compared to 0.078  
642 ([MD], IQR = 0.15,  $N = 7$ ) by chimpanzees that migrated alone. Immigrant chimpanzees that  
643 moved as a pair sampled the previously unPal food, on average, earlier (MD = 475.50s, IQR  
644 = 2668.50,  $N = 4$ ) than individually moved chimpanzees (MD = 1158.00s; IQR = 2798.50,  $N$   
645 = 5).

646         Food preferences during the test phase varied according to individual, as assessed by  
647 comparing food consumption times to what would be expected by chance alone (binomial  
648 tests, see SM Table 2, 3 and 4). Three migratory-minority individuals preferred the  
649 previously unPal food (of 'low', 'medium' and 'high' dominance rank, 1 male) and eight the  
650 previously Pal (one chimpanzee of 'low', five chimpanzees of 'medium' and two  
651 chimpanzees of 'high' dominance rank, 5 male); 12 local-majority individuals preferred the

652 previously unPal food, 23 the previously Pal and 1 displayed no preference; and 11 of the  
653 (11) control individuals displayed a preference for the previously Pal food.

654           There was slight variation in group food preferences, as assessed by comparing food  
655 consumption times to what would be expected by chance alone (binomial tests, see SM Table  
656 5). Data was collated from all participants (including migratory-minority individuals) to  
657 assess whether there was convergence on either Pal or unPal food. Pal food represents the  
658 food that was previously Pal to the local-majority and controls (thus being previously unPal  
659 to the minority). Seven of the experimental groups displayed a preference for the food that  
660 was known to be Pal to the local-majority, one group displayed no preference and one  
661 preferred the food known to be unPal to the local-majority. Both our controls displayed a  
662 preference for their known Pal food during the test phase (see SM Table 5).

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679 **Table 1.**

680 Number, sex and induced food preference of migrating chimpanzees and the local-majority to  
681 which they migrated.

Group	Migratory-minority			Local-majority		
	<i>N</i>	Number of females	Induced food preference	<i>N</i>	Number of females	Induced food preference
PH	2	1	Orange	4	2	Green
GP	1	1	Green	2	1	Orange
AX	1	0	Orange	2	0	Green
NK	1	0	Green	4	2	Orange
JY	1	1	Orange	2	0	Green
SA	2	2	Green	7	2	Orange
HA	1	0	Orange	2	2	Green
NK	1	0	Green	9	6	Orange
MO	1	0	Green	5	4	Orange

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694 **SM Table 1.**

695 Majority size and proportion of foods consumed by migratory-minority subjects.

Group	Migratory-Minority Subject	Majority Size	unPal	Pal
PH	EY	4	0.65	0.35
PH	DE	4	0.29	0.71
GP	GI	2	0	1
AX	JE	2	0.11	0.89
NK	MC	4	0.08	0.92
SA	JSE	7	0.06	0.94
SA	GE	7	0.98	0.02
HA	ME	2	0.72	0.28
JY	PR	2	0.15	0.85
MO	RR	5	0	1
ALX	SM	9*	0.08	0.92

Note: \* one local-majority did not participate, failing to sample any food

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707 **SM Table 2.**

708 Time spent consuming food during the test phase and migratory-minority individual food  
 709 preferences as determined using the binomial test (probability set at 0.5)

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Migratory-minority						
Group	Individual	Sex	Previously pal	Previously unPal	Binomial p-value	Food preference
PH	EY	f	1444	2667	<0.001	previously unpalatable
PH	DE	m	1443	589	<0.001	previously palatable
GP	GI	f	4149	0	<0.001	previously palatable
AX	JE	m	2106	252	<0.001	previously palatable
NK	MC	m	1724	146	<0.001	previously palatable
SA	JSE	f	1703	106	<0.001	previously palatable
SA	GE	f	9	504	<0.001	previously unpalatable
HA	ME	m	1257	3211	<0.001	previously unpalatable
JY	PR	f	2511	434	<0.001	previously palatable
MO	RR	m	2570	0	<0.001	previously palatable
ALX	SN	m	2116	178	<0.001	previously palatable

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723 **SM Table 3.**

724 Time spent consuming food during the test phase and local-majority individual food  
 725 preferences as determined using the binomial test (probability set at 0.5)

Local-majority						
Group	Individual	Sex	Previously pal	Previously unPal	Binomial p-value	Food preference
PH	CE	f	21	3288	<0.001	previously unpalatable
PH	PH	m	4916	0	<0.001	previously palatable
PH	SY	f	1135	17	<0.001	previously palatable
PH	LE	m	688	2014	<0.001	previously unpalatable
GP	PY	f	3040	802	<0.001	previously palatable
GP	GP	m	3355	0	<0.001	previously palatable
AX	TU	m	529	81	<0.001	previously palatable
AX	AX	m	2705	56	<0.001	previously palatable
NK	BA	f	191	322	<0.001	previously unpalatable
NK	MY	f	257	101	<0.001	previously palatable
NK	NK	m	291	881	<0.001	previously unpalatable
NK	CK	m	170	8	<0.001	previously palatable
SA	MI	f	4244	0	<0.001	previously palatable
SA	PH	m	8	0	0.008	previously palatable
SA	SA	f	1237	3385	<0.001	previously unpalatable
SA	PN	m	24	80	<0.001	previously unpalatable
SA	TI	m	136	336	<0.001	previously unpalatable
SA	TO	m	0	162	<0.001	previously unpalatable
SA	SE	m	1078	151	<0.001	previously palatable
HA	UA	f	2441	1097	<0.001	previously palatable
HA	HA	f	0	3247	<0.001	previously unpalatable
JY	JY	m	2482	1537	<0.001	previously palatable
JY	CY	m	1384	53	<0.001	previously palatable
MO	KT	f	0	2266	<0.001	previously unpalatable
MO	NA	f	2880	1424	<0.001	previously palatable
MO	AE	f	1639	297	<0.001	previously palatable
MO	MO	m	1336	1319	0.756	no preference
MO	CI	f	1957	0	<0.001	previously palatable
ALX	MN	m	1930	0	<0.001	previously palatable
ALX	AA	f	1838	0	<0.001	previously palatable
ALX	BTA	f	417	857	<0.001	previously palatable
ALX	SPE	f	925	131	<0.001	previously palatable
ALX	GE	m	300	591	<0.001	previously unpalatable
ALX	AX	m	1243	352	<0.001	previously palatable
ALX	TA	f	107	142	0.031	previously unpalatable
ALX	MN	f	13	99	<0.001	previously palatable

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727 **SM Table 4.**

728 Time spent consuming food during the test phase and controls individual food preferences as  
 729 determined using the binomial test (probability set at 0.5)

Controls						
Group	Individual	Sex	Previously pal	Previously unPal	Binomial p-value	Food preference
AK	ZE	f	1277	25	<0.001	previously palatable
AK	HD	m	2914	0	<0.001	previously palatable
AK	CA	f	499	12	<0.001	previously palatable
AK	AL	m	3310	0	<0.001	previously palatable
AK	MY	f	1637	15	<0.001	previously palatable
AK	MA	f	2542	999	<0.001	previously palatable
AK	TA	f	2638	154	<0.001	previously palatable
JI	JA	m	964	0	<0.001	previously palatable
JI	BE	f	767	0	<0.001	previously palatable
JI	TK	f	2623	0	<0.001	previously palatable
JI	QY	f	3520	0	<0.001	previously palatable

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743 **SM Table 5.**

744 Overall group preferences observed during the test phase (binomial probability set at 0.5).

745 Control groups indicated in bold.

Group Pal	Group unPal	Binomial p- vale	Food preference
7337	5826	<0.001	previously palatable
3486	2243	<0.001	previously palatable
5652	5601	0.637	no preference
1085	3036	<0.001	previously unpalatable
7812	7876	0.615	previously palatable
10016	8206	<0.001	previously palatable
4300	4101	0.031	previously palatable
6395	4951	<0.001	previously palatable
6950	4288	<0.001	previously palatable
<b>14817</b>	<b>1433</b>	<b>&lt;0.001</b>	<b>previously palatable</b>
<b>7874</b>	<b>0</b>	<b>&lt;0.001</b>	<b>previously palatable</b>

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761 **Figure 1.**  
762 Median proportion of time spent consuming previously unPal food (black horizontal line)  
763 according to subject group. Boxes represent the interquartile ranges. Whiskers represent the  
764 minimum and maximum proportion of time spent consuming previously unPal that are not  
765 outliers (unclassified outliers represented by circles or extreme cases by asterisks).

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781 **SM Figure 1.**

782 Proportion of time spent consuming previously unPal food by migratory-minority individuals  
783 according to their local-majority group size.

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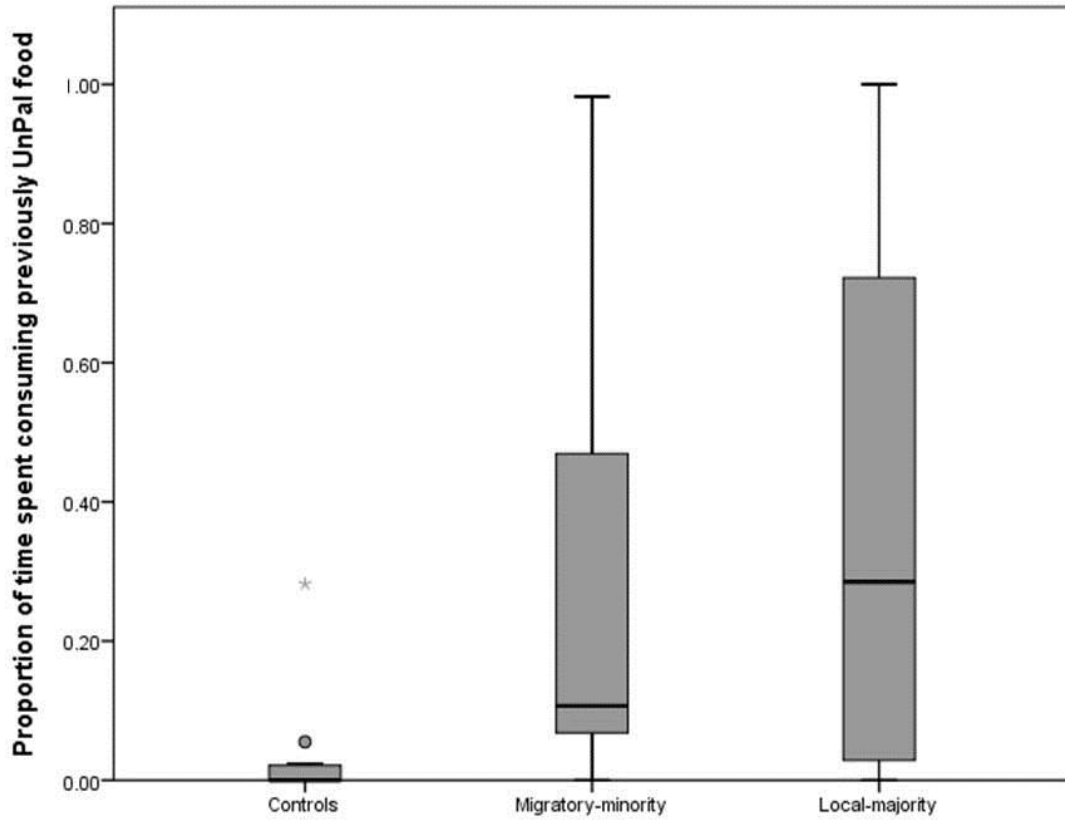
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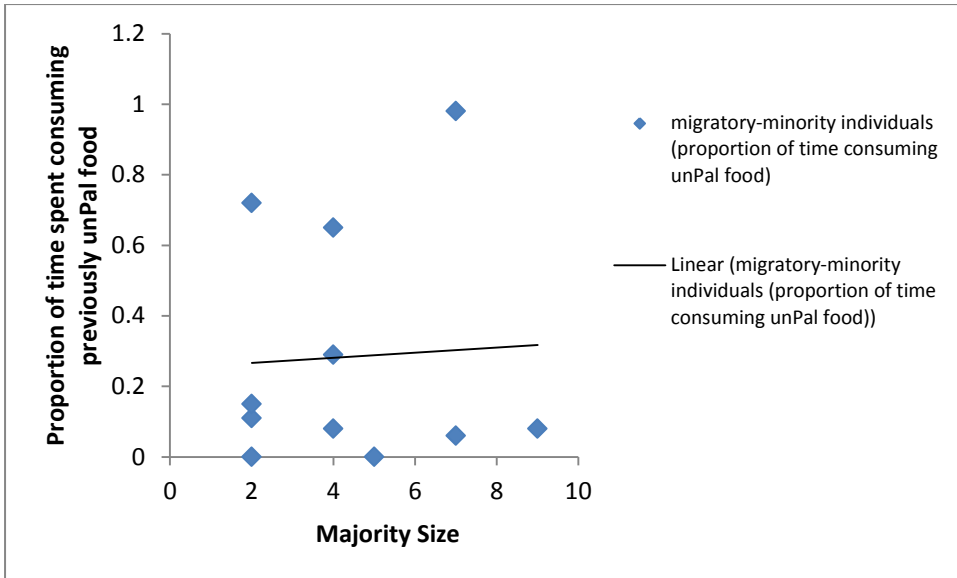
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827 **Supplementary Video**

828 Local-Majority consuming known Pal food during food preference training

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