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5	Lack of conformity to new local dietary preferences in migrating captive
6	chimpanzees
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24 Conformity to the behavioural preferences of others can have powerful effects on intra-group behavioural homogeneity in humans, but evidence in animals remains minimal. In this study, 25 we took advantage of circumstances in which individuals or pairs of captive chimpanzees 26 27 (Pan troglodytes) were "migrated" between groups, to investigate whether immigrants would conform to a new dietary population preference experienced in the group they entered, an 28 29 effect suggested by recent fieldwork. Such 'migratory-minority' chimpanzees were trained to avoid one of two differently-coloured foods made unpalatable, before 'migrating' to, and then 30 observing, a 'local-majority' group consume a different food colour. Both migratory-minority 31 32 and local-majority chimpanzees displayed social learning, spending significantly more time consuming the previously unpalatable, but instead now edible, food, than did control 33 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 local-majority chimpanzees tended to rely primarily upon personal information, consuming 36 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 a previously unpalatable food led to socially learned and adaptive re-exploration of this now-39 40 safe option in both minority and majority participants.

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Key Words: conformity, culture, cultural transmission biases, social learning, social learningstrategies

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

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72 Authors have defined the concept of conformity in other variant ways over the years (Claidiere & Whiten, 2012; van Leeuwen & Haun, 2014). Originally, social psychologists 73 emphasised conformity as the subjugation of personal knowledge or behaviour in favour of 74 75 an alternative displayed by a majority of others. The classic work of Asch (1956), in which participants were prepared to express agreement with the clearly incorrect perceptual 76 judgments of a group of experimental confederates, is an example of this form of conformity. 77 78 Human deference to such group responses has since been replicated many times and has been shown to be sensitive to a number of factors, such as cultural context, audience presence, and 79 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 primate relative, the chimpanzee (Pan troglodytes). However to avoid confusion, we first 82 note that some students of cultural evolution have defined conformity in the more specific 83 84 sense of a *disproportionate* tendency for individuals to copy a majority, even without subjugation of known behaviours (Boyd & Richerson, 1985; Whalen & Laland, 2015), a 85 86 phenomenon that has been labelled 'conformist transmission' (van Leeuwen & Haun, 2014; 87 Whalen & Laland, 2015). Theoretical simulation studies have suggested that such conformist transmission may readily evolve in populations of social learners, although strong conformist 88 tendencies can also be maladaptive in preventing the spread of potentially beneficial 89 innovations (Henrich & Boyd, 1998; Kandler & Laland, 2013; Wakano & Aoki, 2007). 90 Recent studies in fish and birds respectively, have suggested that such disproportionate 91 copying of majorities may occur in non-human animals (e.g., great tit Parus major: Aplin et 92 al., 2015a; nine-spined stickleback Pungitius pungitius: Pike & Laland, 2010) although this 93 conclusion has proved controversial (Aplin et al., 2015b; van Leeuwen, Kendal, Tennie, & 94 Haun, 2015; Whiten & van de Waal, in press). 95

96 In intermediate levels of environmental change and patterns of spatial heterogeneity, social learning becomes an adaptive strategy (reviewed in Vale, Carr, Dean, & Kendal, in 97 press). Conformity may be an important social learning strategy when migrating to a new 98 99 area and entering a new group (Boyd & Richerson, 1985), where there is scope for uncertainty about the optimal ways to behave. 'Copy when uncertain' is one of the other 100 101 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 with 'copy when uncertain' and/or 'conformity' comes from a small but growing set of field 103 104 experiments. In one, after four groups of wild vervet monkeys were trained to prefer just one of two differently coloured corn provisions because one was made severely distasteful, nine 105 106 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). More recently, a similar effect was documented in wild great tits (Parus major) that 109 abandoned an earlier learned preference to peck one side of an artificial foraging device in 110 favour of the opposite method, if this was shown by a majority of the new community they 111 entered (Aplin et al., 2015a). There is thus a growing, if still small and controversial, 112 literature consistent with the existence of this form of conformity to new community 113 114 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).

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

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

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

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

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

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

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177 Local-Majority Subjects

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

185 *Control groups*

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

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192 *Ethical note*

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

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[insert Table 1 around here]

203 Materials

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

216 *Procedure*

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

219 Training Phase

To establish food colour preferences we ran an initial training phase in which all chimpanzees 220 (migratory-minority, local-majority, control individuals) were provisioned with orange and 221 green food in two adjacent, differently coloured feeders, one of which (orange or green) was 222 made unpalatable by spraying it with Fooey Ultra-Bitter Training Aid (Table 1 and 223 224 supplementary video). To ascertain whether migratory-minority subjects adopt the food choice of their new group, different food colour preferences were always induced in resident 225 226 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 above, of subjects and until a maximum of one animal per session sampled the unpalatable 228 229 food across three consecutive sessions. Each session lasted for 20 minutes, during which the food sources were refilled when nearly depleted. To re-bait, both food sources were 230 simultaneously removed from, refilled, and then repositioned within reach of the subjects. 231 232 Both food sources were refilled using this procedure when one or both were nearly depleted. This ensured there was always access to both food sources. This method was employed to 233 234 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

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

259 Test Phase

In the test phase, conducted the day after the observation phase, chimpanzees, now as a
group, were provisioned with untreated orange and green food for three 30-minute sessions.
This phase allowed an assessment of whether chimpanzees switched their food preferences to
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), when both foods were palatable. Again, participation was voluntary. All food sampling was 265 continuously coded, noting the start and end time of the feeding bout and the type of food that 266 was consumed. This allowed the calculation of the overall consumption times according to 267 food type. Chimpanzee food selections during three 30-minute test sessions were also coded 268 by a second researcher and inter-rater reliability was 100%. Due to a limited sample size, data 269 270 were analysed using nonparametric, two-sided, statistical tests. The dependent variable was the proportion of time chimpanzees spent consuming previously unPal food (time spent 271 272 consuming previously unPal food (secs)/total time spent consuming previously unPal and Pal food). 273

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

282 RESULTS

283 The proportion of time spent consuming previously unPal food differed according to subject

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

chimpanzees (median = 0.285) spent proportionately more time consuming their previously

unPal food than did controls (median = 0.00; Mann-Whitney U test: U = 21.00, $N_{\text{controls}} = 11$,

288 $N_{\text{migratory-minority}} = 11, P = 0.008; U = 74.00, N_{\text{controls}} = 11, N_{\text{local-majority}} = 36, P = 0.002,$ respectively, Figure 1; see also supplementary Tables 2 -5 for individual and group food 289 preferences), suggesting that chimpanzees in both categories were affected by witnessing 290 291 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 previously unPal foods (Mann-Whitney U test: U = 166.00, $N_{\text{local-majority}} = 36$, $N_{\text{migratory-minority}}$ 293 294 = 11, P = 0.420; Bonferroni adjustment applied with alphas set at 0.017). Latencies to first sample the previously unPal food also did not differ between local-majority (median = 1800s) 295 296 and migratory-minority (median = 630s) chimpanzees (Mann-Whitney U test: U = 105.00, $N_{\text{local-majority}} = 29, N_{\text{migratory-minority}} = 9, P = 0.39$). 297

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[insert Figure 1 around here]

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

All majority individuals, except one female, that sampled the previously unPal food during the test phase, did so only after a migrant had already sampled it. Local-majority individuals sampled the unPal food after observing, on average, just 2 (median) unPal food sampling events (range 0-8 events, N = 29; 'events' account for observing the same individual sample the food multiple times), or watching, on average, 1 (median) individual sample unPal food (range 0-4)). As migratory-minorities were exposed to an observation phase in which they observed the local-majority consume the food they knew to be unPal, all migratory-minority subjects, during the test phase, that sampled the unPal food did so only after observing the local-majority consume it.

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

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

340 DISCUSSION

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

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

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

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

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

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

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

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

A third possible explanation for the lack of conformity observed relates to 420 421 informational uncertainty. Theoretical analyses also suggest that individuals should use social information when they are uncertain, whether induced by prior information being unreliable, 422 423 a lack of prior personal information (Boyd & Richerson, 1988), personal information 424 becoming outdated (Boyd & Richerson, 1985; Boyd & Richerson, 1988), the accumulated knowledge of conspecifics being more reliable (Giraldeau, Valone, & Templeton, 2002), or 425 426 through environmental variability (Boyd & Richerson, 1985). Environmental heterogeneity in the present study, introducing uncertainty, may not have been within the right parameters for 427 chimpanzees to adopt the dietary preference of their group. Modelling studies and theoretical 428 429 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 was introduced by chimpanzees' migrations to a new enclosure with new residents. However, 433

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

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

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

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 small636 sample size.

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

Food preferences during the test phase varied according to individual, as assessed by comparing food consumption times to what would be expected by chance alone (binomial tests, see SM Table 2, 3 and 4). Three migratory-minority individuals preferred the previously unPal food (of 'low', 'medium' and 'high' dominance rank, 1 male) and eight the previously Pal (one chimpanzee of 'low', five chimpanzees of 'medium' and two chimpanzees of 'high' dominance rank, 5 male); 12 local-majority individuals preferred the previously unPal food, 23 the previously Pal and 1 displayed no preference; and 11 of the(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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Table 1.

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

Group N		Number of females	Induced food preference	N	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
мо	1	0	Green	5	4	Orange

SM Table 1.

Group	Migratory- Minority Subject	Majority Size	unPal	Pal
PH	EY	4	0.65	0.35
РН	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

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

707 SM Table 2.

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

	Migratory-minority								
Group	Individual	Sex	Previously pal	Previously unPal	Binomial p-value	Food preference			
РН	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			
МО	RR	m	2570	0	<0.001	previously palatable			
ALX	SN	m	2116	178	<0.001	previously palatable			

SM Table 3.

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)
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				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	СК	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	то	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
мо	КТ	f	0	2266	<0.001	previously unpalatable
МО	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 <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	107	99	<0.001	previously palatable

727 SM Table 4.

728 Time spent consuming food during the test phase and controls individual food preferences as

determined using the binomial test (probability set at 0.5)	
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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	ТА	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	ТК	f	2623	0	<0.001	previously palatable
JI	QY	f	3520	0	<0.001	previously palatable

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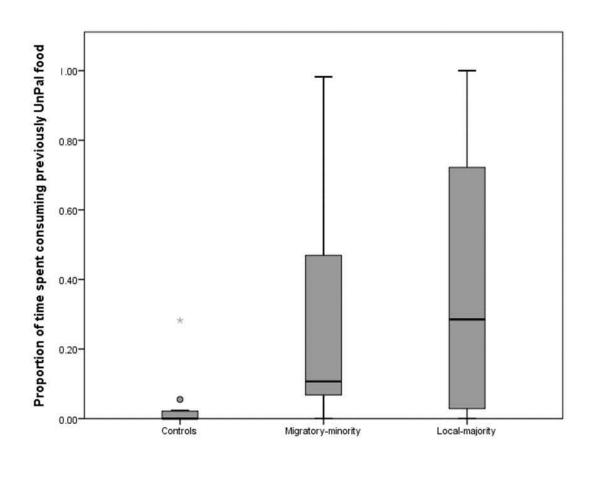
743 **SM Table 5**.

- 744 Overall group preferences observed during the test phase (binomial probability set at 0.5).
- 745 Control groups indicated in bold.

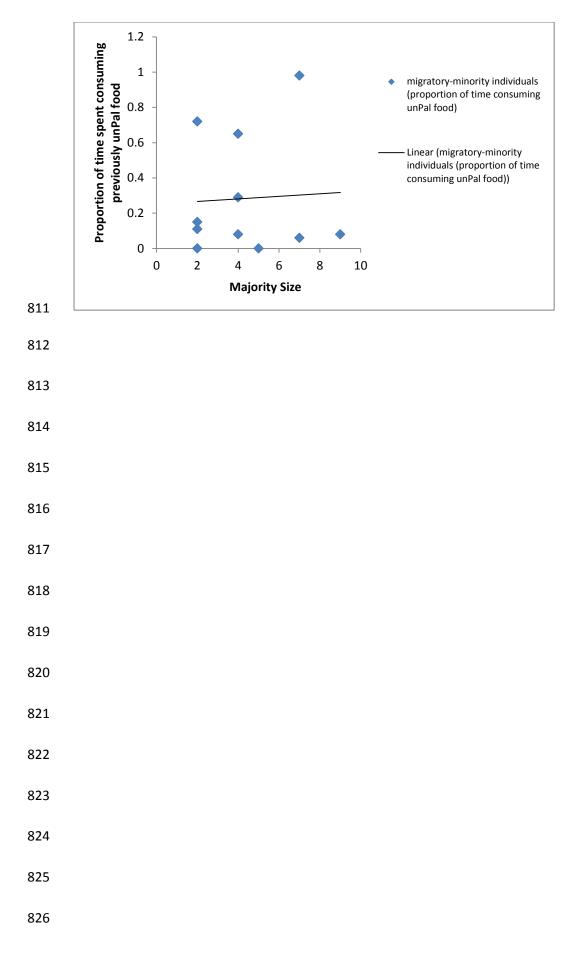
	Group Pal	Group unPal	Binomial p- vale	Food preference
	7337	5826	<0.001	previously palatable
	3486	2243	<0.001	previously palatable
	5652	5601	0.637	no preference
	1085	3036	<0.001	previously unpalatable
	7812	7876	0.615	previously palatable
	10016	8206	<0.001	previously palatable
	4300	4101	0.031	previously palatable
	6395	4951	<0.001	previously palatable
	6950	4288	<0.001	previously palatable
	14817	1433	<0.001	previously palatable
5	7874	0	<0.001	previously palatable
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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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827 Supplementary Video

828	Local-Majority c	onsuming known	Pal food during	food preference	training
020	Local majority c	onsuming known	i ui ioou uuiing	rood preference	nannig