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3 **Chimpanzees copy dominant and knowledgeable individuals:**

4 **Implications for cultural diversity**

5

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8

9 [6450 words, including title page, main text, references & legends]

10

11 **Running head:** chimpanzees copy dominants and experts

12 **ABSTRACT**

13 Evolutionary theory predicts that natural selection will fashion cognitive biases to guide  
14 when, and from whom, individuals acquire social information but the precise nature of these  
15 biases, especially in ecologically valid group contexts, remains unknown. We exposed four  
16 captive groups of chimpanzees (*Pan troglodytes*) to a novel extractive foraging device and,  
17 by fitting statistical models, isolated four simultaneously operating transmission biases.  
18 These include biases to copy (i) higher-ranking and (ii) expert individuals, and to copy others  
19 when (iii) uncertain or (iv) of low rank. High-ranking individuals were relatively un-strategic  
20 in their use of acquired knowledge, which, combined with the bias for others to observe  
21 them, may explain reports that high innovation rates (in juveniles and subordinates) do not  
22 generate a correspondingly high frequency of traditions in chimpanzees. Given the typically  
23 low rank of immigrants in chimpanzees, a ‘copying dominants’ bias may contribute to the  
24 observed maintenance of distinct cultural repertoires in neighboring communities despite  
25 sharing similar ecology and knowledgeable migrants. Thus, a copying dominants strategy  
26 may, as often proposed for conformist transmission, and perhaps in concert with it, restrict  
27 the accumulation of traditions within chimpanzee communities whilst maintaining cultural  
28 diversity.

29

30 **Key words:** Transmission biases, Social learning strategies, Chimpanzees, Culture, Cultural  
31 diversity.

32

33

## 34 INTRODUCTION

35 Many animals acquire information from their social environment, for example pertaining to  
36 foraging, mate choice, and predator avoidance, and such social learning often underlies  
37 behavioral traditions in a diverse array of taxa (see Kendal et al. 2010a and references  
38 therein; Whiten et al. 1999). The strong link between theoretical and empirical work, and the  
39 parallels between the social decision-making of human and non-human animals, has fuelled  
40 an explosion of interest in the psychological rules that underpin social learning. As  
41 highlighted by Rendell et al.'s (2011) review, interest in the decision-making involved in  
42 social learning has increased dramatically in recent years, yet empirical evidence lags behind  
43 theory. Social learning is not inherently adaptive, due to the risk of acquiring misinformation,  
44 but natural selection has fashioned social learning heuristics that combat this problem.  
45 Transmission biases (Boyd & Richerson, 1985; Henrich & McElreath, 2003; also termed  
46 'social learning strategies' by Laland, 2004), guide what, when, and from whom, individuals  
47 acquire social information (Kendal et al. 2005, 2009a; Rendell et al. 2011). For example,  
48 model-based biases influence who is copied and relate to traits such as prestige (e.g. Henrich  
49 & Gil-White, 2001), age (e.g. Dugatkin & Godin, 1993) and rank (e.g. Horner et al. 2010).  
50 While it is widely believed that such biases are crucial for understanding both how human  
51 cultures evolve and the cultural patterns of our closest primate relatives (Biro et al. 2006;  
52 Haun et al. 2012; Luncz et al. 2012; Nishida et al. 2009; Reader & Laland, 2001; Rendell et  
53 al. 2011), researchers currently lack clear experimental evidence for such biases (but see  
54 Chudek et al. 2012, Horner et al. 2010, and van Leeuwen et al. 2013 for the beginnings of  
55 this evidence base). Furthermore, researchers do not know whether transmission biases  
56 operate separately or together, or, in the latter case, how they are combined.

57

58 Our study explored these questions by exposing four groups of captive chimpanzees (two  
59 seeded with one trained mid-ranking female model each, and two without such a model) and  
60 twelve asocial learning control animals to a novel extractive foraging task in which a small  
61 door could be pushed right or left to retrieve a food reward. The study of how social learning  
62 operates in chimpanzees is of particular significance. Since Whiten et al.'s (1999) influential  
63 paper, reporting multiple traditions among wild chimpanzees, much effort has been expended  
64 in understanding chimpanzee culture. Investigation of evolved transmission biases in our  
65 closest living relative has the potential to shed new light on the ancestral features of  
66 humanity's 'adaptations for culture' (Fessler, 2011) and the selection pressures that shaped  
67 them. Such data establish whether certain transmission biases are unique to humans and,  
68 potentially, whether these explain humanity's uniquely strong reliance on culture, in  
69 particular, cumulative culture (Dean et al. 2012).

70

71 The spread of foraging information between chimpanzees was measured by recording - for  
72 every successful task manipulation - who performed it, what method was used, and who  
73 observed it. We aimed to build on the recent strides made in exploring social learning  
74 processes and transmission biases in relatively naturalistic contexts (Kendal et al. 2010a).  
75 Thus, in place of standard inferential tests of hypotheses, we employed pioneering new  
76 analytical methods (Franz & Nunn, 2009; Hoppitt & Laland 2011; Kendal et al. 2009b,  
77 2010b) and model-fitting approaches (McElreath et al. 2008) to examine which biases  
78 influence chimpanzee cultural learning, focusing on 'option' choice (push door left or push  
79 door right to retrieve a reward).

80

81 We then investigated the implications of the findings for understanding cultural transmission  
82 and cultural diversity in wild chimpanzees, and potentially humans. For example, we attempt  
83 to shed light on reports that high innovation rates (in juveniles and subordinates, Biro et al.  
84 2006; Reader & Laland, 2001) do not generate a correspondingly high frequency of traditions  
85 in chimpanzees (Nishida et al. 2009; Brosnan & Hopper, 2014). Similarly, we discuss how  
86 transmission biases might contribute to the observed maintenance of distinct cultural  
87 repertoires in neighboring chimpanzee communities despite them sharing similar ecology and  
88 knowledgeable migrants (Biro et al. 2006; Luncz et al. 2012, 2014). Thus far, conformist  
89 transmission has been proposed to restrict the accumulation of traditions in non-human (Haun  
90 et al. 2012; Luncz et al. 2012; van de Waal et al. 2013) and human (Henrich & Boyd, 1998;  
91 Pagel & Mace, 2004) primate communities, whilst maintaining cultural diversity. It remains  
92 to be seen whether such propositions are valid and whether alternative transmission biases are  
93 involved, either singularly or in concert with others. There is, however, reason to expect that  
94 transmission biases may partially explain the lack of cross-cultural homogenization, and  
95 incredible cultural diversity, observed in modern and prehistoric humans (Pagel & Mace  
96 2004; Pétrequin, 1993).

97

## 98 **METHODS**

99 **Subjects** Fifty-four chimpanzees, housed in social groups in large enriched enclosures at the  
100 Michale E. Keeling Center for Comparative Medicine and Research, UT MD Anderson  
101 Cancer Center, USA (KCCMR), were the subjects. Chimpanzees were never food or water  
102 deprived and the research was approved by the Institutional Animal Care and Use Committee  
103 (IACUC 07-92-03887) and ethical committees of Durham and St Andrews Universities.  
104 KCCMR is accredited by the Association for the Assessment and Accreditation of

105 Laboratory Animal Care-International (AAALAC-I) and the research conformed to  
106 guidelines of ASAB/ABS. Four chimpanzee groups were used; two (T1, T2) seeded with  
107 trained models and two without (N1, N2). T1 comprised 13 chimpanzees (7 female), average  
108 age 25.5 years (range: 7–44); T2 comprised 10 chimpanzees (8 female), average age 19.5  
109 years (range: 9–26); N1 comprised 10 animals (6 female), average age 18.1 years (range: 9–  
110 35); N2 comprised 9 chimpanzees (4 female), average age 22.3 years (range: 9–42). The 12  
111 asocial adult controls (six female), were of average age 27.7 years (range: 15–44).

112

113 **Apparatus** A bidirectional extractive foraging task, the ‘Slide-box’ (Hopper et al. 2008,  
114 2013), which consisted of a cube (32cm<sup>3</sup>) with a food chute (4cm diameter) that opened in  
115 the center of the front panel was used. A door (8cm<sup>2</sup>) covered the aperture of the chute but  
116 could be pushed left or right with equal ease to release a grape from the chute (Fig S1). Based  
117 on observations of wild chimpanzees (Biro et al. 2003), and our previous research with  
118 captive chimpanzees (e.g. Hopper et al. 2007, 2011), indicating the relative utility of different  
119 classes of individuals for both training and model/demonstrator purposes, a mid-ranking adult  
120 female from each T group (T1: CO, 22 years, T2: MU, 26 years) was chosen as the ‘trained  
121 model.’ Observations of wild chimpanzees, suggest that it is the relative rank or age of the  
122 model to an observer that is important, not necessarily their absolute rank (Biro et al., 2003).  
123 Therefore we selected individuals whom were dominant enough to be observed by their  
124 peers, but not so dominant that other individuals avoided them (Drea & Wallen, 1999;  
125 Hopper et al. 2013). Following this, the specific mid-ranking female models were selected  
126 for two reasons. First we wanted a model that could be observed easily by their group mates  
127 such that close access to the apparatus was possible while the demonstrator was in action.  
128 Secondly, these two females were selected because they were both comfortable being briefly

129 separated from their group for training sessions and were known to be fast learners. Although  
130 previous captive studies of social learning with chimpanzees have used dominant females  
131 (e.g., Hopper et al., 2007), other studies of social learning in primates have demonstrated that  
132 younger, less dominant individuals can also represent reliable models (e.g., Hopper et al.,  
133 2013). Each model was trained, individually, over two 15-minute sessions, to push the door  
134 (CO: right, MU: left) using positive reinforcement. By the end of the second session both  
135 models were considered proficient, having pushed the door in the designated direction 30  
136 times in succession during a single training session.

137

138 ***Procedure*** Groups were presented with the Slide-box on the outside of their 21.3m diameter  
139 enclosures. For T groups, initially only the model chimpanzee could access the apparatus (by  
140 reaching through the bars of the enclosure) to enable all group members to observe the Slide-  
141 box in use by the model. If non-models attempted to use the task, the experimenter pulled it  
142 out of reach. During this observations-phase (two 20-minute sessions over consecutive days),  
143 and the subsequent open-diffusion phase, once a chimpanzee retrieved a grape the task was  
144 turned through 180° to re-set the door to the central position reducing emission of inadvertent  
145 experimenter cues (e.g., stimulus or local enhancement). Once re-set, the Slide-box was  
146 repositioned and re-baited in full view of any chimpanzees present. The day following the  
147 final observation-phase (T groups) or immediately (N groups), the chimpanzees entered the  
148 open-diffusion phase where any chimpanzee could operate the Slide-box. No subjects were  
149 called by the experimenter; participation in the study was voluntary such that task  
150 interactions proceeded in a pattern natural for the group. This phase continued until all group  
151 members retrieved a reward 30 times: T1 (9.5 hours) and T2 (7 hours) in April 2007, N1 (10  
152 hours) and N2 (10.5 hours) in January–February 2008. Using video recordings, identities of

153 those manipulating the Slide-box and appearing to observe manipulations were noted. An  
154 ‘observing’ chimpanzee was one that was within 1 meter of the Slide-box, with their body  
155 oriented towards it, during a manipulation (Hopper et al. 2007). A ‘manipulation’ was  
156 physical movement of the Slide-box door, and considered ‘unsuccessful’ or ‘successful’  
157 depending on whether a grape was obtained and eaten.

158

159 Observational data, regarding social relations, were collected for three of the groups using  
160 one-hour instantaneous scan samples over several months prior to, and following, the open-  
161 diffusion study (SI 1.ii). For most of our analyses, however, we were interested in the rank  
162 class of individuals rather than the detail of dominance hierarchies. We chose to rate  
163 dominance using a categorical scale because it facilitated comparisons across the four,  
164 differently sized, groups when compared to assigning individuals a rank order relative to their  
165 group’s size. Thus, each member of the four groups was ranked on a three-point scale for  
166 dominance (where 1 = high, 2 = mid, and 3 = low). These rankings were scored by three  
167 chimpanzee experts, entirely independently of each other, who all had a minimum of two-  
168 years experience working with these chimpanzees; the primary experimenter (LMH), the  
169 facility’s behavioral coordinator and Research Laboratory Manager (SPL) and a trainer.  
170 Inter-rater agreement was high ( $ICC(2,1) = 0.74, P < 0.001$ ) and on the very rare instances in  
171 which the three raters did not agree, the mode rank was selected.

172

173 Finally, asocial controls were voluntarily individually tested in their inside enclosure (2.4 x  
174 2.4 x 1.8m<sup>3</sup>) for 20 minutes. They observed the experimenter bait the Slide-box with a grape  
175 but were not encouraged to interact with it. If they slid the door, in either direction, the task  
176 was re-set and baited as previously described.



177

178 ***Statistical Analyses*** We conducted four types of analysis, all of which overcome issues  
179 which standard inferential statistics cannot, allowing investigation of social learning in  
180 naturalistic conditions: First, we used the established option bias method (Kendal et al.  
181 2009b, 2010b) to assess whether chimpanzees within a group tended to solve the task by  
182 pushing the door in the same direction, as would be expected if the task solution was socially  
183 transmitted within each group. Second, we used Network-Based Diffusion Analysis (Franz  
184 & Nunn 2009; Hoppitt & Laland, 2011) to determine whether the first successful task  
185 interaction spread within groups according to principles of directed social learning (Coussi-  
186 Korb & Fragaszy, 1995) represented via social networks based on different factors (e.g.  
187 affiliation, observation). Since we found no indication that the time of first solving the task  
188 follows such a pattern, the results are reported in the SI (2.i) only. Third, we developed a  
189 time-structured model of option choice to infer which social learning strategies were being  
190 used. Finally, we ran analyses of whom observed whom, so as to determine whether  
191 chimpanzees preferentially chose to watch others of a specific rank. Here we outline the latter  
192 two methods, with further technical details given in the S.I.. All analyses were conducted  
193 using WinBUGS 1.4 and the R statistical environment (2.13.1 (R Core Development Team  
194 2011)).

195

196 For the time-structured stochastic models of option choice we adapted the approach  
197 pioneered by McElreath et al. (2008) to infer the social learning strategies being used by  
198 individuals, by modelling the option choices made as a function of the social information  
199 available to them. Different models are fitted corresponding to different social learning  
200 strategies and asocial learning, and the fit of the models compared using Akaike's

201 Information Criterion (AIC, Burnham & Anderson 1998). Since option bias was only found  
202 in the direction the door was pushed, the analysis was applied to the choice of push left  
203 versus push right. In the Supplementary Information we give details of all models fitted: here  
204 we give an overview. The general model form had a component of asocial learning (L) and a  
205 component of social information (S), with the parameter  $\gamma$  giving the proportion of weight  
206 given to S when making a decision about option choices and  $1 - \gamma$  giving the weight given to  
207 L. For a model of asocial learning alone, we set  $\gamma = 0$ . The exact form of the L and S  
208 components was varied between the different models considered as outlined below.

209

210 For the L component we started with McElreath et al.'s (2008) model of asocial learning,  
211 where an individual's "attraction score" for option  $k$ , is updated as the individual receives  
212 rewards for choosing each option. However, the chimpanzees tended to engage in long runs  
213 of using an option without necessarily settling on that option as a long-term solution, as  
214 would be expected under McElreath et al.'s model. Therefore, we formulated an alternative  
215 model in which individuals make an initial choice of option on their first manipulation. For  
216 each subsequent manipulation, given an individual is using asocial information, there is a  
217 probability they will switch to the alternative option, otherwise they will stick with the option  
218 they chose for their previous manipulation.

219

220 McElreath et al (2008) consider models of social learning in which each observer is sensitive  
221 to the payoff received by those it observes making option choices. For our data, the reward  
222 was always the same (a single grape), and so we only consider the frequency dependent  
223 strategy suggested by McElreath et al. In this model a parameter  $f$  determines how nonlinear  
224 any frequency dependence is: when  $f=1$  copying is unbiased; when  $f>1$  commonly observed

225 choices have more chance of being copied (conformity effect) and when  $f < 1$ , commonly  
226 observed choices have less chance of being copied. We also considered models in which  
227 copying was unbiased, where  $f$  was constrained to be 1.

228

229 We initially found strongest support for the state-switching model with frequency unbiased  
230 copying (see S.I.). However, subsequent examination of plots of the data (see Fig S3 in S.I.)  
231 strongly suggested that the weight given to social information decreased as chimpanzees  
232 gained more experience manipulating the task. We therefore fitted an expanded model in  
233 which chimpanzees were less likely to copy others if it involved switching away from an  
234 option that they had used frequently in the past. This model had much more support than any  
235 others considered (Akaike weight = 0.838; Table 1) so we based our inferences on this model,  
236 to assess whether individuals of different rank employed different strategies of switching  
237 between options, and copying others (see S.I.).

238

239 To investigate whether chimpanzees preferentially chose to watch others of a specific rank  
240 we developed a model of observation to test whether chimpanzees preferred to observe  
241 manipulations by others of a higher, lower or same rank. We did not treat each manipulation  
242 as an independent event, since chimpanzees engaged in bouts of manipulation: if an  
243 individual observed one manipulation at the task, it was more likely to observe the next one.  
244 We therefore formulated a model that allowed for this autocorrelation, and within individual  
245 correlation (see S.I.) and allowed us to calculate the expected long run proportion of  
246 manipulations that would be expected for each combination of manipulator and observer  
247 status. This model allows us to test for evidence of differences in observation patterns

248 between individuals of different relative rank, allowing for individual-level sampling error  
249 and autocorrelations between successive manipulations.

250

251

## 252 **RESULTS & DISCUSSION**

### 253 **Social Learning**

254 Six of twelve control chimpanzees (tested alone, hence reliant on asocial learning) interacted  
255 with the task, with three first pushing the door to the right and three to the left. Across all  
256 individuals, 50% of manipulations were to the right, indicating no inherent directional bias.  
257 Conversely, in experimental groups (where social learning was possible) there was strong  
258 evidence of a group-level bias in the option used (i.e. the direction chimpanzees pushed the  
259 door to gain a food reward). This bias exceeded that expected by asocial learning alone  
260 (Kendal et al. 2009b, 2010b, Option bias test:  $p < 0.001$ , 100,000 randomizations of 35  
261 individuals), but there was no bias in the hand(s) used by the chimpanzees to manipulate the  
262 task (Option bias test:  $p = 0.34$ , 100,000 randomizations of 35 individuals). In groups seeded  
263 with chimpanzees trained to push the apparatus door in a specific direction, the direction  
264 favored by the rest of their group matched that used by the model. In the group seeded with  
265 the left variant 81.8% of manipulations were to the left, and in the group seeded with the right  
266 variant 90.2% of manipulations were to the right. Likewise, in unseeded groups, individuals  
267 matched the direction of the first chimpanzee (or innovator) to solve the task, with 98.3% of  
268 manipulations to the right in one unseeded group and 95.7% to the left in the other unseeded  
269 group (Fig. 1). Thus, despite no inherent directional bias for door manipulation, the  
270 involvement of social learning in the spread of the novel behavior pattern through the  
271 experimental groups was established. The lack of influence of social learning at the level of

272 hand-use accords with studies of wild chimpanzees (Biro et al. 2003, 2006), and is likely due  
273 to existing individual hand-use preferences (Hopkins et al. 2009). We suggest that object-  
274 movement reenactment, a form of emulation (Hopper, 2010), underlay the diffusions.  
275 Consistent with wild (Whiten et al. 1999) and captive (e.g. Franz & Matthews, 2010; Hopper  
276 et al. 2011) studies, we observed high-fidelity copying (of the door strategy) sufficient to  
277 allow the maintenance of arbitrary traditions in chimpanzees. The question that then arises  
278 concerns the transmission biases employed by individuals in the emergence and maintenance  
279 of such traditions.

280

281 [Fig 1]

282

### 283 **Transmission Biases**

284 A time structured model of option choice (push left or right) delivered inferences about  
285 which social learning strategies were used. This dissected an individual's choice into asocial  
286 and social information (copying) components, with a parameter controlling the weight given  
287 to each. We considered various models for each component, expanding those of McElreath et  
288 al. (2008), and compared them using AIC. The final model allowed for chimpanzees that  
289 engaged in runs of choosing one option, with asocial learning affecting the probability of  
290 switching between options (a "state-switching" model). The best-supported statistical model  
291 assumed that chimpanzees copied in proportion to the number of manipulations of each  
292 option they observed. This model had more support than any others considered (Akaike  
293 weight= 0.838; Table 1), including a model without social learning ( $\Delta AIC = 91.8$ ). While we  
294 cannot rule out, or distinguish between, conformity, or anti-conformity, effects (the 95%  
295 confidence interval for  $f$ , a parameter quantifying the conformity effect was 0.6-3.5, where

296  $f > 1$  and  $0 < f < 1$  imply conformity and anti-conformity, respectively), for simplicity, we based  
297 further inferences on a frequency unbiased model. Details of all models fitted (using  
298 Bayesian MCMC techniques) during the subsequent model selection procedure are given in  
299 the SI (2.ii). Here, we report the main results, with estimates taken from the final model,  
300 which closely fitted the data (Fig 3). Estimates are the median of the posterior distribution  
301 with 95% credible intervals (CI). A low posterior probability (PP) against the hypothesis  
302 being reported ( $H_1$ ) indicates strong evidence in its favor.

303

304

[Table 1]

305

306 ***Copy when uncertain.*** The model of option choice fitted the open diffusion data better when  
307 it accounted for the ‘state’ of individuals, in terms of the personal information they  
308 possessed. There was clear evidence that the weight given to social information decreased  
309 rapidly as a chimpanzee manipulated the task more (PP against  $H_1 < 0.001$ ; Figs 2a, 3 & S4).  
310 The data showed evidence that social information (observations of manipulations) had a  
311 decreasing effect upon the behavior of individuals as their personal information (number of  
312 task manipulations) increased (Figs 2a, 3, S4). This corresponds to theoretical (Boyd &  
313 Richerson, 1985) and empirical studies in humans and non-humans (Kendal et al. 2005,  
314 2009a), including chimpanzees (Hirata & Morimura, 2000), that indicate a “copy when  
315 uncertain” bias. This contrasts with a tendency of children, in some studies, to be influenced  
316 by social information even when well-informed (Wood et al. 2013).

317

318

[Fig 2]

319

[Fig 3]

320

321 ***Copy when of low rank.*** The model was expanded to test for parameter differences between  
322 social ranks. There was clear evidence that low- and medium-ranked individuals acquired a  
323 task-opening option through copying. Eight of nine low-ranked individuals, and 11/12 of  
324 medium-ranked individuals, adopted the option, in their initial choice, that they had observed  
325 most. In contrast, there was an indication that high-ranked individuals gave lower weight than  
326 low- and medium-ranked individuals to social information when making their initial choice  
327 of option (i.e. left or right, PP against  $H_1 = 0.026$ ), with only 7/12 choosing the option they  
328 had seen most. This is despite high-ranked individuals having similar social information  
329 available when they made their initial responses (see Fig S4). For later responses, there was  
330 no evidence that chimpanzees of any rank gave different weight to social information (SI  
331 2.ii), thus we defer discussion to the SI (3i).

332

333 There was also strong evidence that asocial learning influenced the option choices of low-  
334 and medium-ranked chimpanzees, but not high-ranked chimpanzees. Low- and medium-  
335 ranked individuals were more likely to switch back to an option they had used more in the  
336 past (PP against  $H_1 < 0.001$ ), whereas there was little evidence for such an effect in high-  
337 ranked individuals (PP against  $H_1 = 0.268$ ; Figs 2b, 4). Moreover, low- and medium- ranked  
338 individuals were less likely to switch away from an option they had used more in the past (PP  
339 against  $H_1 < 0.001$ ), but there was little evidence for such an effect on high-ranked individuals  
340 (PP against  $H_1 = 0.167$ ; Fig S2-3). Low- and medium-ranked individuals rapidly settled on a  
341 preferred option, whereas high-ranked individuals vacillated for a prolonged period of time  
342 (Fig S3). The apparent lack of weight given to prior experience by more dominant individuals  
343 may reflect lack of investment in learning due to an ability to scrounge resources from others

344 (Melis et al. 2011). Similarly, compared to subordinates, dominant individuals experience  
345 less social interference when foraging, and higher energetic intake (Rands et al. 2006), so  
346 they may be less averse to the risk of changing a previously successful foraging method (see  
347 also Caldwell & Millen, 2010). Such findings may pertain to ongoing discussion regarding  
348 conservatism in ape learning (SI 3.i)

349

350 [Fig 4]

351

352 Taken together, however, these findings imply that high-ranked individuals, compared to  
353 low- and medium-ranked individuals, were not strategic information users (whether asocial  
354 or social), which may be consistent with reports that high-ranked individuals do not tend to  
355 be the innovators in wild chimpanzees (Reader & Laland, 2001). This may be because high-  
356 ranked individuals are occupied with other concerns, for example the psychosocial (Sapolsky,  
357 1992) and metabolic costs (Muller & Wrangham, 2004) of maintaining their rank. This may  
358 ensure relatively little motivation for fine-grained (option-level) learning of novel foraging  
359 methods in high-ranked individuals, who have priority of access to resources. Indeed, high-  
360 ranked individuals retrieved food from the task at the same, and higher, rates as low- and  
361 medium-ranked individuals, respectively. Thus, high-ranked individuals learned to access the  
362 food, but the means by which they did so was under minimal social influence.

363

364 ***Copy higher-ranking individuals.*** Further analyses of whom observed whom determined  
365 whether chimpanzees displayed evidence indicative of model-based biases, by preferentially  
366 choosing to watch specific others. These models allowed for correlation between successive  
367 manipulations, individual differences in the probability of observing others, and being



368 observed. Final models of option choice and observation were fitted using MCMC methods  
369 allowing inclusion of random effects for both observer and observed individuals, thus,  
370 simultaneously accounting for sampling effects at the level of individuals and behavior. For  
371 example, if one high-ranked individual ‘A’ happens to produce many manipulations  
372 (compared to individual ‘B’) and is observed frequently, the model allows for the fact we  
373 have more information on individual A than B but does not, as a consequence, infer that  
374 ‘being observed frequently’ is a property of high-ranked individuals in general. Little  
375 evidence was found for age or sex effects (SI 2.iv).

376

377 We found strong evidence of preferential attendance by naïve (as opposed to informed)  
378 chimpanzees to individuals of higher rank, rather than those of the same rank as themselves  
379 (PP against  $H_1 = 0.002$ ; Fig. 5). Intuitively an attendance bias suggests a copying bias, and is  
380 indicative of directed social learning, or transmission biases. However, although  
381 understandable, previous studies (e.g., Biro et al. 2003; Ottoni et al. 2005) have made such  
382 claims without assessing whether preferentially observed individuals are actually  
383 correspondingly influential in determining the behavior of observers. Likely due to  
384 homogeneity of option choice within groups, we found no evidence that observations of  
385 individuals of different relative rank (higher, lower, same) had a quantitatively different  
386 effect on option choice (see S3.iii). However, as chimpanzees rarely acquired conflicting  
387 information (regarding door directionality) from individuals of different rank, we cannot rule  
388 out such an effect of model rank on social information use.

389

390 Our results are, however, highly consistent with a copying bias for several reasons. Firstly, as  
391 only task-naïve individuals exhibited a preference for observing higher-ranked chimpanzees,

392 a learning function would seem to underlie the attendance bias. This corresponds to  
393 observation rates of wild chimpanzee nut-cracking doubling when novel, versus familiar, nuts  
394 are presented (Biro et al. 2006). Moreover, the attendance bias is a ‘choice’, rather than a  
395 byproduct mediated by social dynamics. Although individuals were more likely to displace  
396 task manipulators of relatively low, versus high, rank, this did not artificially inflate our  
397 estimate of observation of relatively higher ranked manipulators (whilst individuals awaited  
398 task access); in the model, an individual’s transition from observing to displacing another at  
399 the task was not counted as “ceasing task observation.”

400

401 [Fig 5]

402

403 To our knowledge this is amongst the first evidence consistent with a ‘copy dominant  
404 individuals’ bias in non-human primates, though such an effect has recently been reported in  
405 young children (Flynn & Whiten 2012). A copying bias for a dominant over a subordinate  
406 individual was reported in a study of two captive chimpanzee groups (Horner et al. 2010), but  
407 age and skill-reputation were conflated with dominance and, unlike here, the potential for  
408 sampling error (e.g., the two dominant individuals being potent models for reasons unrelated  
409 to dominance, such as age or sex) was not accounted for. Consistent with our findings, Biro  
410 et al. (2003, 2006) documented preferential attendance to nut-cracking and leaf-use by older,  
411 or same aged, wild chimpanzees, and age may correlate with dominance in such populations  
412 (Kahlenberg et al. 2008).

413

414 ***Copy knowledgeable individuals.*** There was strong evidence in the two seeded groups that  
415 naïve chimpanzees chose to observe trained models more than individuals of a lower (PP

416 against  $H_1 = 0.011$ ) or same rank (PP against  $H_1 = 0.003$ ) than themselves, and this preference  
417 was also likely greater than that for observing individuals of a higher-rank than themselves  
418 (PP against  $H_1 = 0.097$ ; Fig. 3). Again, due to homogeneity of option choice within groups,  
419 we cannot confirm whether this preferential attendance had a quantitative influence on  
420 behavior. With only two trained models, we cannot estimate the rate of observation of trained  
421 models in general with precision. Nonetheless, our analysis indicated that it was highly  
422 unlikely that we had sampled two individuals whom others watched so frequently by chance,  
423 rather than the effect being a result of their trained status. Several studies have similarly  
424 pointed to a transmission bias to ‘copy knowledgeable individuals.’ In humans, young  
425 children discriminate between competent and incompetent models (Harris & Corriveau,  
426 2011, but see Wood et al. 2012), and ‘copying experts’ enhances individual, and group,  
427 accuracy (King et al. 2012). Wild vervet monkeys (*Chlorocebus pygerythrus*) copy foraging  
428 tactics of dominant females, but not dominant males, (copying of dominants versus  
429 subordinates was not assessed) possibly due to greater locale-relevant knowledge in  
430 philopatric females (van de Waal et al. 2010). Similar reasoning applies to inter-specific  
431 social learning of nesting sites by migrant birds observing residents (Seppänen & Forsman,  
432 2007). Likewise, preferential attendance to skilled nutcrackers in naïve capuchins has been  
433 reported (Ottoni et al. 2005), though this may be a by-product of their tolerance of scrounging  
434 (Ottoni & Izar, 2008). Here, as all task manipulations resulted in reward, it is unlikely that  
435 varying success levels of trained versus untrained individuals were responsible for the  
436 attendance bias. Indeed, there was little evidence that task manipulation rate differed between  
437 high- or medium-ranked individuals and trained models (Fig S5). It is possible that purposive  
438 locomotion towards the task biased the attention of naïve individuals, as previously reported  
439 for chimpanzees (Menzel & Halperin, 1975; SI 3.ii).

440

441 Model-based biases might allow individuals to determine the ‘best’ individual to copy in a  
442 given context with reasonable speed and accuracy. As individuals of higher rank than  
443 observers can be assumed to be generally successful in life skills a, “copy higher-ranking  
444 individuals” bias may, on the whole, be effective. A “copy knowledgeable individuals” bias  
445 may further enhance performance, however. Such a hierarchy in bias-use, in this context, is  
446 potentially indicated by the greater attendance bias towards trained versus relatively higher  
447 ranked individuals. However, neither of these biases is likely to be as effective as copying the  
448 most successful (highest payoff) individual (SI 3ii), and thus it may pay chimpanzees to use  
449 model-based biases in concert. The observed patterns of preferential attendance to dominant  
450 and knowledgeable individuals, and model-based biases in chimpanzees, may correspond to  
451 ancestral, evolutionary precursors of prestige bias in humans (Chudek et al. 2012; Henrich &  
452 Gil-White, 2001; Horner et al. 2010).

453

454 **Implications for understanding cultural patterns.** The indiscriminate use of available  
455 information by high-ranked individuals and their tendency to vacillate between response  
456 options, combined with the “copy higher-ranking individuals” bias, are likely factors limiting  
457 the establishment of behavioral traditions in chimpanzees. This interpretation adds to  
458 arguments that a lack of attention to low-ranking, or young, individuals explains the  
459 discordance between the high frequency of innovation seen in chimpanzees - mostly by low  
460 ranking individuals (Reader & Laland, 2001) or juveniles/infants (Biro et al. 2006) - and the  
461 relative scarcity of reported traditions arising from innovations (Nishida et al. 2009; Brosnan  
462 & Hopper, 2014). Likewise, the likelihood that immigrants enter communities at a low point  
463 in the social hierarchy (Kahlenberg et al. 2008), provides an alternative, or additional,

464 explanation to conformity to group traditions, (Haun et al. 2012; Luncz et al. 2012, 2014) for  
465 the observation that cultural repertoires of neighboring chimpanzee communities may differ  
466 despite shared knowledgeable migrants (Biro et al. 2006; Luncz et al. 2012, 2014, but see  
467 Lind & Lindenfors, 2010; Nunn et al. 2009). Indeed, these findings echo those of Yeaman et  
468 al. (2011) who, in an analytical model, found that opposite biases in individuals who are  
469 learned from, and individuals who migrate, resulted in high cultural trait variation among  
470 groups relative to a genetic model. However, the consistency of our data with chimpanzees  
471 employing a “copy knowledgeable individuals” strategy complicates this interpretation;  
472 females display their alternative behavioral traits for some time following immigration  
473 (Luncz et al. 2014) and thus low-ranked immigrants may still be copied if they exhibit cues  
474 of proficiency with new skills. This area is ripe for further investigation deploying the  
475 analytical methods presented here in concert with seeding of models with different properties  
476 into experimental populations. Likewise, consideration could be given to the role of  
477 transmission biases in cultural patterns when individual learning may be more strongly  
478 favored than it is in this study. For example, when (i) alternative traditions are not arbitrary  
479 but afford differential payoffs to their users, and (ii) when there are multiple copies of the  
480 novel resource available to the group.

481

482 As proposed for conformist transmission (Haun et al. 2012; Henrich & Boyd, 1998; Luncz et  
483 al. 2012; Pagel & Mace, 2004; van de Waal et al. 2013), a “copy dominant individuals” bias  
484 may limit the accumulation of traditions within a culture whilst at the same time maintaining  
485 cultural diversity, including in modern and prehistoric humans (Henrich & Boyd, 1998; Pagel  
486 & Mace, 2004; Pétrequin, 1993). Perhaps several transmission biases, acting in concert,  
487 underlie the spread of learned behavior through populations and preserve cultural diversity.

488

489

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499

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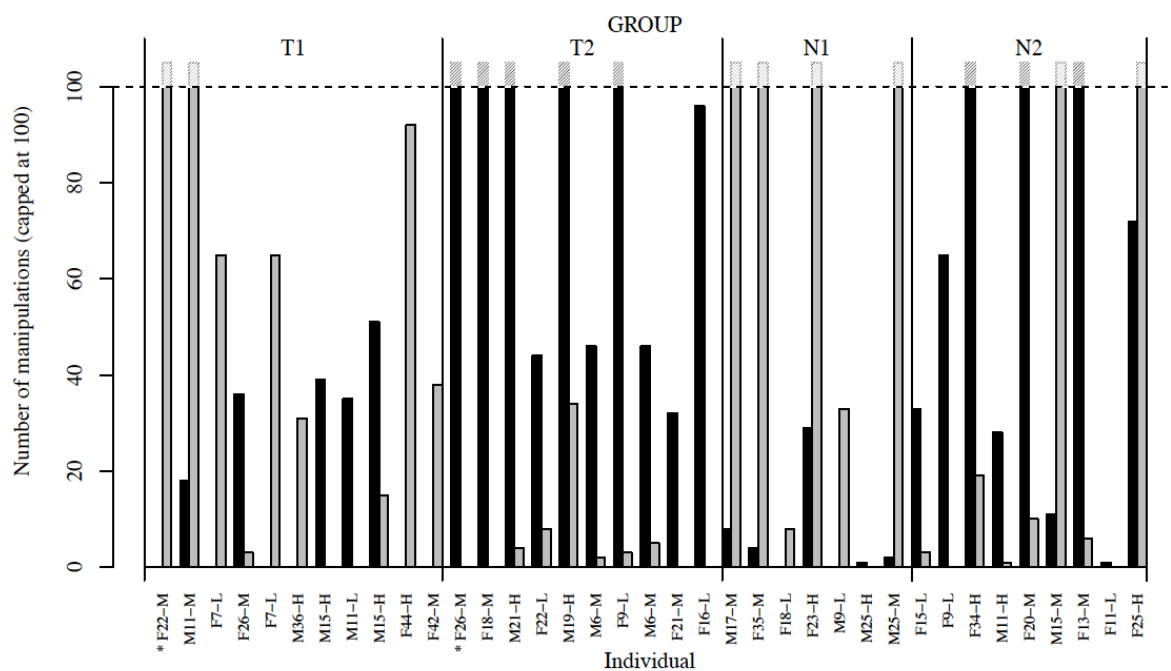
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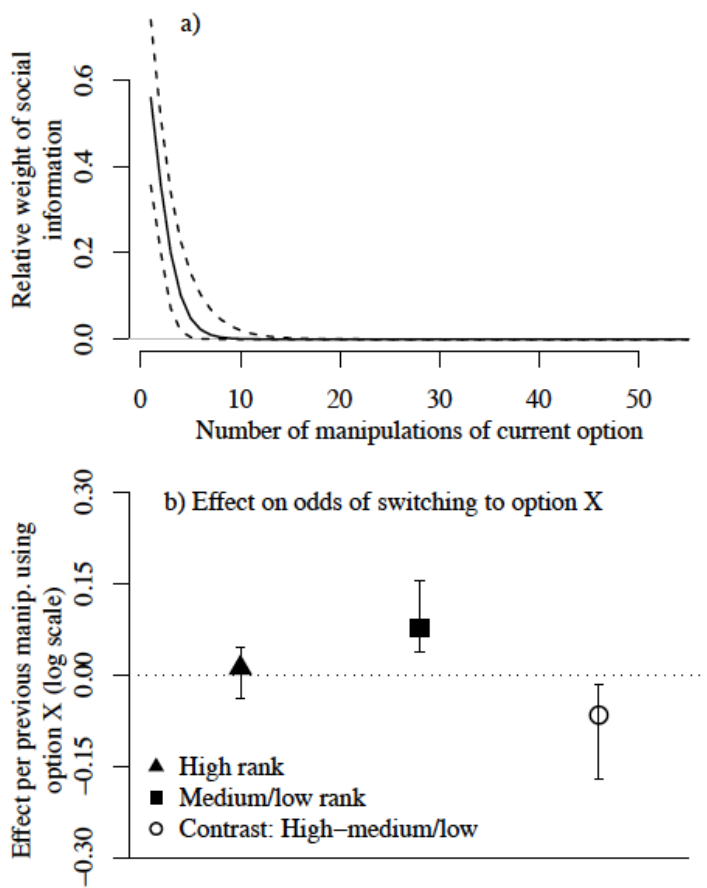


722

723 **Fig. 1:** Number of manipulations, of each option (grey=right, black=left), by individuals in  
 724 each group (shown in order of acquisition), capped at 100 (see Fig S1 for all data). The x-  
 725 axis indicates whether individuals were trained models (\*), male or female (M/F), their age in  
 726 years, and whether of high (-H), medium (-M) or low (-L) rank.

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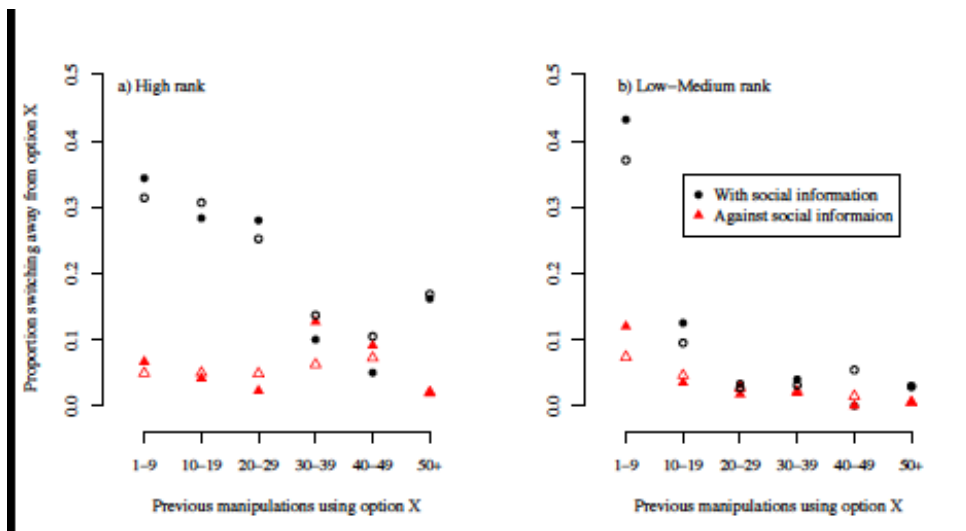
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**Fig. 2:** **a)** Estimated effect that the proportion of switches away from an option decreases with the number of prior successes with that option (see also Fig. S3); **b)** Estimated effect of prior successes on the odds of switching to an option for high and low-medium rank individuals (with estimated difference between the two). Error bars give 95% credible intervals (see also Fig. S2);



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737

**Fig. 3:** Fit of the model of option choice to the data. Solid points are the observed data,

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summed across chimpanzees for each bin on the x-axis. Empty points are the predictions of

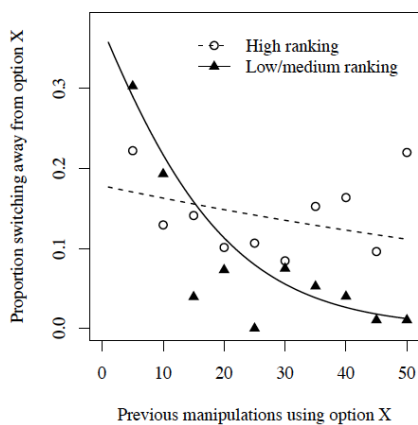
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the model. The latter were obtained from the posterior predictive distribution for each

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manipulation by summing the probability of a switch across the manipulations in each bin.

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**Fig. 4:** Proportion of manipulations that were switches away from the option chosen for the

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previous manipulation as a function of the number of previous manipulations using that

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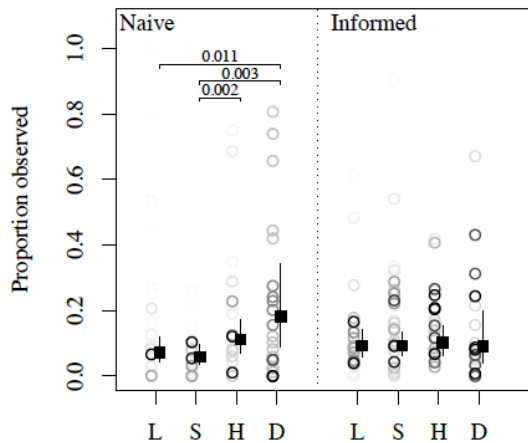
option, for high-ranking chimpanzees and low/medium-ranking chimpanzees. Points are the

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number of switches summed across chimpanzees in bins of width five (i.e. 1-5, 6-10, etc.).

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Lines show the slope predicted by the model of option choice.



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749

**Fig. 5:** The proportion of manipulations observed for each possible pair of

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manipulator/observer, by rank of manipulator relative to observer (L: lower, S: same, H:

751

higher), and whether the observer was naïve (no prior manipulations) or informed. Instances

752

where the manipulator was a trained model (D) are plotted/modeled separately. Darker circles

753

are based on more data. Square points give the estimated long-term proportion (median of the

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posterior distribution with 95% CI) for an average pair of chimpanzees. Posterior

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probabilities are given for differences between ranks of  $<0.025$  only.

756

**Table 1.** Relative fit of time-structured stochastic models of option choice

Asocial Learning	Social Learning	df	AIC	$\Delta$ AIC	Akaike Weight
Updates attraction score	None	2	2069.7	403.7	$<<0.001$
	Frequency dependent*	4	2004.2	338.2	$<<0.001$
	Updates social attraction score $\xi$	3	2064.1	398.1	$<<0.001$
Affects switching rate	None	4	1757.8	91.8	$<<0.001$
	Manipulations observed: frequency dependent#	8	1669.3	3.3	0.161
	Manipulations observed: frequency non-dependent	6	1666.0	0	0.838
	Manipulators observed: frequency dependent $\xi$	8	1698.2	32.2	$<0.001$
	Manipulators observed: frequency non-dependent	6	1714.7	48.7	$<0.001$
	Updates social attraction score $\xi$	8	1685.2	19.2	$<0.001$

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758

**Table 1:** Akaike weights give the weight of evidence in favor of the model being that which

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best approximates the true distribution for the dependent variable, out of those presented

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(Burnham & Anderson, 2002). \*Parameter  $f$  estimated at 0, effectively excluding social

761

learning (see text). #Parameter  $f$  estimated as very close to 1, thus frequency dependence was

762

weak.  $\xi$ See SI for details of these strategies.