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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]

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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

INTRODUCTION

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

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 ($32cm^3$) with a food chute (4cm diameter) that opened in

115   the center of the front panel was used. A door ($8cm^2$) 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 1.8m3) 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   Korbel & 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 γ 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) <u>against</u> 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]

14

320

Copy when of low rank. The model was expanded to test for parameter differences between

social ranks. There was clear evidence that low- and medium-ranked individuals acquired a

task-opening option through copying. Eight of nine low-ranked individuals, and 11/12 of

medium-ranked individuals, adopted the option, in their initial choice, that they had observed

most. In contrast, there was an indication that high-ranked individuals gave lower weight than

low- and medium-ranked individuals to social information when making their initial choice

of option (i.e. left or right, PP against $H_1 = 0.026$), with only 7/12 choosing the option they

had seen most. This is despite high-ranked individuals having similar social information

available when they made their initial responses (see Fig S4). For later responses, there was

no evidence that chimpanzees of any rank gave different weight to social information (SI

2.ii), thus we defer discussion to the SI (3i).

332

There was also strong evidence that asocial learning influenced the option choices of low-

and medium-ranked chimpanzees, but not high-ranked chimpanzees. Low- and medium-

ranked individuals were more likely to switch back to an option they had used more in the

past (PP against $H_1 < 0.001$), whereas there was little evidence for such an effect in high-

ranked individuals (PP against $H_1 = 0.268$; Figs 2b, 4). Moreover, low- and medium- ranked

individuals were less likely to switch away from an option they had used more in the past (PP

against $H_1 < 0.001$), but there was little evidence for such an effect on high-ranked individuals

(PP against $H_1 = 0.167$; Fig S2-3). Low- and medium-ranked individuals rapidly settled on a

preferred option, whereas high-ranked individuals vacillated for a prolonged period of time

(Fig S3). The apparent lack of weight given to prior experience by more dominant individuals

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

16

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.

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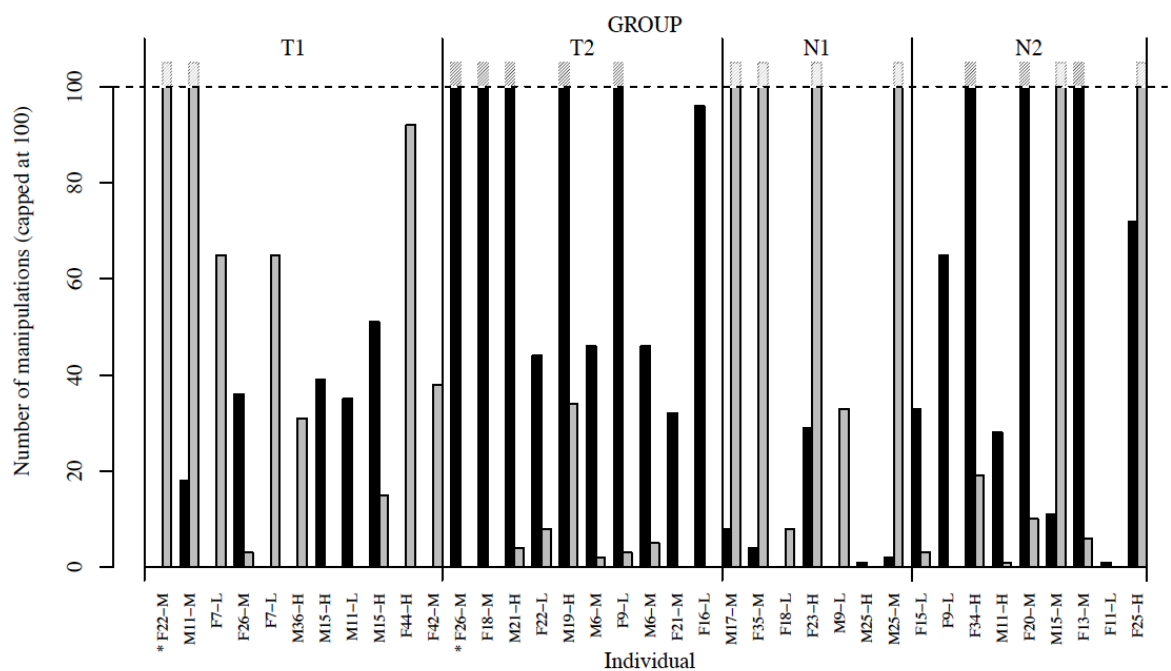
Fig. 1: Number of manipulations, of each option (grey=right, black=left), by individuals in each group (shown in order of acquisition), capped at 100 (see Fig S1 for all data). The x-axis indicates whether individuals were trained models (*), male or female (M/F), their age in years, and whether of high (-H), medium (-M) or low (-L) rank.
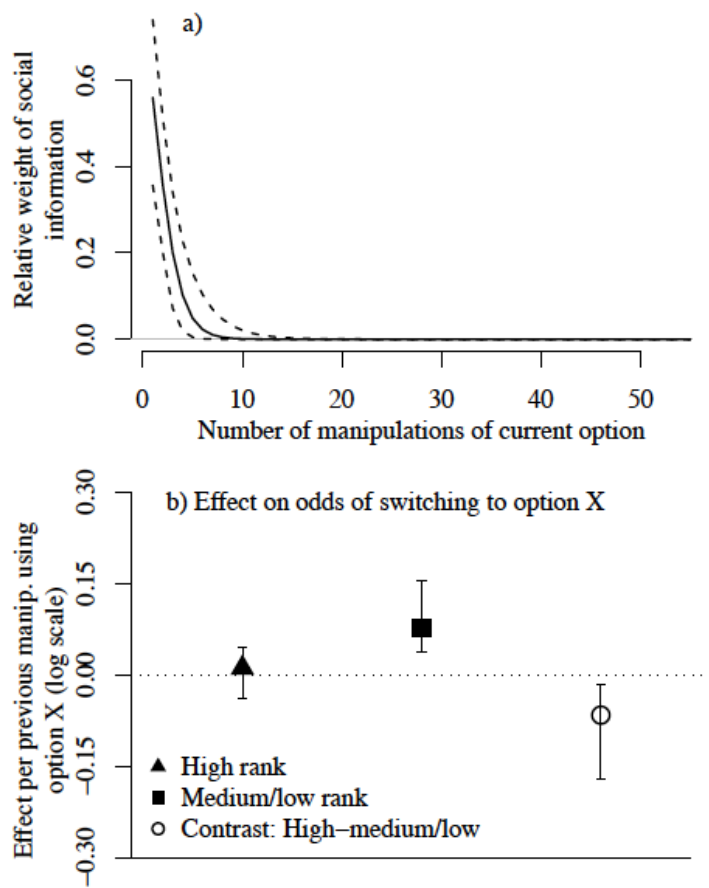
Fig. 2: a) Estimated effect that the proportion of switches away from an option decreases

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
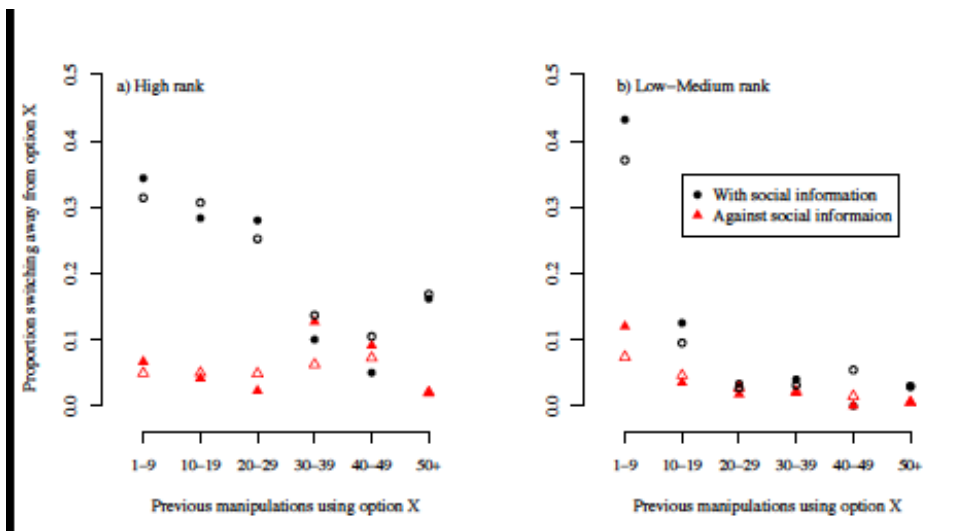
intervals (see also Fig. S2);

736

Fig. 3: Fit of the model of option choice to the data. Solid points are the observed data, summed across chimpanzees for each bin on the x-axis. Empty points are the predictions of the model. The latter were obtained from the posterior predictive distribution for each manipulation by summing the probability of a switch across the manipulations in each bin.
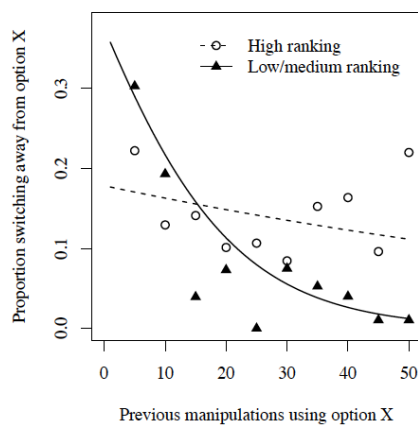
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Fig. 4: Proportion of manipulations that were switches away from the option chosen for the previous manipulation as a function of the number of previous manipulations using that option, for high-ranking chimpanzees and low/medium-ranking chimpanzees. Points are the number of switches summed across chimpanzees in bins of width five (i.e. 1-5, 6-10, etc.). Lines show the slope predicted by the model of option choice.
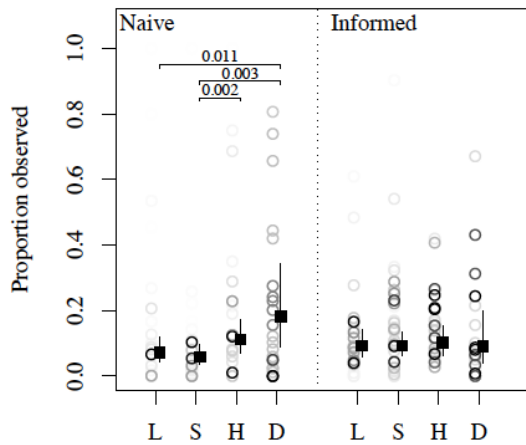
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Fig. 5: The proportion of manipulations observed for each possible pair of

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

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

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

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

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

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	ΔAIC	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 scoreξ	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 dependentξ	8	1698.2	32.2	<0.001
	Manipulators observed: frequency non-dependent	6	1714.7	48.7	<0.001
	Updates social attraction scoreξ	8	1685.2	19.2	<0.001

757
758 Table 1: Akaike weights give the weight of evidence in favor of the model being that which

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

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

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

weak. ξSee SI for details of these strategies.