[In Press, *Evolution and Human Behaviour*]

Chimpanzees copy dominant and knowledgeable individuals: Implications for cultural diversity

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

Running head: chimpanzees copy dominants and experts

ABSTRACT

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

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

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.

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

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

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

METHODS

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

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

Apparatus A bidirectional extractive foraging task, the 'Slide-box' (Hopper et al. 2008, 2013), which consisted of a cube (32cm^3) with a food chute (4cm diameter) that opened in the center of the front panel was used. A door (8cm^2) covered the aperture of the chute but could be pushed left or right with equal ease to release a grape from the chute (Fig S1). Based on observations of wild chimpanzees (Biro et al. 2003), and our previous research with captive chimpanzees (e.g. Hopper et al. 2007, 2011), indicating the relative utility of different classes of individuals for both training and model/demonstrator purposes, a mid-ranking adult female from each T group (T1: CO, 22 years, T2: MU, 26 years) was chosen as the 'trained model.' Observations of wild chimpanzees, suggest that it is the relative rank or age of the model to an observer that is important, not necessarily their absolute rank (Biro et al., 2003). Therefore we selected individuals whom were dominant enough to be observed by their peers, but not so dominant that other individuals avoided them (Drea & Wallen, 1999; Hopper et al. 2013). Following this, the specific mid-ranking female models were selected for two reasons. First we wanted a model that could be observed easily by their group mates such that close access to the apparatus was possible while the demonstrator was in action. Secondly, these two females were selected because they were both comfortable being briefly separated from their group for training sessions and were known to be fast learners. Although previous captive studies of social learning with chimpanzees have used dominant females (e.g., Hopper et al., 2007), other studies of social learning in primates have demonstrated that younger, less dominant individuals can also represent reliable models (e.g., Hopper et al., 2013). Each model was trained, individually, over two 15-minute sessions, to push the door (CO: right, MU: left) using positive reinforcement. By the end of the second session both models were considered proficient, having pushed the door in the designated direction 30 times in succession during a single training session.

Procedure Groups were presented with the Slide-box on the outside of their 21.3m diameter enclosures. For T groups, initially only the model chimpanzee could access the apparatus (by reaching through the bars of the enclosure) to enable all group members to observe the Slide-box in use by the model. If non-models attempted to use the task, the experimenter pulled it out of reach. During this observations-phase (two 20-minute sessions over consecutive days), and the subsequent open-diffusion phase, once a chimpanzee retrieved a grape the task was turned through 180° to re-set the door to the central position reducing emission of inadvertent experimenter cues (e.g., stimulus or local enhancement). Once re-set, the Slide-box was repositioned and re-baited in full view of any chimpanzees present. The day following the final observation-phase (T groups) or immediately (N groups), the chimpanzees entered the open-diffusion phase where any chimpanzee could operate the Slide-box. No subjects were called by the experimenter; participation in the study was voluntary such that task interactions proceeded in a pattern natural for the group. This phase continued until all group members retrieved a reward 30 times: T1 (9.5 hours) and T2 (7 hours) in April 2007, N1 (10 hours) and N2 (10.5 hours) in January–February 2008. Using video recordings, identities of those manipulating the Slide-box and appearing to observe manipulations were noted. An ‘observing’ chimpanzee was one that was within 1 meter of the Slide-box, with their body oriented towards it, during a manipulation (Hopper et al. 2007). A ‘manipulation’ was physical movement of the Slide-box door, and considered ‘unsuccessful’ or ‘successful’ depending on whether a grape was obtained and eaten.

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

Finally, asocial controls were voluntarily individually tested in their inside enclosure (2.4 x 2.4 x 1.8m3) for 20 minutes. They observed the experimenter bait the Slide-box with a grape but were not encouraged to interact with it. If they slid the door, in either direction, the task was re-set and baited as previously described.

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

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

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

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

McElreath et al (2008) consider models of social learning in which each observer is sensitive to the payoff received by those it observes making option choices. For our data, the reward was always the same (a single grape), and so we only consider the frequency dependent strategy suggested by McElreath et al. In this model a parameter f determines how nonlinear any frequency dependence is: when f=1 copying is unbiased; when f>1 commonly observed choices have more chance of being copied (conformity effect) and when $f<1$, commonly observed choices have less chance of being copied. We also considered models in which copying was unbiased, where f was constrained to be 1.

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

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

RESULTS & DISCUSSION

Social Learning

Six of twelve control chimpanzees (tested alone, hence reliant on asocial learning) interacted with the task, with three first pushing the door to the right and three to the left. Across all individuals, 50% of manipulations were to the right, indicating no inherent directional bias. Conversely, in experimental groups (where social learning was possible) there was strong evidence of a group-level bias in the option used (i.e. the direction chimpanzees pushed the door to gain a food reward). This bias exceeded that expected by asocial learning alone (Kendal et al. 2009b, 2010b, Option bias test: $p<0.001$, 100,000 randomizations of 35 individuals), but there was no bias in the hand(s) used by the chimpanzees to manipulate the task (Option bias test: $p=0.34$, 100,000 randomizations of 35 individuals). In groups seeded with chimpanzees trained to push the apparatus door in a specific direction, the direction favored by the rest of their group matched that used by the model. In the group seeded with the left variant 81.8% of manipulations were to the left, and in the group seeded with the right variant 90.2% of manipulations were to the right. Likewise, in unseeded groups, individuals matched the direction of the first chimpanzee (or innovator) to solve the task, with 98.3% of manipulations to the right in one unseeded group and 95.7% to the left in the other unseeded group (Fig. 1). Thus, despite no inherent directional bias for door manipulation, the involvement of social learning in the spread of the novel behavior pattern through the experimental groups was established. The lack of influence of social learning at the level of hand-use accords with studies of wild chimpanzees (Biro et al. 2003, 2006), and is likely due to existing individual hand-use preferences (Hopkins et al. 2009). We suggest that object-movement reenactment, a form of emulation (Hopper, 2010), underlay the diffusions. Consistent with wild (Whiten et al. 1999) and captive (e.g. Franz & Matthews, 2010; Hopper et al. 2011) studies, we observed high-fidelity copying (of the door strategy) sufficient to allow the maintenance of arbitrary traditions in chimpanzees. The question that then arises concerns the transmission biases employed by individuals in the emergence and maintenance of such traditions.

[Fig 1]

Transmission Biases

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

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

[Table 1]

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

[Fig 2]

[Fig 3]

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).

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

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

[Fig 4]

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

Copy higher-ranking individuals. Further analyses of whom observed whom determined whether chimpanzees displayed evidence indicative of model-based biases, by preferentially choosing to watch specific others. These models allowed for correlation between successive manipulations, individual differences in the probability of observing others, and being observed. Final models of option choice and observation were fitted using MCMC methods allowing inclusion of random effects for both observer and observed individuals, thus, simultaneously accounting for sampling effects at the level of individuals and behavior. For example, if one high-ranked individual ‘A’ happens to produce many manipulations (compared to individual ‘B’) and is observed frequently, the model allows for the fact we have more information on individual A than B but does not, as a consequence, infer that ‘being observed frequently’ is a property of high-ranked individuals in general. Little evidence was found for age or sex effects (SI 2.iv).

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

Our results are, however, highly consistent with a copying bias for several reasons. Firstly, as only task-naïve individuals exhibited a preference for observing higher-ranked chimpanzees, a learning function would seem to underlie the attendance bias. This corresponds to observation rates of wild chimpanzee nut-cracking doubling when novel, versus familiar, nuts are presented (Biro et al. 2006). Moreover, the attendance bias is a ‘choice’, rather than a byproduct mediated by social dynamics. Although individuals were more likely to displace task manipulators of relatively low, versus high, rank, this did not artificially inflate our estimate of observation of relatively higher ranked manipulators (whilst individuals awaited task access); in the model, an individual’s transition from observing to displacing another at the task was not counted as “ceasing task observation.”

[Fig 5]

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

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

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

Implications for understanding cultural patterns. The indiscriminate use of available information by high-ranked individuals and their tendency to vacillate between response options, combined with the “copy higher-ranking individuals” bias, are likely factors limiting the establishment of behavioral traditions in chimpanzees. This interpretation adds to arguments that a lack of attention to low-ranking, or young, individuals explains the discordance between the high frequency of innovation seen in chimpanzees - mostly by low ranking individuals (Reader & Laland, 2001) or juveniles/infants (Biro et al. 2006) - and the relative scarcity of reported traditions arising from innovations (Nishida et al. 2009; Brosnan & Hopper, 2014). Likewise, the likelihood that immigrants enter communities at a low point in the social hierarchy (Kahlenberg et al. 2008), provides an alternative, or additional, explanation to conformity to group traditions, (Haun et al. 2012; Luncz et al. 2012, 2014) for the observation that cultural repertoires of neighboring chimpanzee communities may differ despite shared knowledgeable migrants (Biro et al. 2006; Luncz et al. 2012, 2014, but see Lind & Lindenfors, 2010; Nunn et al. 2009). Indeed, these findings echo those of Yeaman et al. (2011) who, in an analytical model, found that opposite biases in individuals who are learned from, and individuals who migrate, resulted in high cultural trait variation among groups relative to a genetic model. However, the consistency of our data with chimpanzees employing a “copy knowledgeable individuals” strategy complicates this interpretation; females display their alternative behavioral traits for some time following immigration (Luncz et al. 2014) and thus low-ranked immigrants may still be copied if they exhibit cues of proficiency with new skills. This area is ripe for further investigation deploying the analytical methods presented here in concert with seeding of models with different properties into experimental populations. Likewise, consideration could be given to the role of transmission biases in cultural patterns when individual learning may be more strongly favored than it is in this study. For example, when (i) alternative traditions are not arbitrary but afford differential payoffs to their users, and (ii) when there are multiple copies of the novel resource available to the group.

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

Acknowledgements

RLK was funded by a Royal Society Dorothy Hodgkin Fellowship; LMH by a BBSRC studentship (BBS/S/K/2004/11255 supervised by AW) and, at the time of writing, is funded by the Guthman Fund; WH by a BBSRC grant (BB/I007997/1); SFB by a NSF CAREER award (SES 0847351) and (SES 0729244). The chimpanzee colony is supported by NIH U42 (RR-15090). Thanks to staff at KCCMR for their help with this study and for providing the highest quality of care for the chimpanzees housed there, and to Bryan Paenitz who made the Slide-box. We are grateful to Kevin Laland, Mathias Franz, Jamie Tehrani, Jeremy Kendal, and Alex Mesoudi for discussion.

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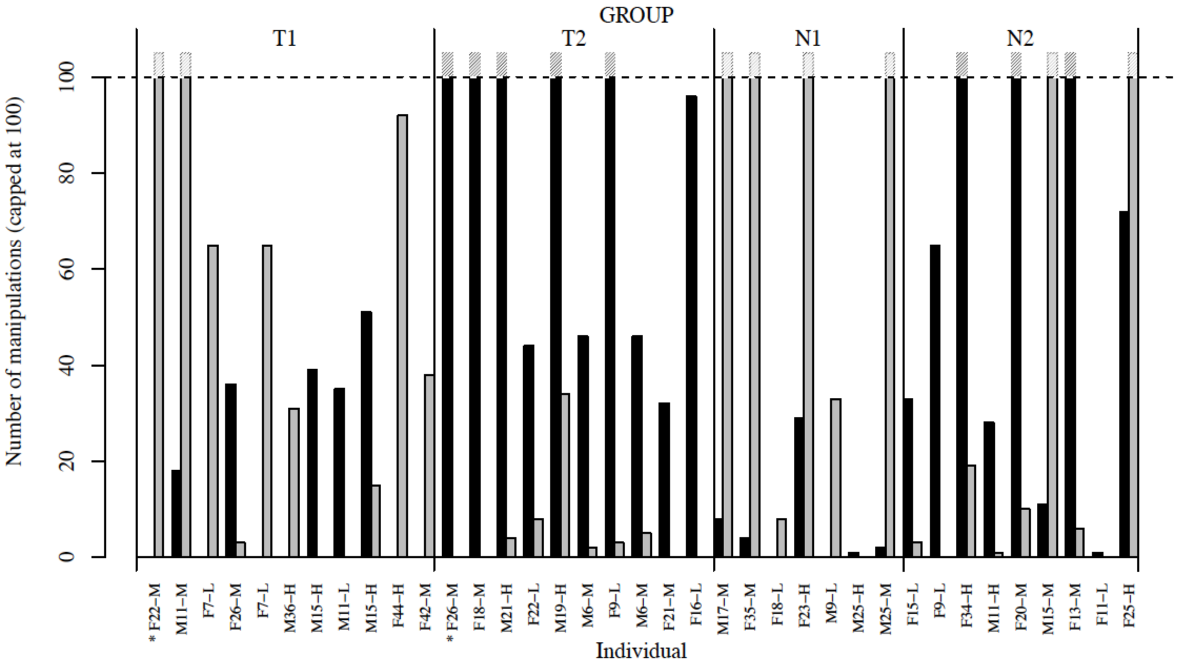

Fig. 1: Number of manipulations, of each option (grey=right, black=left), by individuals in each group (shown in order of acquisition), capped at 100 (see Fig S1 for all data). The x-axis indicates whether individuals were trained models (*), male or female (M/F), their age in years, and whether of high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

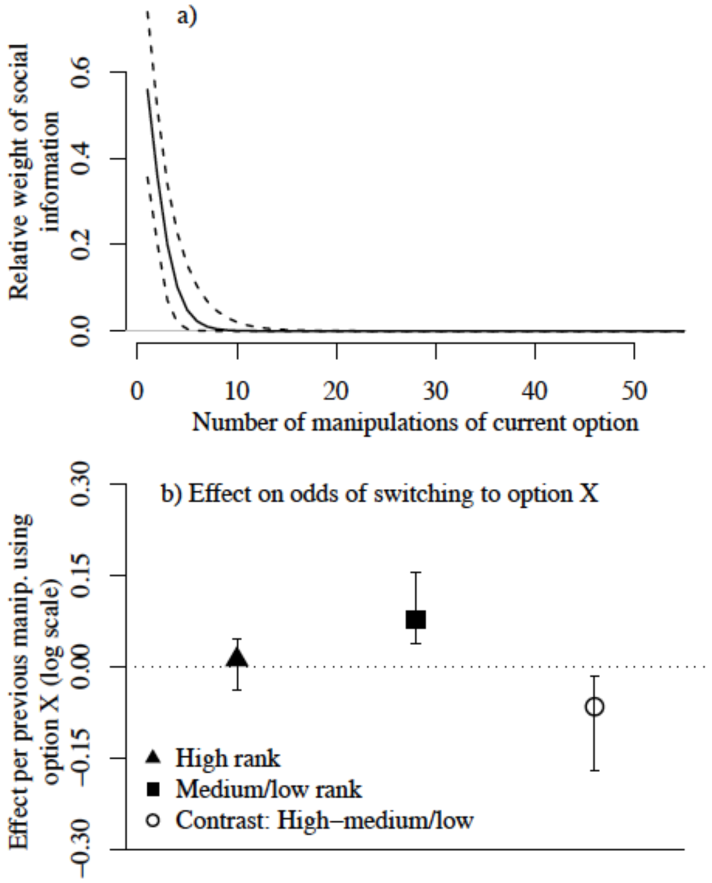

Fig. 2: a) Estimated effect that the proportion of switches away from an option decreases with the number of prior successes with that option (see also Fig. S3); **b)** Estimated effect of prior successes on the odds of switching to an option for high and low-medium rank individuals (with estimated difference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

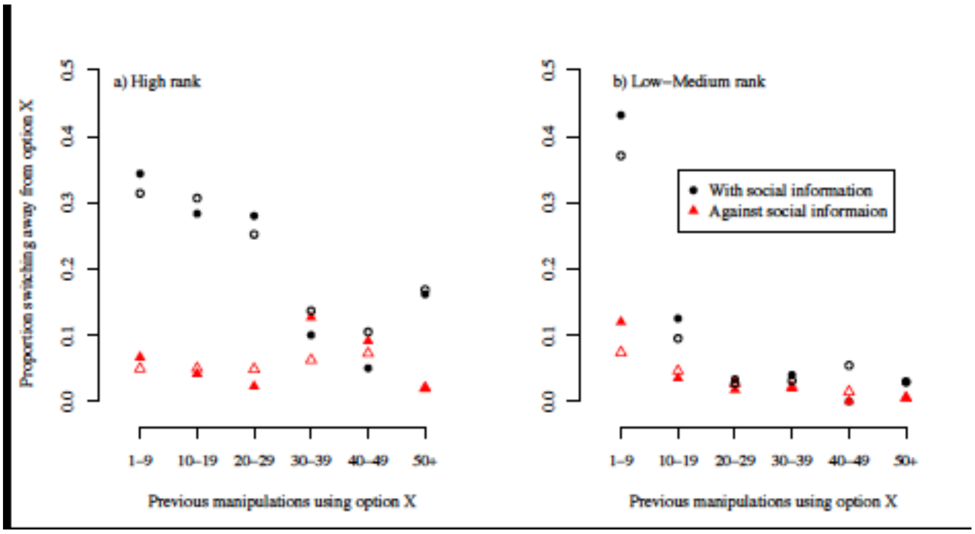

Fig. 3: Fit of the model of option choice to the data. Solid points are the observed data, summed across chimpanzees for each bin on the x-axis. Empty points are the predictions of the model. The latter were obtained from the posterior predictive distribution for each manipulation by summing the probability of a switch across the manipulations in each bin.

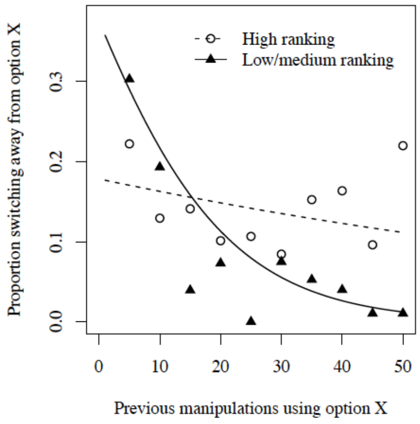

Fig. 4: Proportion of manipulations that were switches away from the option chosen for the previous manipulation as a function of the number of previous manipulations using that option, for high-ranking chimpanzees and low/medium-ranking chimpanzees. Points are the number of switches summed across chimpanzees in bins of width five (i.e. 1-5, 6-10, etc.). Lines show the slope predicted by the model of option choice.

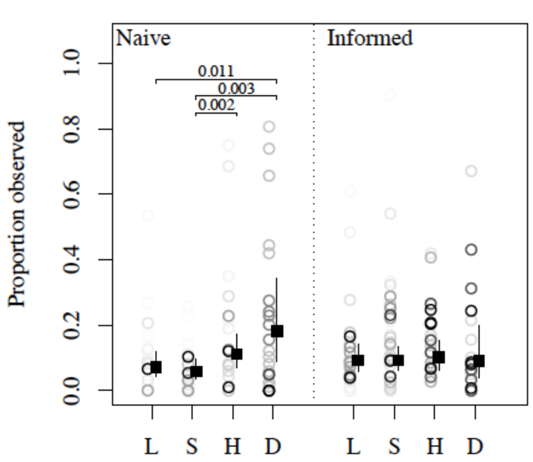

Fig. 5: The proportion of manipulations observed for each possible pair of manipulator/observer, by rank of manipulator relative to observer (L: lower, S: same, H: higher), and whether the observer was naïve (no prior manipulations) or informed. Instances where the manipulator was a trained model (D) 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.

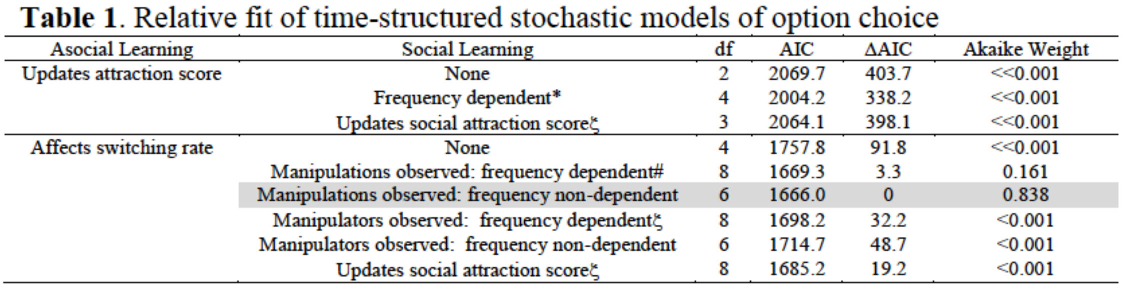

Table 1. Relative fit of time-structured stochastic models of option choice

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

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.