

TITLE PAGE INFORMATION

Title: Effects of indirect reputation and type of rearing on food choices in chimpanzees (*Pan troglodytes*)

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Abstract:

Chimpanzees and humans establish preferences over individuals they may benefit more from through scoring indirect reputation. However, humans prefer prosocial individuals even at their own cost. Giving preference to prosocial reputation over material rewards might have permitted the establishment of cooperative human societies. We tested the evolutionary roots of this propensity: importantly, in our study, the reputation scored had no food involved. Eighteen chimpanzees watched a performance where an antisocial experimenter hit a human victim and a prosocial experimenter interrupted the fight and consoled the victim. Next, the chimpanzees begged food from one of them. In Phase 2, the experimenters offered different food amounts (antisocial+4 vs. prosocial+1). Chimpanzees significantly prioritized rewards over reputation (i.e. chose antisocial). In Phase 3 both experimenters offered two pieces of food. Most of the subjects showed indifference to reputation (i.e. chose randomly). Watching fights produced significantly more arousal than consolations. Emotional engagement could not account for chimpanzees' choices since their choices varied between phases but their arousal did not. Ontogeny and rearing history might play a role in chimpanzees' choices: the adolescent males (n=3) consistently chose the antisocial individual whereas hand-reared subjects chose significantly different from mother-reared. We discuss whether the valence of the reputation is species-specific.

Significance statement:

From an evolutionary perspective, being able to learn indirect reputation is relevant for the individual's fitness. Both chimpanzees and humans have previously proved to choose those who will presumably behave in the future in a way they could benefit from, suggesting similar underlying cognitive processes that would have emerged at an earlier common ancestor. However, both species approach differently to prosocial individuals. Humans live in societies where there is common agreement about certain universal rights which should always prevail, and thus they are more willing to approach prosocial individuals, even at their own cost. By contrast, in our study, chimpanzees, whose societies are based on unequitable distribution of power and resources, were not that willing to consistently and costly approach prosocial individuals. Moreover, other interpersonal factors, such as the type of upbringing or age-related changes in behavior (aggressiveness during adolescence) might have accounted for these differences.

Keywords: reputation; image scoring; chimpanzees; morality.

Authors' contributions: All authors contributed to the study conception and design. Material preparation and data collection were performed by NB-G. Analysis were performed by NB-G and JC. The first draft of the manuscript was written by NB-G and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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80 Effects of indirect reputation and type of rearing on food choices in chimpanzees (*Pan troglodytes*)

81 **Introduction**

82 Indirect reputation is acquired through the observation of others' typical behavior as an uninvolved
83 bystander (Nowak and Sigmund 1998). Humans are good at monitoring reputation: children prefer to
84 acquire things from nice rather than from mean people (e.g. Herrmann et al. 2013) and adults take
85 individuals' reputation into account when deciding whom to cooperate with (Milinski et al. 2001, 2002).
86 Other species also share this ability, such as chimpanzees (*Pan troglodytes*), which prefer to beg for food
87 from experimenters who gave food to third parties (Russell et al. 2008; Subiaul et al. 2008), or tufted
88 capuchin monkeys (*Sapajus apella*), who chose those experimenters who cooperated with others (Anderson
89 et al. 2013b, a). Therefore, it is conceivable that image scoring (meaning eavesdropping' on third-party
90 interactions), is evolutionarily selected because the ability to anticipate potential cooperators and defectors
91 has an evident effect on the individual's welfare (Alexander 1987). By contrast, Engelmann and colleagues
92 (2012) showed that preschool children, but not chimpanzees, changed their behavior (ie. share more, steal
93 less) when conspecifics were watching them. It might be that being aware that the self-image is judged by
94 others, the so-called impression management, is a more cognitive complex capacity that humans, but not
95 non-human primates, are capable of.

96 Interestingly, when there is no potential reward from choosing the nice character, humans still tend to
97 choose them. As young as 5 months of age, human infants are willing to touch prosocial actors more than
98 antisocial actors (Hamlin et al. 2007, 2011) and as they grow up, children reduce their niceness towards an
99 individual that harmed another one (Vaish et al. 2010; Kenward and Dahl 2011). Even more strikingly, they
100 also do this when it is costly, therefore prioritizing the interaction with prosocial individuals over
101 maximizing their outcome, at least to a certain extent. In a recent study (Tasimi and Wynn 2016), 5- and 8-
102 year-olds were given the opportunity to choose between a prosocial character offering few rewards and an
103 antisocial character offering many rewards. The authors showed that children would keep incurring a cost
104 up to a ratio of 1:8 (1 reward from prosocial vs. 8 rewards from antisocial), meaning that from 1:16 on
105 children would change their choice and, as the authors said, would start "dealing with the devil". It is
106 interesting that children are willing to pay some cost, at least to a certain limit, in order to interact with
107 prosocial individuals. Probably selecting prosocial individuals is evolutionarily meaningful for humans
108 because it enhances the stability of societies through reinforcing an abstract body of shared rules such as
109 social norms (i.e. social agreements about the fairest thing to do Chudek and Henrich 2011; Schmidt and

110 Tomasello 2012) and moral norms (i.e. actions addressed to favor others' welfare Nichols 2004). However,
111 prosociality can be also evolutionarily selected in other non-normative forms such as mutualism, as it
112 happens in client and cleaner fishes' interactions when cleaner fishes cheat clients by eating available mucus
113 instead of hidden parasites. In those cases, defeated clients punished cheat cleaners by chasing them, and
114 this made the cheaters returned to mutual benefit (Bshary and Noë 2003). So far, what remains unanswered
115 is whether other species in addition to humans would also preferentially interact with prosocial individuals
116 as opposed to maximize their material outcomes.

117 One could argue that chimpanzees may not be willing to incur costs when a better deal is available,
118 regardless of the giver's reputation, for two reasons. First, chimpanzees have been largely considered
119 rational maximizers (Jensen et al. 2007, 2013). Previous research has shown that they failed to consistently
120 incur costs to be generous with a conspecific in platform and token tasks (Amici et al. 2014), in a dyadic
121 test of inequity (Hopper et al. 2013) as well as in bargaining tasks such as the ultimatum game (Jensen et
122 al. 2007; Kaiser et al. 2012; Bueno-Guerra et al. 2019) or the negotiation game (Melis et al. 2009).
123 Moreover, they hardly ever reject any food in an inequity aversion set-up (Bräuer et al. 2009). Second,
124 chimpanzees do not seem to care about third-party conflicts over food in experimental settings (Riedl et al.
125 2012). However, there are also some examples in which chimpanzees' responses challenged the rational
126 maximization hypothesis and incurred some costs. For instance, chimpanzees preferred equal distributions
127 in a token exchange task similar to the ultimatum game by incurring costs in terms of rewards (Proctor et
128 al. 2013) and tend to invest effort in giving their partner a high-value resource, taking the risk to be not
129 reciprocated in a trust game (Engelmann et al. 2015). In addition, observational studies show that
130 chimpanzees care about third-party conflicts since bystanders usually console attacked friends (Fraser and
131 Aureli 2008; Fraser et al. 2008); they police (von Rohr et al. 2012) and mediate in conflicts (de Waal 2000).
132 Therefore, chimpanzees could potentially incur some food costs and also care about certain third-party
133 behavior. Probably, the decision to combine both (i.e. incur a cost in order to interact with prosocial
134 individuals) will vary depending on what actions are presented as "prosocial" or "antisocial" and whether
135 those actions are relevant enough to be prioritized over outcomes by the particular species.

136 Previous studies in non-human primates have mainly used giving food to others (Russell et al. 2008; Subiaul
137 et al. 2008; Herrmann et al. 2013) and interrupting the action of giving food (Russell et al. 2008; Herrmann
138 et al. 2013), refusing to give food by turning their back or making food inaccessible (Subiaul et al. 2008)
139 as prosocial and antisocial actions, respectively. However, the action of spontaneous giving (without a prior

140 request) is rare among chimpanzees unless it is justified by a complex system of previous actions (Silk et
141 al. 2013 but see recent findings on teaching by costly tool provisioning; Musgrave et al. 2016). Moreover,
142 a wider concept of prosocial individuals might focus on the actions *per se*, regardless of the potential
143 outcome associated to them (i.e. giving is good *per se* and does not depend on whether the given content is
144 pleasant). That is why it would be interesting to present the chimpanzees with individuals who perform
145 actions that could be interpreted as antisocial or prosocial actions *per se*, without the inference of the given
146 content (i.e. unpleasant content/potential gift), and let them choose who they want to interact with
147 afterwards. In this way we could explore whether chimpanzees preferentially select prosocial individuals
148 and whether they do so at their own cost. Importantly, the prosocial and antisocial actions to be scored
149 should be chosen from observational studies in order to be ecologically relevant for the subjects tested.

150 There are certainly some actions in the chimpanzees' natural repertoire that are regularly performed both
151 in captivity and in the wild that can stand on their own as prosocial or antisocial without the need of a
152 particular content. As it has been mentioned, when chimpanzees engage in conflicts, aggression (i.e.
153 harmful action) can be followed by mediation (i.e. interrupting a fight) and reassuring (i.e. consoling).
154 These actions do not involve any exchange of contents but they themselves can be interpreted by a bystander
155 as antisocial and prosocial respectively since they always generate different outcomes in the recipient (i.e.
156 fearful facial expression vs. calming down). The relevance of the present study is that chimpanzees watched
157 common species-specific situations in which the action but not the content was scored: antisocial agents
158 were "experimenters who harmed others" and prosocial agents were "experimenters who interrupted fights
159 and consoled victims". To investigate who they preferred to interact with, chimpanzees were asked to beg
160 from one of the agents, a dependent variable common to previous studies with children (Tasimi and Wynn
161 2016) and apes (Russell et al. 2008; e.g. Herrmann et al. 2013). We presented two forced choices to eighteen
162 captive chimpanzees. After they saw a fight (antisocial agent hitting a victim) followed by a consolation
163 event (prosocial agent interrupting the fight and consoling the victim), the chimpanzees chose between the
164 antisocial agent and the prosocial agent, both of whom offered food to the chimpanzee, although the
165 antisocial agent offered more food. If they consistently chose the antisocial agent, we would confirm the
166 rational maximization hypothesis. If they consistently chose the prosocial agent, then we may provide
167 experimental evidence of chimpanzees incurring a cost to interact with individuals who were previously
168 prosocial in a different context. In addition, we explored whether chimpanzees shared the human preference
169 for prosocial agents by teasing the effect of the rewards apart. Therefore, in the second forced choice the

170 chimpanzees chose between the prosocial and the antisocial agents, both of them offering the same amount
171 of rewards. With the second forced choice we explored whether indirect reputation led to prosocial
172 preference or by contrast they were indifferent to reputation derived from third-party interactions. Given
173 that chimpanzees watched interactions between human actors (not conspecifics), we also analyzed whether
174 the amount of interspecific contact during upbringing (nursery- vs. mother-reared) affected their choices.

175 **Methods**

176 *Subjects.* We tested eighteen chimpanzees (*P. troglodytes*, 12 females) between 10 and 40 years of age
177 housed in the Wolfgang Köhler Primate Research Center in Leipzig (Germany). There were 8 individuals
178 who were nursery-reared: 3 subjects (two females and one male) received full daily human care for about
179 3 years while 5 subjects (four females and one male) received sporadic human care. The remaining 10
180 subjects were mother-reared (see Tables S1, S2, demographic, housing info, exclusion criteria and
181 participation in previous studies in Supplementary Materials, SM). One female was excluded from Phase 3
182 due to absence of motivation to participate (Ulla, see Table S2 in SM). The subjects were fed as a daily
183 basis with fruit, vegetables and leaves and occasionally with meat, eggs and worms. They were never food
184 deprived and had access to water *ad libitum*.

185 *Procedure*

186 The experiment consisted of three phases. In Phase 1 (Reward Baseline) we checked that apes preferred
187 larger over smaller amounts of food. Phases 2 and 3 started with chimpanzees watching three human
188 experimenters engaged in a fight (the antisocial experimenter hits the victim experimenter) followed by a
189 consolation event (the prosocial experimenter stops the fight, expulses the antisocial experimenter and
190 consoles the victim). We are aware that we did not counterbalance the order of appearance of the actions
191 performed by the experimenters within or across the phases (all subjects first watched the aggression and
192 then the consolation). This is because we wanted to keep a logic and coherent course of actions similar to
193 the situations they faced in their daily routine, in which individuals console victims who have been
194 previously attacked. After the performance, the chimpanzees received two trials in which the prosocial and
195 the antisocial experimenters offered food. In Phase 2, the prosocial experimenter offered 1 piece of food
196 and the antisocial experimenter offered 4 pieces of food. In Phase 3, both the prosocial and the antisocial
197 experimenters offered the same amount of food, 2 pieces each. With this procedure we wanted to see
198 whether chimpanzees changed their response from Phase 2 (Rewards vs. Reputation) to Phase 3

199 (Reputation). If chimpanzees wanted to choose the experimenter who had engaged in positive actions in
200 Phase 2 they must incur a cost, whereas this cost was absent in Phase 3 since the two experimenters offered
201 the same amount of food.

202 We conducted each phase in three different consecutive days and each phase was conducted only once to
203 avoid excessive arousal in the chimpanzees that could affect their welfare. All the trials were videotaped.
204 We tested the subjects individually. To prevent carry over effects between phases, the experimenters
205 participating in Phase 1 never participated in the following phases with the same subject. However, the
206 experimenters of Phase 2 and 3 were the same and kept their roles per subject to maintain coherence in their
207 reputation (ie. Tabea and Carol offered food in Phase 1 to chimpanzee Alex and in Phases 2 and 3 Anke
208 played the antisocial role and Nereida the prosocial role). The victim was a research assistant familiar to
209 the apes (about one-year exposure) and remained the same all trials across subjects. However, to prevent
210 the potential interference of familiarity of the agents, both the prosocial and the antisocial experimenters
211 were naïve to the subjects (only one experimenter had been exposed approx. 9 non-consecutive months to
212 the apes) and their roles were fully counterbalanced between subjects. We always used half-grapes as food
213 rewards, which were high quality food for these chimpanzees. After the experiment, we watched the videos
214 and coded their behavior and vocalizations in Phases 2 and 3 as measures of chimpanzees' emotional
215 arousal (see Analysis, second tab in the datasheet and ethogram and Table S3 in SM). All procedures
216 followed all applicable international, national, and/or institutional guidelines for the care and use of
217 animals. Besides, all procedures performed were in accordance with the ethical standards and granted the
218 permission of the Wolfgang Köhler Primate Research Center, at which the studies were conducted.

219 *Phase 1: Reward Baseline*

220 Two experimenters entered in the room with a dish in their hands, one of them carrying 1 piece of food and
221 the other carrying 4 pieces of food. After they showed the food to the subject, both of them moved to
222 opposite equidistant sides of the room (approx. 1.5 meters) and offered their food by pushing a sliding table
223 towards the subject. The chimpanzee could beg from them by inserting some fingers through a hole.
224 Immediately after the choice, both experimenters pushed their sliding table backwards and the chimpanzee
225 received food only from the experimenter she had begged from. Then both experimenters left the room so
226 that the ape understood he would only receive food from the first experimenter he begged from. We
227 repeated the same procedure counterbalancing the sides where the experimenters stayed as well as the order

228 in which they entered in the room. The chimpanzees passed to the next phase only if they chose 4 pieces of
229 food in the two first trials or across 4 consecutive trials. We ran a maximum of 14 trials per subject.

230 *Phase 2: Rewards vs. Reputation*

231 In this phase, three experimenters different from those who participated in Phase 1 performed one of these
232 three roles in front of the chimpanzee: victim, antisocial agent and prosocial agent. First, the victim entered
233 in the room, sat down on a plastic stool facing the middle point of the cage and pretended to be busy. After
234 5s, the antisocial experimenter entered with a red water noodle (1m long) and hit the victim three times on
235 her shoulder, who protected herself by covering her head with her arms while exclaiming “Au” in a painful
236 voice after each hit (see Fig. S1 in SM). Right before the fourth hit was produced, the prosocial experimenter
237 entered in the room, took the water noodle from the antisocial experimenter, threw it outside and made her
238 leave the room by firmly saying “Get out, leave” while making a gesture of expulsion with her hands
239 (shaking the hands towards the antisocial). The antisocial experimenter went out while the prosocial one
240 squatted next to the victim consoling her by semi-hugging and caressing her arm repeatedly for 5s (see Fig.
241 S2 in SM). After that, both experimenters left. During the fight the victim had remained covered and
242 sobbing whereas during the consolation the victim stopped sobbing to show recovery. After 5 seconds, the
243 prosocial and the antisocial experimenters entered again in the room to offer food in two consecutive trials
244 (prosocial+1 vs. antisocial+4) in the same way as it was conducted in Phase 1 (see Fig. S3 in SM).

245 *Phase 3. Reputation*

246 We repeated the same procedure of Phase 2 but this time both experimenters offered the same amount of
247 food (prosocial+2 vs. antisocial+2), also in two consecutive trials.

248 *Data availability*

249 All data generated during this study are included in this published article and its supplementary information
250 files. Also, the datasets are available in the Comillas repository (public, downloadable, permanent link:
251 <http://hdl.handle.net/11531/45604>) and ResearchGate repository (private, deliverable upon request,
252 permanent link: shorturl.at/aTY23).

253 **Analysis**

254 To compare Phases 2 and 3 and explore which factors may explain the chimpanzees' choices, we ran a
255 logistic GLMM with choice (prosocial or antisocial experimenter) as the dependent variable, which
256 modeled as a binary outcome (0 they chose antisocial; 1 they chose prosocial); condition (phases 2 or 3),
257 rearing (mother or human reared) and sex (male or female) as factors; age as a covariate and subject as a
258 random effect (intercept). We excluded the double interaction of rearing and condition because the
259 descriptive data showed that in Phase 2 only two subjects out of eighteen responded differently from the
260 rest, so we did not want to pollute the analysis or produce any spurious results.

261 With regard to the emotional arousal, we elaborated an ad-hoc ethogram (see details in SM), based on the
262 well-known Nishida et al.'s (1999) and Goodall's (1989) chimpanzee ethograms. We selected those
263 behaviors that entailed physical activation (e.g. genital erection, piloerection), interest in the action (e.g.
264 physical proximity, look) or were usually performed in aggressive encounters (e.g. hit): physical proximity,
265 balancing, bipedalism, enter hands through hole, genital erection, hit, kick, jump, look, move around,
266 nodding, piloerection, scratch and vocalizations. We watched the videos after the experiment and counted
267 whether any of these behaviors occurred (see coding in Table S3). We wanted to see whether chimpanzees
268 consistently displayed aggressive behaviors in front of fights but not in front of consolations. If this
269 happened, we acknowledge that it cannot prove the understanding of the actions displayed by the
270 experimenters but it might show that chimpanzees consistently and emotionally emulated what they were
271 watching (because of that, we ended up excluding physical proximity, enter hands through the hole and
272 look as they did not provide crucial information about their emotional arousal).

273 Due to the very few instances of vocalizations we registered (N=12) and its distribution across events
274 (fight=11 and consolation=1), it made no sense to run separated GLMMs (one for behavior, one for
275 vocalizations). Rather than excluding vocalizations from the analysis, we summed vocalizations to
276 behaviors (as vocalizing is indeed a behavior), and considered this sum our dependent variable
277 (nevertheless, we provide a GLMM with behaviors but not vocalizations in Tables S9 and S10, which yields
278 similar results to the ones reported here). Thus, to compare the emotional arousal between conditions and
279 fight/consolation events and to explore whether rearing would produce any difference in that, we ran a
280 Poisson GLMM with emotional arousal (the sum of behaviors and vocalizations) as the dependent variable;
281 condition (phases 2 or 3), event (fight or consolation), rearing (peer group or nursery) and the double
282 interactions of condition*event and event*rearing, keeping subject as a random effect (intercept). In both
283 models, as an overall test of the effect of the predictor variables we compared the full model with a null

284 model lacking the fixed effects and interactions but comprising the same random effect structure as the full
285 model (Forstmeier and Schielzeth 2011) using a likelihood ratio test (Dobson and Barnett 2008). The
286 models were fitted in JAMOVI (The jamovi project 2020) using the function lmer of the R package lme4
287 (Bates et al. 2015) adapted to the JAMOVI program by Gallucci (2019). To minimize observer bias, we
288 used blinded methods during the data analysis. Inter-observers watched a random selection of 15% of the
289 videos and coded both chimpanzees' choices and individual emotional arousal during fight and consolation
290 events. Their reliability was high ($\kappa = 0.97$).

291 **Results**

292 *Phase 1. Reward Baseline*

293 All eighteen subjects preferred four pieces of food and passed through the next phases. The mean average
294 of trials to reach the criteria was 5 (min.= 2, max.= 14).

295 *Choices and rearing*

296 The GLMM with condition, rearing, sex and age was significant compared to the null model (likelihood
297 ratio test: $\chi^2=28.648$, $df=4$, $p<0.001$). Adding condition ($\chi^2=19.218$, $df=1$, $p=0.001$) and rearing ($\chi^2=6.928$,
298 $df=1$, $p=0.01$) improved model fit, while adding sex ($\chi^2=2.008$, $df=1$, $p=0.16$) and age ($\chi^2=0.439$, $df=1$,
299 $p=0.51$) did not (see Table 1, S4, S5). With regard to condition, chimpanzees responded differently in
300 Phases 2 and 3. Fig. 1a shows the number of choices of the prosocial and the antisocial experimenters as a
301 function of phase. As it can be seen, in Phase 2, the 88% of the sample (sixteen out of eighteen subjects)
302 consistently begged from the antisocial experimenter offering four pieces of food, therefore chimpanzees
303 preferred the quantity of the rewards over the reputation of the humans who performed prosocial actions to
304 others (Bonferroni test: $Z=-3.73$, $p<0.001$). However, in Phase 3, chimpanzees as a group chose randomly
305 between the two experimenters (each experimenter was chosen 17 times). We also looked at their choice at
306 the first trial for the potential existence of primacy effect, but data in Table S2 confirms that chimpanzees
307 chose randomly: only 52% chose the prosocial agent first. Furthermore, Table 1 and Fig. 1b show that those
308 chimpanzees that had some human contact during their rearing chose the prosocial agent more than those
309 who were mother-reared (Bonferroni test: $Z=-2.10$, $p=0.036$).

310 ** Table 1 around here **

311 ** Figures 1a and 1b around here **

312 *Emotional Arousal*

313 The GLMM with condition, event, rearing and the double interactions condition*event and event*rearing
314 was significant compared to the null model (likelihood ratio test: ($\chi^2=64.232$, $df=5$, $p<0.001$). Adding event
315 ($\chi^2=63.379$, $df=1$, $p=0.001$) improved model fit, while adding condition ($\chi^2=0.28$, $df=1$, $p=0.59$), rearing
316 ($\chi^2=0.104$, $df=1$, $p=0.74$) and the double-way interactions between condition and event ($\chi^2=0.582$, $df=1$,
317 $p=0.44$) and between event and rearing ($\chi^2=0.112$, $df=1$, $p=0.73$) did not (see Table 2, S6, S7). In other
318 words, chimpanzees emotionally reacted very similarly regardless of their rearing in both phases and events.
319 Also, as the fight and consolation events were repeated the same across phases, it is a sign of consistency
320 (of the experimenters' performance) that we did not find any effect of condition on the chimpanzees'
321 emotional arousal. However, as it can be seen in Fig. 2, chimpanzees reacted differently between events.
322 Post-hoc test confirmed that during the fights, subjects produced significantly more arousal-activate or
323 aggressive-like behaviors (included vocalizations) than during the consolations (Bonferroni test: $Z=-5.59$,
324 $p<0.001$).

325 ** Table 2 around here **

326 **Figure 2 around here**

327 **Discussion**

328 Chimpanzees did not beg food from humans based on the reputation scored but on the amount of food they
329 were offering. More specifically, they preferred to maximize the food that they obtained even when it came
330 from a human who had previously harmed another one. When the effect of the rewards was controlled and
331 both humans offered the same amount of food, most of the chimpanzees did not show a clear preference
332 for the prosocial experimenter. However, the type of rearing was a predictor for their choice, so the
333 chimpanzees with most human contact during their upbringing were less likely to choose the antisocial
334 human compared to mother-reared chimpanzees. Interestingly, by contrast, the three adolescent males in
335 our sample, which regularly harass, hit and bully females in their group, consistently chose the antisocial
336 human. Finally, chimpanzees produced more arousal-activate or aggressive-like behaviors and
337 vocalizations during the fights than consolation events. As these differences in the arousal remained

338 comparable between the phases while their choices changed, we can rule out order effects and emotional
339 contagion as potential explanations for their preferences.

340 Our first main finding is that chimpanzees seem to prefer rewards over social reputation, at least with
341 heterospecific actors. Humans, in experiments with conspecifics, may choose individuals based in their
342 indirect reputation rather than in their own potential benefits, at least until a certain ratio of rewards (Tasimi
343 and Wynn 2016) and may prefer those who choose prosocial over antisocial individuals (e.g. Hamlin and
344 Wynn 2010). Chimpanzees also seem to behave differently from other non-human primates species such
345 as capuchin monkeys (*Cebus apella*) (Anderson et al. 2013a, b) and common marmosets (*Callithrix*
346 *jacchus*) (Kawai et al. 2014). In these studies, capuchin monkeys and marmosets scored the reputation of
347 humans performing food or non-food related actions (cooperative or non-cooperative / reciprocal or non-
348 reciprocal interactions) and significantly chose cooperative and reciprocal humans in ulterior food
349 distribution tasks. Therefore, two different evolutionary pathways might exist: the human/capuchin
350 monkeys/common marmosets pathway, highly social-oriented, with intermediate or full cooperative
351 breeding societies and without the need for a big brain (1300g in humans versus 8g in common marmosets),
352 which can be even prone to incur costs to interact with individuals who care about the conspecifics' welfare,
353 at least in the case of humans, and the chimpanzee pathway, highly self-oriented, with fission-fusion
354 societies, which will rarely loose the opportunity to maximize their outcome regardless of the reputation of
355 the individual they interact with. However, we must be cautious with this conclusion in light of the
356 following three caveats (which apply to our study but also to other experimental studies on this topic done
357 with non-human animals) plus, importantly, the role that rearing may play over chimpanzees' decisions,
358 since in our study human reared chimpanzees chose differently from their (mother reared) conspecifics.

359 First, we used human actors (not conspecifics) to present the forced choices to chimpanzees. The logistic
360 and ethical difficulties of using chimpanzee actors in an experimental setting involving physical aggression
361 are evident, which is why previous studies have also used human actors (Russell et al. 2008; Subiaul et al.
362 2008; Herrmann et al. 2013). However, as rearing appeared to influence chimpanzees' behavior, we think
363 it is important to discuss this aspect briefly. Even though the rearing history had no effect over the
364 chimpanzees' emotional arousal during the fighting-consolation events, it did affect their subsequent
365 decisions regarding the prosocial and the antisocial agents. The literature on how human rearing,
366 particularly enculturation, affects apes' behavior has mainly focused on their cognitive capacities (e.g., Call
367 and Tomasello 1998). Enculturated chimpanzees outperform non-enculturated ones in tool-use (e.g.

368 Furlong et al. 2007), imitative learning (e.g. Nagell et al. 1993 vs. Buttelmann et al. 2007) or communicative
369 skills (Call and Tomasello 1996). Even the mere exposure to human partners and their surroundings enables
370 them to display referential pointing (e.g., Call and Tomasello 1994; Leavens and Hopkins 1999; Leavens
371 et al. 2005). Leavens and colleagues wrote that: “Pointing emerges as a consequence of ecological factors
372 that come into play in some developmental contexts (captivity) but not in others (wild habitats)” (Leavens
373 et al. 2005 p. 187). Although Call and Tomasello (1996) originally argued that certain forms of
374 enculturation had a deep impact on apes cognitive abilities, more recently these authors have revised their
375 position by proposing that enculturation facilitates or enhances pre-existing abilities: “Since even non-
376 enculturated apes understand some aspects of intentional actions, it is likely that human experience only
377 serves to modify existing social interactional and attentional skills—rather than creating new ones”
378 (Tomasello and Call 2004 p. 214). It is unclear whether this human-triggered facilitation also happens in
379 chimpanzees’ acquisition and use of indirect reputation. Chimpanzees may possess some preference for
380 prosocial agents that emerges after repeated contact with humans. Bering (2004) argued that one of the key
381 effects of enculturation was that human-reared apes learned to pay more attention to humans. This means
382 that human-reared chimpanzees may be more likely to consider humans as potential social partners than
383 mother-reared chimpanzees. Future studies are needed to assess to what extent human-reared chimpanzees
384 are more likely to consider humans as part of their social environment than mother-reared chimpanzees
385 (see also Hayes 1951).

386 A second caveat was to assign some valence to fights and consolation that may not totally correspond to
387 the valence that chimpanzees assign to those same actions. It is important to bear in mind that those human
388 societies which are based on the universal right of “all are the same” do not see hitting as a regular way of
389 behaving. In fact, in those societies, humans who hit other humans are usually incarcerated, socially rejected
390 or labeled as “antisocial”. However, chimpanzee societies are hierarchically organized with adult males
391 being dominant over females. Male status does not only reflect fighting ability but it is also determined by
392 coalitions with other males and other group members (Nishida 1979; de Waal 1982; Goodall 1986).
393 Adolescent males typically ascend the adult male ranking order by physical harassing (e.g., hitting and
394 stomping) other group members beginning with females and low ranking individuals until they challenge
395 the top ranking males (Nishida 2003; Anestis 2006; Wobber et al. 2013). Thus, low rank individuals are
396 usually hit by adolescent males who seek strong allies to establish coalitions with them in potential conflicts
397 (van Schaik et al. 2004; Gilby et al. 2013). Therefore, after a fight, chimpanzees might not see the aggressor

398 as “antisocial”, as humans would do, but just see the regular set of actions that usually happens in their life
399 according to their social status. Indeed, even though age did not yield any significant result in our models,
400 when exploring the data we saw that the subjects who chose to beg from the antisocial experimenter both
401 times in Phase 3 were the three adolescent males we tested (see the choices of Lobo, Lome and Kofi in
402 Table S2). This is just a descriptive data based in very few subjects and observations with no comparison
403 with female adolescents available, so no strong inference may be extracted from it. However, this data
404 might warn us that looking at ontogeny when performing experiments about those behaviors that may be
405 affected by changes through development might be a potential source of revealing how lifespan evolution
406 occurs in non-human animals. Future studies should attempt to confirm this result with a larger sample of
407 adolescent males.

408 Third, we used “begging food” from one of the two experimenters as the dependent variable to assess
409 preferences. Even though this is the measure that has been used with apes in many other studies (Russell et
410 al. 2008; Subiaul et al. 2008; Herrmann et al. 2013), chimpanzees’ willingness to maximize their food
411 intake might have interfered with the assessment of their social preferences. In order to study how apes
412 score reputation in a wider sense, it would be interesting to know whether apes transfer their preferences
413 (prosocial or antisocial) to different contexts and whether they would have shown the same preference
414 without having visual access to the food carried by the agents. At least this is how humans conceive
415 reputation - a general construct that is not simply tied to a particular context but applicable to multiple
416 contexts. For example, being “prosocial” entails multiple attributes (provide objects, help, console,
417 cooperate). Although our dependent variable was performed in a different context (food) from the context
418 of the events the apes witnessed (fight and consolation), this might have been confusing for the apes. After
419 all, why would an antisocial individual offer food to the chimpanzee? Despite its usefulness, the food
420 begging measure raises further interpretative problems. Apes begging from the prosocial experimenter may
421 mean that they preferred individuals who performed prosocial actions but it could also mean that they
422 avoided the proximity of someone who may attack them. Our results at least show a change in chimpanzees’
423 preferences between phases: whereas most of the chimpanzees preferred the antisocial human in Phase 2,
424 when she was offering much food, the majority chose at random in Phase 3, when both experimenters
425 offered the same. Future studies should consider using tasks that do not involve food acquisition but that
426 require the chimpanzee to enlist the human for an action (e.g. help in a problem-solving situation). It would
427 also be desirable to explore to what extent the reputation scored in a particular situation can be transferred

428 to a different novel one (see Anderson et al. 2017). Finally, we also recommend to bearing in mind the
429 species' umwelt and its preferences through lifespan during the elaboration of the experimental design and
430 the interpretation of the data to avoid incurring in anthropomorphism.

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434 **Compliance with Ethical Standards:**

435 **Funding:** This study was funded by a FPU12/00409 scholarship from the Ministry of Education of Spain
436 granted by NBG.

437 **Conflict of Interest:** The authors declare that they have no conflict of interest.

438 **Ethical approval:** All applicable international, national, and/or institutional guidelines for the care and
439 use of animals were followed. Besides, all procedures performed were in accordance with the ethical
440 standards of the Wolfgang Köhler Primate Research Center at which the studies were conducted.

441 **Informed consent:** The human participants had signed a working contract with the Max Planck Institute
442 for Evolutionary Anthropology in Leipzig.

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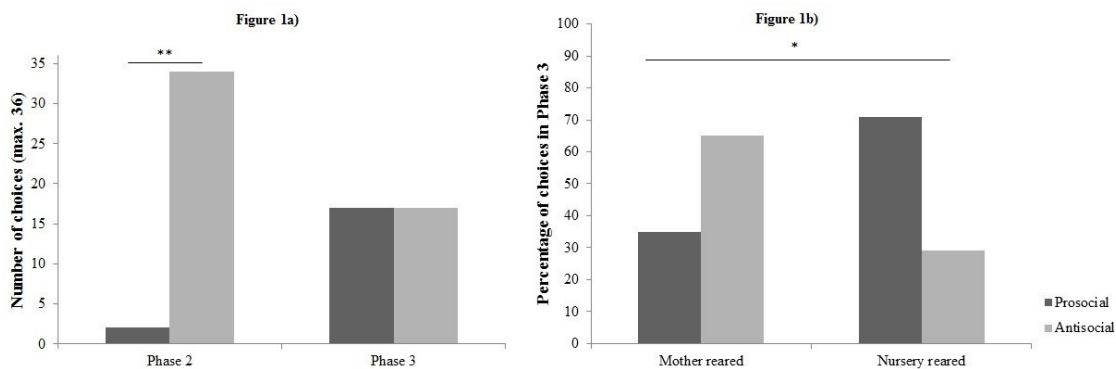
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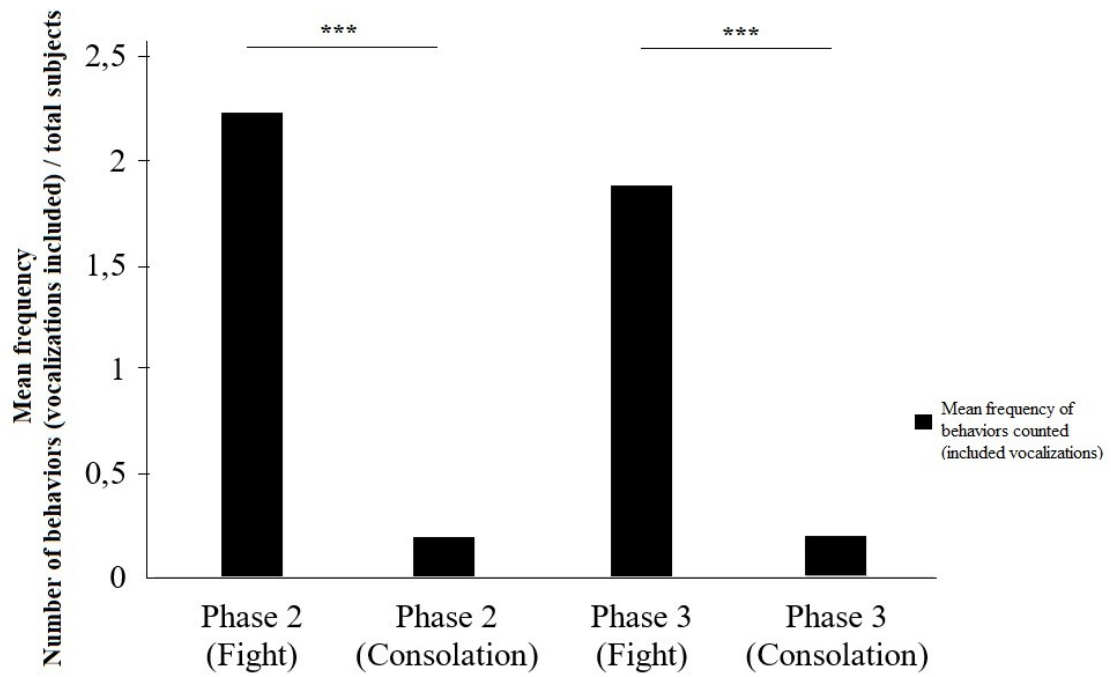


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600 **Fig. 1a** Number of choices in Phases 2 and 3 sorted by the reputation of the agent (prosocial vs.
601 antisocial). **Fig. 1b** Percentages of choices (prosocial vs. antisocial) in Phase 3 sorted by type of
602 chimpanzees' rearing (mother vs. nursery). * $p < 0.05$, ** $p < 0.01$

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606 **Fig. 2** Mean frequency of behaviors (vocalizations included) produced during the fight and consolation
 607 events of each phase. *** $p < 0.001$

608

Table 1 GLMM output (choices)
Fixed Effects Parameter Estimates

Names	Estimate	SE	z	p
(Intercept)	-1.6618	0.4667	-3.560	<0.001
Condition	3.4217	0.9182	3.727	<0.001
Rearing	1.6286	0.7748	2.102	0.036
Sex	0.9441	0.7603	1.242	0.214
Age	0.0223	0.0338	0.660	0.509

609

Table 2 GLMM (emotional arousal)
Fixed Effects Parameter Estimates

Names	Estimate	SE	z	p
(Intercept)	-0.6977	0.268	-2.608	0.009
Condition	-0.0521	0.426	-0.122	0.903
Event	2.5102	0.449	5.586	<0.001
Rearing	-0.1326	0.517	-0.257	0.798
Condition * Event	-0.1603	0.851	-0.188	0.851
Event * Rearing	0.5754	0.899	0.640	0.522

610

611 Find data sheet here: <http://hdl.handle.net/11531/45604>