



HAL
open science

Prosociality and reciprocity in capybaras (*Hydrochoerus hydrochaeris*) in a non-reproductive context

Mathilde Lalot, Agatha Liévin-Bazin, Aude Bourgeois, Michel Saint Jalme,
Dalila Bovet

► To cite this version:

Mathilde Lalot, Agatha Liévin-Bazin, Aude Bourgeois, Michel Saint Jalme, Dalila Bovet. Prosociality and reciprocity in capybaras (*Hydrochoerus hydrochaeris*) in a non-reproductive context. *Behavioural Processes*, 2021, 188, pp.104407. 10.1016/j.beproc.2021.104407 . hal-04367163

HAL Id: hal-04367163

<https://hal.science/hal-04367163v1>

Submitted on 22 Jul 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **Prosociality and reciprocity in capybaras**
2 **(*Hydrochoerus hydrochaeris*) in a non-reproductive**
3 **context.**

4

5

6 Mathilde Lalot^{1*}, Agatha Liévin-Bazin¹, Aude Bourgeois², Michel Saint Jalme², & Dalila
7 Bovet¹

8

9

10 ¹ Laboratoire Ethologie Cognition Développement, Université Paris Nanterre, Nanterre,
11 France

12 ² Ménagerie du Jardin des Plantes, Muséum National d'Histoire Naturelle, Paris, France

13

14 * Corresponding author

15 E-mail: mathilde.lalot@gmail.com (ML)

16 <http://orcid.org/0000-0003-3375-4194>

17

18 **Abstract**

19 Prosocial behaviours (providing benefits to a recipient with or without cost for the
20 donor) have been found to be highly influenced by sex and by hierarchy. Rodents, in
21 particular, are good model for studying prosocial responses, as they were found to exhibit
22 intentional prosocial behaviours to reward a conspecific, and are very sensitive to reciprocity.
23 In our study, we conducted a Prosocial Choice Test (PCT) in which four capybaras
24 (*Hydrochoerus hydrochaeris*) living in a social group could choose between three tokens:
25 choosing the prosocial token rewarded simultaneously the subject and a recipient, while
26 choosing the selfish token only rewarded the subject; and choosing the null token provided no
27 reward to anyone. Dominance within each dyad was also studied, both before and during the
28 PCT experiment. Our results showed an influence of hierarchy: subjects were more prosocial
29 towards the recipient when it was a subordinate than when it was a dominant individual.
30 These results could be interpreted as a desire of strengthening a hierarchical rank regarding
31 the subordinate, of punishing aggressive conspecifics (usually the subject's direct dominant),
32 and of weakening dominant individuals in order to modify the pre-existing hierarchy.
33 Additionally, our results highlighted a direct reciprocity phenomenon, a subject being more
34 likely to be prosocial towards a prosocial recipient. All these findings suggest that prosociality
35 could be well developed in other taxa than Primates and that, in long enough PCT
36 experiments, subtle rules could influence individual prosocial strategies.

37

38

39 **Keywords:** Prosociality – Sex – Dominance – Reciprocity – Capybaras – *Hydrochoerus*
40 *hydrochaeris*

41

42 **Introduction**

43 Recently, prosocial behaviours, defined as behaviours providing benefits to a recipient
44 with or without cost for the donor (Jensen et al., 2014) have been proven to exist outside
45 primates. Rodents, in particular, were found to be prosocial in experiments using paradigms
46 comparable to those used with primates. Studying this behaviours and determining whether it
47 can be exhibited by other taxa than primates is particularly important and would support the
48 Social Brain Hypothesis. Dunbar (1998) proposed the Social Brain Hypothesis as an
49 explanation for brain evolution. According to this concept, social complexity, not only the
50 size of a social group (Dunbar, 2009) but also the importance and flexibility of social
51 relationships, like fission-fusion society or monogamous bond (Shultz & Dunbar, 2007),
52 would be the main constraint to shape evolution of the size of the brain in vertebrate taxa.
53 Furthermore, finding prosociality outside primates would help to dissociate what is
54 specifically human (or purely exhibited by primate) and what is not.

55 Because of their developed sociality, rodents are considered as good candidates to
56 study prosociality. Many studies highlighted their skills in social behaviour and
57 communication (Decety & Svetlova, 2012; Mogil, 2012; Panksepp & Panksepp, 2013;
58 Preston, 2013), in emotional contagion (Paré & Glavin, 1986; Glavin et al., 1994; Langford et
59 al., 2006; Chen et al., 2009; Jeon et al., 2010; Romero et al., 2010; Knapska et al., 2010; Mohr
60 et al., 2010; Panksepp & Lahvis, 2011; Atsak et al., 2011; Akyazi & Eraslan, 2014), in
61 cooperation (Rutte & Taborsky, 2007; Viana et al., 2010; Tsoory et al., 2012), and in helping
62 behaviours (Church, 1959; Rice & Gainer, 1962; Ben-Ami Bartal et al., 2014), the latter being
63 a type of prosocial behaviours.

64 Most of studies about prosocial abilities in non-human subjects used Giving
65 Assistance Tests (GAT) or Prosocial Choice Tests (PCT). In GAT procedures, a recipient
66 individual needs the subject to give him a token or a tool to access a food source, and the
67 subject can choose either to do this action or not (Yamamoto et al., 2009, 2012). In PCT
68 procedures, subject could choose between several tokens associated with different outcomes,
69 usually a prosocial one and a selfish one (Stevens, 2010; Cronin et al., 2010). Choosing the
70 prosocial token induce to simultaneously reward the subject and a recipient individual (1/1
71 option), while choosing the selfish token only rewards the subject (1/0 option).

72 Several experiments highlighted the existence of prosocial abilities in rodents using
73 GAT or PCT procedures. For instance, Hernandez-Lallement and colleagues (2015) used a
74 spatial PCT (in a T-maze setup) and showed that rats preferred the prosocial option. They also
75 showed that rats became increasingly prosocial over sessions. Ben-Ami Bartal and colleagues
76 (2011) reported that rats behave prosocially when they perceive a conspecific experiencing
77 non-painful restraint stress: rats opened the door to free their cagemate but did not open the
78 door when the tube was empty or when the cagemate was replaced by an object. Sato and
79 colleagues (2015) also found prosociality in rats, subjects being more prompt to free a
80 conspecific in distress (forced to swim in a pool) than a non distressed one. Moreover, rats
81 that had previously experienced a forced swimming were quicker to help a cagemate than
82 those that had never been in this situation. In these two studies (Ben-Ami Bartal et al., 2011;
83 Sato et al., 2015), when given the choice to get a food reward or to help a distressed
84 cagemate, rats preferred the later.

85 Several studies also suggested that rodents' prosocial responses could be modulated by
86 the same factors that affect primates' prosociality, *i.e.*: subject's and recipient's sex and
87 dominance rank, as well as reciprocal pattern between them (Rutte & Taborsky, 2007, 2008;
88 Ben-Ami Bartal et al., 2011, 2014; Sato et al., 2015; Dolivo & Taborsky, 2015). Most of the
89 previously mentioned studies on rodents' prosocial abilities only involved females and used
90 species in which only the female invests in parental care. Besides, numerous studies involving
91 mammals of both sexes reported a difference between males and females, suggesting that
92 females would act more prosocially (in vampire bats: Wilkinson, 1984; in macaques: Massen
93 et al., 2010).

94 Prosociality might also be highly influenced by hierarchy (see Cronin, 2012 for a
95 review). Asymmetrical relationships hierarchies are thought to be a factor decreasing the
96 likelihood for prosociality to occur (Connor & Norris, 1982). In most species, dominance
97 hierarchies dictate priority of access to resources such as food, and subordinate individuals
98 may concede resources to more dominant individuals to avoid aggression (Preuschoft & van
99 Schaik, 2000). Then, if resource transfer in artificial tasks reflected the patterns of resource
100 allocation in the wild, one would predict that prosociality would be more likely to occur in
101 favour of dominant recipients rather than subordinate ones. However, in studies using a PCT
102 procedure in primates, more prosocial choices were performed by dominant individuals
103 towards subordinate ones (Colman et al., 1969; Lakshminarayanan & Santos, 2008; Takimoto
104 et al., 2010; Massen et al., 2010; Horner et al., 2011; Chang et al., 2011; Massen et al., 2011).

105 In contrast, female rats provide more food to heavy (dominant) conspecifics than to lighter
106 rats if the subjects were not hungry (Schneeberger et al. 2012).

107 While studies have reported reciprocity in primates (Hauser et al., 2003; Dufour et al.,
108 2009; Jaeggi et al., 2010; Jaeggi et al., 2013), some recent findings highlighted that rodents
109 could constitute a good model for studying reciprocity in their prosocial tendencies. Rutte &
110 Taborsky (2007) trained female Norway rats (*Rattus norvegicus*) in an instrumental prosocial
111 task in which subjects could pull a stick to provide food for a partner, and showed that
112 prosocial behaviour of rats was influenced by prior receipt of help, irrespective of the identity
113 of the partner. Rats acted according to a generalised reciprocity mechanism (defined as a
114 mechanism in which an individual A rewarded an individual B because an unknown
115 individual rewarded A before). In another study, Rutte & Taborsky (2008) showed that rats
116 could also act according to a direct reciprocity mechanism (defined as a mechanism in which
117 an individual A rewarded an individual B because B rewarded A before), and that direct
118 reciprocity generated a higher prosocial propensity than generalised reciprocity did. Rats'
119 prosocial responses were thus influenced by partner-specific information.

120 Therefore, we chose to study prosocial abilities in a highly sociable rodent species:
121 capybaras (*Hydrochoerus hydrochaeris*). They are the largest rodent species in the world and
122 present a developed and complex sociality (Burton & Burton, 2002). These rodents live in
123 stable groups of around 10 adults of both sexes; they are polygynous and breed cooperatively,
124 as it is not rare to see females suckling other pups than their own (Courchamp et al., 1999;
125 Herrera et al., 2011). Capybaras could be considered as a suitable species to study the
126 influence of sex and hierarchy on prosociality. According to Decety & Cowell (2014),
127 differences between sexes in prosociality appear because empathy has evolved in the context
128 of parental care and group living. In species presenting mostly maternal care, females would
129 be more often prosocial than male. Female capybaras being cooperative breeders, we could
130 expect that female subjects would be more prosocial than males. However, because our
131 experiment was conducted in a non-reproductive context, we did not assume that females
132 would be widely more prosocial than males. A strict linear social dominance hierarchy
133 enforced by chasing and, rarely, fights has been described in male capybaras (Herrera &
134 Macdonald, 1989, 1993; Maldonado-Chaparro & Blumstein, 2008), and more recently in
135 female capybaras (Nogueira-Filho et al., 2017). Considering the stable and linear hierarchy
136 within our subjects (both males and females), subordinates might be more prosocial towards
137 dominants to avoid punishment. However, as PCT procedures have been shown to elicit more

138 prosociality from dominant towards subordinate in numerous studies, we assumed that each
139 individual would be more prosocial towards subordinate than towards dominant. Capybaras
140 fulfil the conditions proposed by Trivers (1971) to be likely to favour reciprocity. Indeed, they
141 present a long lifespan and a low dispersal rate in adults; their society is relatively stable over
142 time; group membership changes rarely and a territory can be maintained by one group for
143 over three years (Burton & Burton, 2002). This social context allows many repeated
144 interactions. Because we conducted a long experiment relying on repeated tests, a reciprocal
145 pattern was likely to settle.

146

147

148 **Materials and Methods**

149

150 **Subjects & housing**

151 This experiment involved four capybaras (*Hydrochoerus hydrochaeris*): two males
152 (three and seven years old) and two females (three and five years old), all born in captivity
153 and not castrated. They were all sexually mature and their social group was stable: all the
154 subjects were housed together for more than two years before the experiment. Our subjects
155 had no experience in cognitive or behavioural testing before the present study. They were
156 housed outdoors, in a 600 m² enclosure in the Paris' Ménagerie of Jardin des Plantes.
157 Capybaras being a semi-aquatic species, especially regarding reproductive behaviours, as
158 copulation usually occurs in the water (Burton & Burton, 2002; Wolff & Sherman, 2007),
159 their enclosure presented a 10 m² x 30 cm deep pool. A food ration composed of fruits and
160 vegetables (apples, carrots, celery, broccoli, and zucchini), bread, and pellets (Mazuri® Zoo
161 A) was distributed daily in the morning. During the experiment, portions of fruits and
162 vegetables from this ration were used as food rewards (the rest of it being distributed after the
163 testing session).

164

165 **Measuring hierarchy**

166 We assessed the hierarchical rank of each individual before and during the experiment,
167 measuring the rate of won attacks (aggressive behaviour that made the conspecific to flee;
168 *e.g.*, chasing, threatening display) in each dyad and using David's score (David, 1987, 1988),
169 considered as the most appropriate dominance ranking method for this social group structure
170 (Gammell et al., 2003; Bang et al., 2010). Dominance asymmetry was also calculated for each
171 dyad, by subtracting the score of the subordinate individual to the score of the dominant
172 individual.

173

174 **Apparatus**

175 At the beginning of each session, the apparatus was placed in the capybaras'
176 enclosure. This apparatus was made of a 200 x 50 cm wooden board, crossed by three wooden
177 levers. On each lever, a token was fixed; the three tokens had an equal area but differed in
178 shape and colour (and colour contrast) to be easily distinguishable by capybaras (see Figure
179 1). Each lever was retained by a spring attached to the back of the board; therefore, after a
180 capybara's push down on the token, the lever would get back up to its previous position. The
181 board was set against the grid of the capybaras' enclosure. The experimenter, from behind the
182 grid outside the enclosure, distributed food rewards (portion of fruits and vegetables)
183 according to the capybara's choice, through one of three pipes placed behind the board and
184 reaching an opening below each item. A fourth pipe was placed at two metres from the board,
185 always at the same spot, and was used to provide food to the recipient individual in case of
186 prosocial choice of the subject.

187 [Figure 1 about here]

188 At each phase of this experiment (familiarisation, training, and test phases), the
189 relative location of the tokens on the levers was randomised between sessions. Rewards were
190 always the same (same fruit or vegetable, same volume of reward) for a subject and a
191 recipient, to avoid any inequity aversion effect. As the type of reward given was randomized
192 across the trials, it was not possible for the individuals to associate any type of reward with a
193 particular token or situation.

194

195 **Familiarisation phase**

196 A familiarisation phase was conducted before the training phase, to let capybaras
197 explore the apparatus and learn to push the lever. The aim of this phase was also to teach our
198 subjects to push the lever thoroughly, to ensure that choosing involves an effort. All tokens
199 provided a food reward. We conducted 30 sessions of 20 minutes to let each capybaras the
200 time to learn to approach the apparatus in less than 5 seconds and to push the lever frankly
201 and explicitly to receive food. At their first sessions, it took them 7 minutes on average.
202 Subjects needed 6 to 15 sessions to begin to approach and properly use the apparatus in less
203 than 5 seconds.

204

205 **Training and Test phases**

206 During the training and the test phases, each individual could either be subject or be
207 recipient. The subject had the possibility to choose a token among the three on the apparatus,
208 while the recipient just had to wait for a possible reward (according to the token chosen by the
209 subject) at a specific location.

210 During the training phase, different consequences were associated to each token (see
211 Table 1). The subject could then choose between the “prosocial” token (a blue square), which
212 induced two similar rewards distributed simultaneously (one to the subject and one to the
213 recipient individuals, 1/1 income), the “selfish” token (a red triangle), which involved a
214 reward distributed only to the subject (1/0 income), and the “null” one (a yellow disk), which
215 provided no food to anyone (0/0 income).

216 [Table 1 about here]

217 An individual was considered as a recipient when his head was less than 50 cm from
218 the bottom of the “recipient pipe” (located at two meters from the apparatus, presented on the
219 left side in Figure 1). Individuals having free access to the apparatus, it happened that no
220 individual was at the recipient area (66 times out of 334), this condition allowed us to study
221 subjects’ choices when no recipient were around.

222 We conducted one session of 20 minutes per day, five days per week, each day at
223 10:00 am, which was capybaras’ usual feeding time. In each session, the identity of both
224 subject and recipient, the token chosen by the subject and the attacks and other behaviours of
225 the subject and the recipient both before and during the tests were reported. Training phase

226 and test phase only differed for the analyses. Each individual was considered in test phase as
227 soon as it passed and maintained the criterion of less than 10% of null choices throughout the
228 rest of the experience (within and between the sessions).

229

230 **Ethical note**

231 The capybaras were not food deprived during this experiment. This study complies
232 with French and European legislation for animal care and was approved by the Committee on
233 the Ethics of Animal Experimentation N° 5 Charles Darwin (authorization number
234 Ce5/2012/089).

235

236 **Statistical analysis**

237 Statistical analyses were performed using the program R, version 3.1.0 (R
238 Development Core Team 2014), with the lme4 package (Bates et al., 2014), and were
239 conducted, for each subject, on the data in which they have passed and maintained the
240 criterion (choosing the “null” dish less than 10% of the trials in each session) through the
241 whole experiment. For a better visibility and understanding, results were reported in all
242 figures as means of the percentage of prosocial choices (*i.e.*, (number of prosocial choices /
243 (number of prosocial choices + number of selfish choices))*100) + S.E.M., while GLMM
244 studied proportion of prosocial choices (*i.e.*, number of prosocial choices / (number of
245 prosocial choices + number of selfish choices)). Statistical analyses were considered
246 significant at $P < 0.05$. Data were non-parametric, repeated and the number of sessions was
247 different from one subject to another. Therefore, for each test session, the proportion of
248 prosocial choices (among prosocial and selfish choices only) was studied using Generalized
249 Linear Mixed Models (GLMM).

250 For each session, the proportion of prosocial choices (among prosocial and selfish
251 choices only) was studied using Generalized Linear Mixed Models (GLMM).

252 First, we analysed data in which there was only one recipient. The fitted model
253 included proportion of prosocial choices according to subject sex (male versus female) and
254 recipient hierarchical rank regarding the subject (dominant versus subordinate). We weighted

255 the animals' responses by their number of trials in the model and used subjects' identity as
256 random factor. Example of syntax: “*modell = glmer(cbind(NbProsocial/NbTrial) ~*
257 *Tested_Sex * Recipient_Status + (1|Tested), weights = NbTrial, family = 'binomial', data =*
258 *data1)*”. We studied the possibility of the existence of prosocial tendencies in our subjects
259 (compared to random pattern) by conducting Z test. We also verified the possible existence of
260 a location bias or any preference for a particular token conducting analyses on the subjects'
261 proportion of choices for each token in familiarisation phase (when all token induced the
262 same consequence, *i.e.*, food reward), and in analysing their proportion of choices according
263 to the location of the token on the board. We also estimated subjects' reciprocal patterns.
264 Within each session the percentages of prosocial choices between each dyad were calculated
265 (A towards B, B towards A, A towards C, C towards A, etc.). Reciprocity was measured using
266 Spearman correlations between both individual percentages of prosocial choices in each dyad.
267 We analysed separately the few data in which they were no recipient, 2 recipient or even 3
268 recipients. The fitted model included the number of recipients. We weighted the animals'
269 responses by their number of trials in the model and used subjects' identity as random factor.
270 Regarding GLMM significant results, χ^2 value, z value, P value, fixed-effect estimates, 95%
271 confidence intervals (C.I.) were reported.

272

273

274 **Results**

275 The subjects' choices during the 30 sessions of the familiarisation phase confirmed the
276 absence of any location bias ($\chi^2 = 2.83$, $P = 0.243$), as well as any preferences for a particular
277 token ($\chi^2 = 0.59$, $P = 0.744$). After four months of training, all our subjects succeeded to pass
278 and maintain our criterion (*i.e.*, less than 10% of null choices). Our test data represented 55
279 test-sessions (including 110 trials per session on average and 6040 trials in total).

280

281 Considering GLMM analysis, the model that presented the best quality, *i.e.* with the
282 lowest Akaike information criterion (AIC) and Bayesian information criterion (BIC), included
283 proportion of prosocial choices according to subject sex (male versus female) and recipient
284 hierarchical rank regarding the subject (dominant versus subordinate).

285

286 The sex of the subject seemed to influenced the response, females being more
287 prosocial than males ($\chi^2 = 12.32$, $z = -3.511$, $P < 0.001$, *Estimate* = -0.7511, *C.I.* = [-1.247; -
288 0.210]). Females chose the prosocial token significantly more often than expected if ($|Z| =$
289 2.50, $P < 0.05$). On the other hand, males were neither particularly prosocial nor selfish ($|Z| =$
290 1.35, $P > 0.05$).

291

292 Capybaras' hierarchical ranks were linear and highly constant over sessions, as
293 subject's rank did not change between sessions and as won attacks and chasing rates were
294 stable over sessions. Therefore, we calculated an individuals' David's scores representing
295 interactions of the whole experiment (reported in the Table 2). Hierarchy seemed to influence
296 individuals' prosociality (see Figure 2). Subjects were more prosocial towards subordinates
297 than towards dominants ($\chi^2 = 24.62$, $z = 4.961$, $P < 0.001$, *Estimate* = 1.291, *C.I.* = [0.822;
298 1.823]). Comparing their percentages of prosocial responses to those expected if capybaras
299 chose randomly, we found that subjects' choices did not differ from chance towards dominant
300 recipient ($W = -87.00$, $P = 0.699$), while they were significantly prosocial towards subordinate
301 recipients ($W = -148.00$, $P = 0.038$).

302 [Table 2 about here]

303 [Figure 2 about here]

304

305 The capybaras were more aggressive towards subordinates than towards dominants (χ^2
306 = 712.90, $z = 26.700$, $P < 0.001$, *Estimate* = 85.663, *C.I.* = [80.832; 92.499]). Dominance
307 asymmetry (which is the difference between the subject's rank and the recipient's rank) was,
308 as well, related to the aggressions rate within the dyad (which is the percentage of the
309 aggressions in the dyad, initiated by the subject): the greater the asymmetry, the greater the
310 aggression rate within the dyad (Spearman's $r_s = 0.944$, $P < 0.001$, $N = 12$).

311

312 Capybaras chose according to a direct reciprocity phenomenon. Subjects were more
313 likely to reciprocate a prosocial choice if the recipient was prosocial as well during the session
314 (Spearman's $r_s = 0.534$, $P = 0.009$, $N = 30$).

315 We verified if this result could be related to a stimulus enhancement effect (*i.e.*,
316 choosing the same token by mere imitation) by analysing the training data. Training data did
317 not correlate between each subject's prosociality towards each recipient (A = subject, B =
318 recipient) and the recipient's prosociality when become subject (B = subject, A = recipient),
319 suggesting this phenomenon would not be due to imitation (Spearman's $r_s = 0.170$, $P = 0.365$,
320 $N = 30$).

321

322 While all the previous analyses focused on data in which there was only one recipient
323 individual, it happened sometimes that an individual chose a token when there was no
324 recipient (66 times) or several individuals (two individuals 53 times and even the three
325 individuals 5 times) at the recipient area. When we analysed all these data together, we found
326 a positive effect of the number of recipients individuals on subject prosociality (see Figure 3):
327 the more recipient individuals there were, the more the subject was prosocial ($\chi^2 = 128.3$, $P <$
328 0.001). Subjects were more prosocial when there was one recipient than when there was none
329 ($\chi^2 = 73.63$, $z = 8.581$, $P < 0.001$, *Estimate* = 0.8717, *C.I.* = [0.674; 1.072]), and were more
330 prosocial when there was two or three recipients than when there was only one ($\chi^2 = 36.97$, z
331 = 6.080, $P < 0.001$, *Estimate* = 0.7742, *C.I.* = [0.527; 1.027]).

332 [Figure 3 about here]

333

334

335 **Discussion**

336 Since only four capybaras were involved in our experiment, we have to be careful with
337 our findings. Despite null model was not the fittest one, we should consider that each effect
338 discussed bellow could also be impacted by inter-individual differences. Our subjects were
339 highly familiar with each other and their relationships were different from one dyad to
340 another. Results could be explained by their relationship specificities as well. However, when

341 a result appeared in several dyads sharing different relationships but being consistent with
342 other variables (sex of the subject, status of the recipient, presence of a witness), we allowed
343 ourselves to look for wider explanations and interpretations of their behaviours. Our
344 discussion should be regarded only as suggestions of possible explanations if we found them
345 at a larger scale.

346 Our results suggest that our experimental design succeeded to elicit prosocial
347 behaviours in capybaras. In our experiment, we used the null token as a control, allowing the
348 experimenter to follow individuals learning progress, as stopping choosing it suggested that
349 the subject might begin to distinguish the three tokens and to associate them different
350 consequences. All our subjects succeeded to choose it less than 10% of the time, after four
351 months of training. We designed our task in order to avoid complex apparatus, eliminate
352 location biases, avoid competitive behaviours (the food reward not visible before the subject's
353 choice, a feature well known to inhibit prosociality), and make the choice and consumption of
354 reward visible and audible for other individuals; not controlling these factors having been
355 proved to cause negative results in many studies (Warneken & Tomasello, 2006, 2009;
356 Horner et al., 2011; Melis et al., 2011; Silk & House, 2011; House et al., 2014).

357 Our experiment was also designed to be as naturalistic as possible, capybaras being
358 tested with unconstrained access to their social group, having free access to the apparatus and
359 having the possibility to participate in the test or not. Some other studies tested animals in
360 their social group (Chalmeau, 1994; Chalmeau & Gallo, 1996; Cronin et al., 2014), and it was
361 often reported that letting the subject choose their partner was important for these kinds of
362 tasks (Nishida & Turner, 1996; de Waal, 1997; Mitani, 2006; Melis et al., 2006; Boesch et al.,
363 2006; Langergraber et al., 2007; Mitani, 2009). Whereas more controlled conditions are a
364 better way of separating variables, free access represents a more ecologically relevant setting
365 in which individuals can choose by themselves with whom they want to cooperate.

366 However, this free access design let to the subjects the possibility to steal the subject's
367 reward in a case of selfish choice. We observed a few instances of food stealing (in 28 out of
368 our 6040 trials, representing 0.46% of the trials). Nevertheless, these behaviours were quite
369 passive (grabbing the food when the subject did not find it soon enough) and did not induce
370 any decrease of participation in the task in any individual. In contrast, Massen and colleagues
371 (2015) reported that ravens became less likely to participate in a cooperation task after being
372 cheated on (cheaters displacing their partner to grab both rewards).

373

374 Data seemed to suggest that female capybaras could exhibit more prosociality than
375 males. None of the female was the mother of any member of the group; thus, it is unlikely that
376 kinship explain this result. Wilkinson (1984), as well, reported that female vampire bats
377 shared food more often than males and explained this difference arguing that female bats were
378 more stable in their relationships. Other studies found that male vampire bats rarely shared
379 food in the wild, where their social relationships are transient (Wilkinson, 1985), but shared
380 food in captivity (DeNault & McFarlane, 1995), where male associations are more stable. In
381 addition, Massen and colleagues (2010) found that female long-tailed macaques were more
382 prosocial than males. In this species, females remain in the same group for their whole life
383 (van Noordwijk & van Schaik, 1987), and have “family ranks”, since they inherit their rank
384 from their mother (Hill & Okayasu, 1996), in contrast to males. Females would thus be more
385 prosocial to sustain their hierarchical rank, in case of family turnover (Chance et al., 1977).

386 If the effect of sex was confirmed by more studies using a greater sample size, it could
387 be explained by the difference in both sexes’ tendency to disperse. When capybaras are in
388 high density groups, males disperse more and females become philopatric (Herrera et al.,
389 2011). Therefore, it would be possible that female capybaras tend to build stronger bonds, like
390 in long-tailed macaques (Massen et al., 2010). Of course, this hypothesis would need further
391 studies in the wild to conclude.

392 Another explanation could be that differences between males and females prosociality
393 would be due to females’ prevalence in mammals to be in charge of parental care. Indeed,
394 according to many researchers, (Eibl-Eibesfeldt, 1973; MacLean, 1985; Decety & Cowell,
395 2014), this difference between sexes might occur because “empathy” evolved in a context of
396 parental care. The selection pressures to emotionally connect with the young, would have
397 shaped the caregivers’ prosocial and empathic abilities (Bowlby, 1958; Acebo & Thoman,
398 1995), the indifferent ones being more likely to see their reproductive success decrease if the
399 young needs to be fed, cleaned and warmed to survive. This hypothesis could be tested by
400 studying capybaras prosocial tendencies in various conditions, comparing, for instance, our
401 data with their prosociality in reproductive context, with and without young, as it was done in
402 Guinea pigs, another rodent species from the *Caviidae* Family. Indeed, Guinea pigs showed
403 prosociality towards their mate and their young, as well as a selfish pattern towards
404 competitors, during the reproductive period but not during the non-reproductive period (Lalot

405 et al., *submitted*). Another study shown that Guinea pigs stress level decreased when they
406 were with a mate during a reproductive period (Kaiser et al., 2003).

407

408 As expected, the capybaras we tested were prosocial towards subordinates. This result
409 is also consistent with those we found studying Guinea pigs (Lalot et al., *submitted*), in which
410 we reported the same pattern of choice. The effect of hierarchical rank we found in capybaras
411 is not likely to be linked to a predisposal from the dominant subjects to approach the
412 apparatus (by being less anxious for instance) because all individuals interacted with the
413 apparatus with no significantly different latencies (being all ready and in the testing area
414 every morning, even before the apparatus was set up).

415 Wild capybaras are known for their very stable and strictly linear hierarchy, which
416 settles through stereotyped agonistic interactions (Herrera & Macdonald, 1993; Salas, 1999;
417 Herrera et al., 2011; Nogueira-Filho et al., 2017). Our capybaras were no exception, their
418 hierarchy being highly consistent over the seven months we studied them. Therefore, we were
419 not surprised to see that these features modulated their prosociality.

420 Despite the variability of definitions of dominance, most focus on easily observable
421 behaviours such as aggression. Drews (1993) defined dominance as “an attribute of the
422 pattern of repeated, agonistic interactions between two individuals, characterized by a
423 consistent outcome in favour of the same dyad member and a default yielding response of its
424 opponent rather than escalation; the status of the consistent winner is dominant and that of the
425 loser subordinate.” We ourselves used the measures of aggressions and threats to estimate the
426 hierarchy of our subjects. However, although agonistic behaviours (highly stereotyped non-
427 openly violent behaviours as well as aggressions) have long been considered to be the main
428 way to achieve and maintain dominance, this position has recently been questioned by some
429 researchers, especially those studying prosocial behaviours.

430 In literature, two possible ways for dominance to affect prosociality were reported.
431 Either the subordinate individuals were particularly prosocial towards dominants, in which
432 case their behaviour was interpreted as a seeking of dominance tolerance or future support
433 (Seyfarth, 1977; Noë et al., 1991), or the dominant individuals were especially prosocial
434 towards subordinates, in which case their prosociality was interpreted as a strategy to enhance

435 and maintain their status (Moore, 1984; de Waal, 1989). The latter strategy is the most
436 observed in PCT experiment.

437 In PCT experiments, humans (Dovidio & Gaertner, 1981; Mast & Bischof, 1999),
438 chimpanzees (Horner et al., 2011), long-tailed macaques (Massen et al., 2010), and capuchins
439 monkeys (Lakshminarayanan & Santos, 2008; Takimoto et al., 2010) were more prosocial
440 towards subordinate than towards dominant recipient. Authors suggested that dominant
441 individuals could use prosocial behaviours to emphasise their hierarchical position.
442 Prosociality was interpreted as a strategy by the dominants to enhance and/or maintain a
443 status (Moore, 1984; de Waal, 1989), as well as to advertise their dominance to others,
444 probably to convince subordinates to accept their high-ranking situation and inhibiting their
445 possible rebellions (Zahavi, 1977, 2004).

446 Other findings in rats also suggested that they would be more prosocial towards
447 subordinate than towards dominant conspecifics in PCT procedures. Hernandez-Lallement
448 and colleagues (2015) and Schneeberger and colleagues (2012) showed that rats were more
449 prosocial when the recipient was lighter. Considering that the heavier a rat is, the more
450 dominant it is supposed to be (Smith et al., 1994), it is probable that rats would have been
451 more prosocial towards subordinate recipients than towards dominant ones. Note that the
452 results of Schneeberger and colleagues (2012) depended on the need of the partner: if the rats
453 were satiated, focal individuals provided more food to dominant (heavier) than to subordinate
454 (lighter) rats. Unfortunately, we did not measure our subjects' weight.

455 The hypothesis that dominance could be maintained, not only by exhibiting agonistic
456 behaviours, but also by being prosocial when having the opportunity is well described by
457 Massen and colleagues (2010), who considered their macaques acting as “benevolent leaders
458 rather than despots” ruling by fear. The fact that the prosocial way is, for now, less described
459 than the aggressive way might be due to two factors: first, prosociality studies are way more
460 recent than studies about mere hierarchy, second, levels of aggressions are easier and faster to
461 assess than prosociality in a PCT procedure. Therefore, estimating which one of the two ways
462 is the most important in an animal society would require numerous further studies.

463 The constraints perceived by the group (limited resources, frustrations) could also
464 affect individuals' strategies. Indeed, studying long-tailed macaques in captivity (not food
465 deprived), Schaub (1996) found that dominants were more prosocial than subordinates, letting
466 them access a food source longer. Rank influenced prosociality whereas kinship did not. In

467 PCT experiments, dominants were, as well, more prosocial than subordinate. However,
468 studies using a GAT (Giving Assistant Test) procedure showed that benefits were transferred
469 “up” the hierarchy, subordinates being more prosocial than dominants, in chimpanzees
470 (Yamamoto et al., 2009; Melis et al., 2011) as in bird species like keas (Tebbich et al., 1996).
471 GAT induces constraints, needs and frustrations that might not be induced by PCT. It would
472 be interesting to study the influence of dominance in prosociality according to different level
473 of constraint/effort/cost for the donor.

474

475 Capybaras exhibited a direct reciprocal pattern in their prosocial responses, regardless
476 of the sex and dominance effect. This is a phenomenon known to take some time to settle
477 (Dufour et al., 2009; Gomes & Boesch, 2009; Gomes et al., 2009; Gilby et al., 2010). Since
478 no reciprocity appeared during the training phase, it is unlikely that this result could be due to
479 an imitation strategy (choosing the same token just because it rewarded the subject right
480 before). This direct reciprocity did not seem to be linked to neither the subject’s sex nor the
481 recipient’s sex.

482 While some studies suggested that some levels of prosociality, reciprocity and
483 cooperation should appear in more socially complex species (Brosnan et al., 2010), others
484 argued that taking account of the emotional results of previous encounter (*i.e.*, “emotional
485 bookkeeping”) might be sufficient to elicit and maintain stable cooperation, prosociality and
486 reciprocity without complex cognition (Evers et al., 2015). Repeated social interactions with a
487 conspecific would lead to associate an emotional state with this conspecific, allowing long-
488 term tracking of prosocial interactions for instance. According to Rutte & Taborsky (2007),
489 reciprocity would be the main factor that promotes the evolution of prosociality among
490 unfamiliar nonrelatives.

491

492 For some trials, the number of recipients was different from one: there was no
493 recipient or, in contrast, two or three individuals at the recipient area. We analysed these data
494 according to the number of recipients and found that subjects chose more often the item
495 associated with a prosocial consequence when there was one or several recipients compared to
496 none, and that they were even more prosocial when there were two or more “recipients”
497 (compared to one and to none).

498 The data in which no recipient was present informed us about subject tendencies when
499 their choice did not have any consequence for a conspecific. These data could be related to
500 those obtained in the non-social condition (also called the empty-cage condition) that
501 occurred in some PCT studies conducted in primates (Silk et al., 2005; Horner et al., 2011).
502 Our capybaras chose the prosocial option significantly more often when there was a recipient.
503 In our experiment, as in Horner and colleagues' (2011), subjects were less prosocial when no
504 one was at the recipient area, suggesting that subject chose prosocially in order to reward the
505 recipient individual rather than to go take the reward for itself.

506 The fact that our subjects were increasingly prosocial as the number of individual at
507 the recipient area increased could be interpreted as a prosocial enhancement due to greater
508 stakes and social constraints. They might have more to lose not showing prosociality to
509 several members of their social group. Moreover, a greater number of "recipients" enhanced
510 the likelihood for one of them to elicit prosociality from the subject (being a subordinate) or
511 to elicit reciprocal prosocial response (in having been prosocial before).

512 This result could be compared with those found on audience effect. Audience effect
513 has been shown to increase some prosocial tendencies. In vervet monkeys, males were less
514 aggressive and more affiliative towards young when their mothers were in sight (Hector et al.,
515 1989). Audience effect also appeared to modulate helping behaviours in cooperative breeding
516 species (McDonald et al., 2008). Indeed, in sociable weaver, individuals helping parents to
517 take care of the young helped them longer and more often when an audience was present
518 (Doutrelant & Covas, 2007). In cleaner fishes, individuals behave more cooperatively when
519 observed (Bshary & Grutter, 2006) and were less likely to cheat (Pinto et al., 2011).

520 The fact that the mere presence of an audience could increase subjects' prosociality
521 has often been interpreted as an interest in their reputation and a desire of reciprocity (Bshary
522 & Grutter, 2006 ; Chevallier et al., 2012 ; Engelmann et al., 2012 ; Leimgruber et al., 2012).
523 For instance, in chimpanzees, individuals signalling to the whole social group their generosity
524 each time they shared food rose more easily in the hierarchy (de Waal, 1982).

525

526

527 Our experiment suggested that, like primates and rats, capybaras seem able to show
528 some prosociality and to modulate their prosocial responses according to the identity, status

529 and previous behaviour of the recipients. As Macdonald and colleagues (2013) highlighted,
530 capybaras present elements in their social system that reflect those of other mammals, while
531 being unusual amongst rodents, and some aspects of their social behavior, like their
532 behavioural flexibility are even unique (Macdonald et al., 2007). Capybara is considered as
533 “an excellent model for the study of variation in mammalian social systems and its adaptive
534 significance” (Macdonald et al., 2013). Obviously, the size of our sample does not allow us to
535 draw firm conclusions about the influence of sex and rank on Capybaras’ prosocial tendencies
536 (which could be due to individual traits). Further studies are needed to confirm each effect we
537 suggested.

538 Nonetheless, the fact that prosociality and reciprocity could be found outside primates
539 supports the idea that social relationships could be a more important factor than mere
540 phylogenetic proximity from humans to exhibit these behaviours. According to Dunbar’s
541 (1998, 2009) Social Brain Hypothesis, bonded relationships would be cognitively demanding
542 enough to modulate the evolution towards a bigger brain (especially a bigger neocortex).
543 Considering the scale of an individual’s lifespan rather than evolution of species, Dale and
544 colleagues (2020) highlighted the importance of social relationship over cognition for
545 prosociality and cooperation tasks. They tested wolves in three experimental tasks:
546 prosociality, cooperation, and inequity aversion task. They showed that social bonds between
547 the subject and the recipient influenced subjects’ performances in all tasks, while non-social
548 factors they measured did not. More and more studies show us that most of what were thought
549 to be human specificities (or primate specificities) may not be. Convergent evolution, driven
550 by social cognition, incites us to search those “specificities” outside primates.

551

552

553 **Acknowledgments**

554 I would like to thank the trainers for their time, and the students who participated in
555 this experiment: Anne-Sophie Feret, Sophie Le Ray and Chloé Serrÿn.

556

557

558 **References**

- 559 Acebo, C., & Thoman, E. B. (1995). Role of infant crying in the early mother-infant
560 dialogue. *Physiology & behavior*, *57*(3), 541-547.
- 561 Akyazi, I., & Eraslan, E. (2014). Transmission of stress between cagemates: a study in rats.
562 *Physiology & behavior*, *123*, 114-118.
- 563 Atsak, P., Orre, M., Bakker, P., Cerliani, L., Roozendaal, B., Gazzola, V., Moita, M., &
564 Keysers, C. (2011). Experience modulates vicarious freezing in rats: a model for
565 empathy. *PloS one*, *6*(7), e21855.
- 566 Bang, A., Deshpande, S., Sumana, A., & Gadagkar, R. (2010). Choosing an appropriate
567 index to construct dominance hierarchies in animal societies: a comparison of three
568 indices. *Animal Behaviour*, *79*(3), 631-636.
- 569 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects
570 models using lme4. arXiv. org. *preprint*]. doi, 10.
- 571 Ben-Ami Bartal, I., Decety, J., & Mason, P. (2011). Empathy and pro-social behavior in
572 rats. *Science*, *334*(6061), 1427-1430.
- 573 Ben-Ami Bartal, I., Rodgers, D. A., Sarria, M. S. B., Decety, J., & Mason, P. (2014). Pro-
574 social behavior in rats is modulated by social experience. *Elife*, *3*, e01385.
- 575 Boesch, C., Boesch, H., & Vigilant, L. (2006). Cooperative hunting in chimpanzees:
576 kinship or mutualism? In: Schaik, C. P., & Kappeler, P. M. (Eds), *Cooperation in*
577 *primates and humans*. (pp. 139-150). Springer Berlin Heidelberg.
- 578 Bowlby, J. (1958). The nature of the child's tie to his mother. *The International journal of*
579 *psycho-analysis*, *39*, 350-373.
- 580 Brosnan, S. F., Salwiczek, L., & Bshary, R. (2010). The interplay of cognition and
581 cooperation. *Philosophical Transactions of the Royal Society B: Biological*
582 *Sciences*, *365*(1553), 2699-2710.
- 583 Bshary, R., & Grutter, A. S. (2006). Image scoring and cooperation in a cleaner fish
584 mutualism. *Nature*, *441*(7096), 975-978.

- 585 Burton, M., & Burton, R. (2002). *International Wildlife Encyclopedia: Index volume* (Vol.
586 22). Marshall Cavendish.
- 587 Chalmeau, R. (1994). Do chimpanzees cooperate in a learning task? *Primates*, 35(3), 385-
588 392.
- 589 Chalmeau, R., & Gallo, A. (1996). What chimpanzees (*Pan troglodytes*) learn in a
590 cooperative task. *Primates*, 37(1), 39-47.
- 591 Chance, M. R. A., Emory, G. R., & Payne, R. G. (1977). Status referents in long-tailed
592 macaques (*Macaca fascicularis*): Precursors and effects of a female
593 rebellion. *Primates*, 18(3), 611-632.
- 594 Chang, S. W., Winecoff, A. A., & Platt, M. L. (2011). Vicarious reinforcement in rhesus
595 macaques (*Macaca mulatta*). *Frontiers in neuroscience*, 5, 27.
- 596 Chen, Q., Panksepp, J. B., & Lahvis, G. P. (2009). Empathy is moderated by genetic
597 background in mice. *PloS one*, 4(2), e4387.
- 598 Chevallier, C., Kohls, G., Troiani, V., Brodtkin, E. S., & Schultz, R. T. (2012). The social
599 motivation theory of autism. *Trends in cognitive sciences*, 16(4), 231-239.
- 600 Church, R. M. (1959). Emotional reactions of rats to the pain of others. *Journal of*
601 *comparative and physiological psychology*, 52(2), 132.
- 602 Colman, A. D., Liebold, K. E., & Boren, J. J. (1969). A method for studying altruism in
603 monkeys. *The Psychological Record*, 19, 401-405.
- 604 Connor, R. C., & Norris, K. S. (1982). Are dolphins reciprocal altruists? *American*
605 *Naturalist*, 119(3), 358-374.
- 606 Courchamp, F., Grenfell, B., & Clutton-Brock, T. (1999). Population dynamics of obligate
607 cooperators. *Proceedings of the Royal Society of London B: Biological*
608 *Sciences*, 266(1419), 557-563.
- 609 Cronin, K. A. (2012). Prosocial behaviour in animals: the influence of social relationships,
610 communication and rewards. *Animal Behaviour*, 84(5), 1085-1093.

- 611 Cronin, K. A., Schroeder, K. K., & Snowdon, C. T. (2010). Prosocial behaviour emerges
612 independent of reciprocity in cottontop tamarins. *Proceedings of the Royal Society of*
613 *London B: Biological Sciences*, 277(1701), 3845-3851.
- 614 Cronin, K. A., Van Leeuwen, E. J., Vreeman, V., & Haun, D. B. (2014). Population-level
615 variability in the social climates of four chimpanzee societies. *Evolution and Human*
616 *Behavior*, 35(5), 389-396.
- 617 Dale, R., Marshall-Pescini, S., & Range, F. (2020). What matters for cooperation? The
618 importance of social relationship over cognition. *Scientific reports*, 10(1), 1-14.
- 619 David, H. A. (1987). Ranking from unbalanced paired-comparison data. *Biometrika*, 74(2),
620 432-436.
- 621 David, H. A. (1988). *The Method of Paired Comparisons*. London: Charles Griffin.
- 622 de Waal, F. B. (1989). Food sharing and reciprocal obligations among
623 chimpanzees. *Journal of Human Evolution*, 18(5), 433-459.
- 624 de Waal, F. B. (1997). The chimpanzee's service economy: food for grooming. *Evolution*
625 *and Human Behavior*, 18(6), 375-386.
- 626 de Waal, F. B. M. (1982). *Chimpanzee Politics*. Harper & Row. New York.
- 627 Decety, J., & Cowell, J. M. (2014). The complex relation between morality and
628 empathy. *Trends in cognitive sciences*, 18(7), 337-339.
- 629 Decety, J., & Svetlova, M. (2012). Putting together phylogenetic and ontogenetic
630 perspectives on empathy. *Developmental cognitive neuroscience*, 2(1), 1-24.
- 631 DeNault, L. K., & McFarlane, D. A. (1995). Reciprocal altruism between male vampire
632 bats, *Desmodus rotundus*. *Animal Behaviour*, 49(3), 855-856.
- 633 Dolivo, V., & Taborsky, M. (2015). Norway rats reciprocate help according to the quality
634 of help they received. *Biology letters*, 11(2), 20140959.
- 635 Doutrelant, C., & Covas, R. (2007). Helping has signalling characteristics in a
636 cooperatively breeding bird. *Animal Behaviour*, 74(4), 739-747.

637 Dovidio, J. F., & Gaertner, S. L. (1981). The effects of race, status, and ability on helping
638 behavior. *Social Psychology Quarterly*, 44, 192-203.

639 Drews, C. (1993). The concept and definition of dominance in animal
640 behaviour. *Behaviour*, 125(3-4), 283-313.

641 Dufour, V., Pelé, M., Neumann, M., Thierry, B., & Call, J. (2009). Calculated reciprocity
642 after all: computation behind token transfers in orang-utans. *Biology letters*, 5, 172-
643 175.

644 Dunbar, R. I. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues,*
645 *News, and Reviews: Issues, News, and Reviews*, 6(5), 178-190.

646 Dunbar, R. I. (2009). The social brain hypothesis and its implications for social
647 evolution. *Annals of human biology*, 36(5), 562-572.

648 Eibl-Eibesfeldt, I. (1973). *Love and hate: On the natural history of basic behaviour*
649 *patterns*. Aldine Transaction.

650 Engelmann, J. M., Herrmann, E., & Tomasello, M. (2012). Five-year olds, but not
651 chimpanzees, attempt to manage their reputations. *PLoS One*, 7(10), e48433.

652 Evers, E., de Vries, H., Spruijt, B. M., & Sterck, E. H. (2015). Emotional bookkeeping and
653 high partner selectivity are necessary for the emergence of partner-specific reciprocal
654 affiliation in an agent-based model of primate groups. *PloS one*, 10(3), e0118921.

655 Fehr, E., Bernhard, H., & Rockenbach, B. (2008). Egalitarianism in young
656 children. *Nature*, 454(7208), 1079-1083.

657 Gammell, M. P., Vries, H. D., Jennings, D. J., Carlin, C. M., & Hayden, T. J. (2003).
658 David's score: a more appropriate dominance ranking method than Clutton-Brock et
659 al.'s index. *Animal behaviour*, 66(3), 601-605.

660 Gilby, I. C., Thompson, M. E., Ruane, J. D., & Wrangham, R. (2010). No evidence of
661 short-term exchange of meat for sex among chimpanzees. *Journal of human*
662 *evolution*, 59(1), 44-53.

- 663 Glavin, G. B., Paré, W. P., Sandbak, T., Bakke, H. K., & Murison, R. (1994). Restraint
664 stress in biomedical research: an update. *Neuroscience & Biobehavioral*
665 *Reviews*, 18(2), 223-249.
- 666 Gomes, C. M., & Boesch, C. (2009). Wild chimpanzees exchange meat for sex on a long-
667 term basis. *PLoS One*, 4(4), e5116.
- 668 Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in
669 wild West African chimpanzees. *Proceedings of the Royal Society of London B:*
670 *Biological Sciences*, 276(1657), 699-706.
- 671 Hauser, M. D., Chen, M. K., Chen, F., & Chuang, E. (2003). Give unto others: genetically
672 unrelated cotton-top tamarin monkeys preferentially give food to those who
673 altruistically give food back. *Proceedings of the Royal Society of London B:*
674 *Biological Sciences*, 270(1531), 2363-2370.
- 675 Hector, A. C. K., Seyfarth, R. M., & Raleigh, M. J. (1989). Male parental care, female
676 choice and the effect of an audience in vervet monkeys. *Animal Behaviour*, 38(2),
677 262-271.
- 678 Hernandez-Lallement, J., van Wingerden, M., Marx, C., & Kalenscher, T. (2015). Rats
679 prefer mutual rewards in a prosocial choice task. *Frontiers in Neuroscience*, 8, 1-9.
- 680 Herrera, E. A., & Macdonald, D. W. (1989). Resource utilization and territoriality in
681 group-living capybaras (*Hydrochoerus hydrochaeris*). *The Journal of Animal*
682 *Ecology*, 58(2), 667-679.
- 683 Herrera, E. A., & Macdonald, D. W. (1993). Aggression, dominance, and mating success
684 among capybara males (*Hydrochaeris hydrochaeris*). *Behavioral Ecology*, 4(2), 114-
685 119.
- 686 Herrera, E. A., Salas, V., Congdon, E. R., Corriale, M. J., & Tang-Martínez, Z. (2011).
687 Capybara social structure and dispersal patterns: variations on a theme. *Journal of*
688 *Mammalogy*, 92(1), 12-20.
- 689 Hill, D. A., & Okayasu, N. (1996). Determinants of dominance among female macaques:
690 demography nepotism and danger. In: Fa, J. E., & Lindburg, D. G. (Eds.), *Evolution*
691 *and Ecology of Macaque Societies*. (pp. 459-472). Cambridge University Press.

- 692 Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. (2011). Spontaneous prosocial
693 choice by chimpanzees. *Proceedings of the National Academy of Sciences*, *108*(33),
694 13847-13851.
- 695 House, B. R., Silk, J. B., Lambeth, S. P., & Schapiro, S. J. (2014). Task design influences
696 prosociality in captive chimpanzees (*Pan troglodytes*). *PloS one*, *9*(9), e103422.
- 697 Jaeggi, A. V., Burkart, J. M., & Van Schaik, C. P. (2010). On the psychology of
698 cooperation in humans and other primates: combining the natural history and
699 experimental evidence of prosociality. *Philosophical Transactions of the Royal
700 Society of London B: Biological Sciences*, *365*(1553), 2723-2735.
- 701 Jaeggi, A. V., De Groot, E., Stevens, J. M., & Van Schaik, C. P. (2013). Mechanisms of
702 reciprocity in primates: testing for short-term contingency of grooming and food
703 sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, *34*(2), 69-77.
- 704 Jensen, K., Vaish, A., & Schmidt, M. F. (2014). The emergence of human prosociality:
705 aligning with others through feelings, concerns, and norms. *Frontiers in
706 psychology*, *5*(822).
- 707 Jeon, D., Kim, S., Chetana, M., Jo, D., Ruley, H. E., Lin, S. Y., Rabah, D., Kinet, J. P., &
708 Shin, H. S. (2010). Observational fear learning involves affective pain system and
709 Cav1.2 Ca²⁺ channels in ACC. *Nature neuroscience*, *13*(4), 482-488.
- 710 Kaiser, S., Kirtzeck, M., Hornschuh, G., & Sachser, N. (2003). Sex-specific difference in
711 social support - a study in female guinea pigs. *Physiology & behavior*, *79*(2), 297-
712 303.
- 713 Knapska, E., Mikosz, M., Werka, T., & Maren, S. (2010). Social modulation of learning in
714 rats. *Learning & memory*, *17*(1), 35-42.
- 715 Lakshminarayanan, V. R., & Santos, L. R. (2008). Capuchin monkeys are sensitive to
716 others' welfare. *Current Biology*, *18*(21), R999-R1000.
- 717 Lalot, M., Bourgeois, A., Saint Jalme, M., & Bovet, D. Family first! Influence of parental
718 investment in Guinea pigs (*Cavia porcellus*) prosocial choices. *Submitted*.

- 719 Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on
720 cooperation in wild chimpanzees. *Proceedings of the National Academy of*
721 *Sciences*, *104*(19), 7786-7790.
- 722 Langford, D. J., Crager, S. E., Shehzad, Z., Smith, S. B., Sotocinal, S. G., Levenstadt, J. S.,
723 Chanda, M. L., Levitin, D. J., & Mogil, J. S. (2006). Social modulation of pain as
724 evidence for empathy in mice. *Science*, *312*(5782), 1967-1970.
- 725 Leimgruber, K. L., Shaw, A., Santos, L. R., & Olson, K. R. (2012). Young children are
726 more generous when others are aware of their actions. *PLoS One*, *7*(10), e48292.
- 727 Macdonald, D. W., Herrera, E. A., Ferraz, K. M. P., & Moreira, J. R. (2013). The
728 Capybara paradigm: from sociality to sustainability. In *Capybara* (pp. 385-408).
729 Springer, New York, NY.
- 730 Macdonald, D. W., Herrera, E. A., Taber, A. B., Moreira, J. R., Wolff, J. O., & Sherman,
731 P. W. (2007). Social organization and resource use in capybaras and maras. *Rodent*
732 *societies: An ecological and evolutionary perspective*, 393-402.
- 733 MacLean, P. D. (1985). Brain evolution relating to family, play, and the separation
734 call. *Archives of General Psychiatry*, *42*(4), 405-417.
- 735 Maldonado-Chaparro, A., & Blumstein, D. T. (2008). Management implications of
736 capybara (*Hydrochoerus hydrochaeris*) social behavior. *Biological*
737 *Conservation*, *141*(8), 1945-1952.
- 738 Massen, J. J., Luyten, I. J., Spruijt, B. M., & Sterck, E. H. (2011). Benefiting friends or
739 dominants: prosocial choices mainly depend on rank position in long-tailed
740 macaques (*Macaca fascicularis*). *Primates*, *52*(3), 237-247.
- 741 Massen, J. J., Ritter, C., & Bugnyar, T. (2015). Tolerance and reward equity predict
742 cooperation in ravens (*Corvus corax*). *Scientific reports*, *5*.
- 743 Massen, J. J., Van Den Berg, L. M., Spruijt, B. M., & Sterck, E. H. (2010). Generous
744 leaders and selfish underdogs: pro-sociality in despotic macaques. *PLoS One*, *5*(3),
745 e9734.
- 746 Mast, M. S., & Bischof, N. (1999). An experimental study of altruism in rank relationships.
747 *Journal of Psychology*, *207*, 1-34.

- 748 McDonald, P. G., Te Marvelde, L., Kazem, A. J., & Wright, J. (2008). Helping as a signal
749 and the effect of a potential audience during provisioning visits in a cooperative
750 bird. *Animal Behaviour*, 75(4), 1319-1330.
- 751 Melis, A. P., Hare, B., & Tomasello, M. (2006). Chimpanzees recruit the best
752 collaborators. *Science*, 311(5765), 1297-1300.
- 753 Melis, A. P., Warneken, F., Jensen, K., Schneider, A. C., Call, J., & Tomasello, M. (2011).
754 Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the*
755 *Royal Society of London B: Biological Sciences*, 278, 1405-1413.
- 756 Mitani, J. C. (2006). Reciprocal exchange in chimpanzees and other primates. In: van
757 Schaik, C. P. & Kappeler P. M. (Eds.), *Cooperation in primates and humans*. (pp.
758 107-119). Springer Berlin Heidelberg.
- 759 Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal*
760 *Behaviour*, 77(3), 633-640.
- 761 Mogil, J. S. (2012). The surprising empathic abilities of rodents. *Trends in cognitive*
762 *sciences*, 16(3), 143-144.
- 763 Mohr, C., Rowe, A. C., & Blanke, O. (2010). The influence of sex and empathy on putting
764 oneself in the shoes of others. *British Journal of Psychology*, 101(2), 277-291.
- 765 Moore, J. (1984). The evolution of reciprocal sharing. *Ethology and Sociobiology*, 5(1), 5-
766 14.
- 767 Nishida, T., & Turner, L. A. (1996). Food transfer between mother and infant chimpanzees
768 of the Mahale Mountains National Park, Tanzania. *International journal of*
769 *primatology*, 17(6), 947-968.
- 770 Noë, R., Schaik, C. P., & Hooff, J. A. (1991). The market effect: An explanation for
771 pay-off asymmetries among collaborating animals. *Ethology*, 87(1-2), 97-118.
- 772 Nogueira-Filho, S. L., Lopes, P. C., Ferreira, D. N., & Nogueira, S. S. (2017). Flexibility in
773 the social behavior of captive female capybaras (Mammalia, Rodentia). *Behavioural*
774 *processes*, 142, 29-32.

- 775 Panksepp, J. B., & Lahvis, G. P. (2011). Rodent empathy and affective
776 neuroscience. *Neuroscience & Biobehavioral Reviews*, *35*(9), 1864-1875.
- 777 Panksepp, J., & Panksepp, J. B. (2013). Toward a cross-species understanding of
778 empathy. *Trends in neurosciences*, *36*(8), 489-496.
- 779 Paré, W. P., & Glavin, G. B. (1986). Restraint stress in biomedical research: a
780 review. *Neuroscience & Biobehavioral Reviews*, *10*(3), 339-370.
- 781 Pinto, A., Oates, J., Grutter, A., & Bshary, R. (2011). Cleaner wrasses *Labroides*
782 *dimidiatus* are more cooperative in the presence of an audience. *Current*
783 *Biology*, *21*(13), 1140-1144.
- 784 Preston, S. D. (2013). The origins of altruism in offspring care. *Psychological*
785 *bulletin*, *139*(6), 1305-1341.
- 786 Preuschoft, S., & van Schaik, C. P. (2000). Dominance and communication: conflict
787 management in various social settings. In: Aureli, F., & F. B. M. de Waal, F. B. M.
788 (Eds.), *Natural Conflict Resolution*. (pp. 77-105). Berkeley: University of California
789 Press.
- 790 R Core Team (2014). R: A language and environment for statistical computing. R
791 Foundation for Statistical Computing, Vienna, Austria. URL [http://www.R-](http://www.R-project.org/)
792 [project.org/](http://www.R-project.org/).
- 793 Rice, G. E., & Gainer, P. (1962). "Altruism" in the albino rat. *Journal of comparative and*
794 *physiological psychology*, *55*(1), 123-125.
- 795 Romero, T., Castellanos, M. A., & de Waal, F. B. (2010). Consolation as possible
796 expression of sympathetic concern among chimpanzees. *Proceedings of the National*
797 *Academy of Sciences*, *107*(27), 12110-12115.
- 798 Rutte, C., & Taborsky, M. (2007). Generalized reciprocity in rats. *PLoS Biology*, *5*(7),
799 e196.
- 800 Rutte, C., & Taborsky, M. (2008). The influence of social experience on cooperative
801 behaviour of rats (*Rattus norvegicus*): direct vs generalised reciprocity. *Behavioral*
802 *Ecology and Sociobiology*, *62*(4), 499-505.

- 803 Salas, V. (1999). *Social organisation of capybaras in the Venezuelan Llanos*. Doctoral
804 dissertation, University of Cambridge.
- 805 Sato, N., Tan, L., Tate, K., & Okada, M. (2015). Rats demonstrate helping behavior toward
806 a soaked conspecific. *Animal cognition*, 18(5), 1039-1047.
- 807 Schaub, H. (1996). Testing kin altruism in long-tailed macaques (*Macaca fascicularis*) in a
808 food-sharing experiment. *International journal of primatology*, 17(3), 445-467.
- 809 Schneeberger, K., Dietz, M., & Taborsky, M. (2012). Reciprocal cooperation between
810 unrelated rats depends on cost to donor and benefit to recipient. *BMC evolutionary
811 biology*, 12(1), 41.
- 812 Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal
813 of theoretical Biology*, 65(4), 671-698.
- 814 Shultz, S., & Dunbar, R. I. (2007). The evolution of the social brain: anthropoid primates
815 contrast with other vertebrates. *Proceedings of the Royal Society B: Biological
816 Sciences*, 274(1624), 2429-2436.
- 817 Silk, J. B., & House, B. R. (2011). Evolutionary foundations of human prosocial
818 sentiments. *Proceedings of the National Academy of Sciences*, 108(Supplement 2),
819 10910-10917.
- 820 Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S.,
821 Lambeth, S. P., Mascaró, J., & Schapiro, S. J. (2005). Chimpanzees are indifferent to
822 the welfare of unrelated group members. *Nature*, 437(7063), 1357-1359.
- 823 Stevens, J. R. (2010). Donor payoffs and other-regarding preferences in cotton-top
824 tamarins (*Saguinus oedipus*). *Animal cognition*, 13(4), 663-670.
- 825 Takimoto, A., Kuroshima, H., & Fujita, K. (2010). Capuchin monkeys (*Cebus apella*) are
826 sensitive to others' reward: an experimental analysis of food-choice for
827 conspecifics. *Animal cognition*, 13(2), 249-261.
- 828 Tebbich, S., Taborsky, M., & Winkler, H. (1996). Social manipulation causes cooperation
829 in keas. *Animal Behaviour*, 52(1), 1-10.

830 Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly review of biology*,
831 46, 35-57.

832 Tsoory, M. M., Youdim, M. B., & Schuster, R. (2012). Social-cooperation differs from
833 individual behavior in hypothalamic and striatal monoamine function: evidence from
834 a laboratory rat model. *Behavioural brain research*, 232(1), 252-263.

835 van Noordwijk, M. A., & van Schaik, C. P. (1987). Competition among female long-tailed
836 macaques, *Macaca fascicularis*. *Animal Behaviour*, 35(2), 577-589.

837 Viana, D. S., Gordo, I., Sucena, E., & Moita, M. A. (2010). Cognitive and motivational
838 requirements for the emergence of cooperation in a rat social game. *PLoS one*, 5(1),
839 e8483.

840 Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young
841 chimpanzees. *Science*, 311(5765), 1301-1303.

842 Warneken, F., & Tomasello, M. (2009). The roots of human altruism. *British Journal of*
843 *Psychology*, 100(3), 455-471.

844 Wilkinson, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature*, 308(5955),
845 181-184.

846 Wilkinson, G. S. (1985). The social organization of the common vampire bat I and
847 II. *Behavioral Ecology and Sociobiology*, 17(2), 111-134.

848 Wolff, J. O., & Sherman, P. W. (Eds.). (2008). *Rodent societies: an ecological and*
849 *evolutionary perspective*. University of Chicago Press.

850 Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees help each other upon
851 request. *PLoS One*, 4(10), e7416.

852 Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees' flexible targeted helping
853 based on an understanding of conspecifics' goals. *Proceedings of the National*
854 *Academy of Sciences*, 109(9), 3588-3592.

855 Zahavi, A. (2004). The details of food-sharing interactions - their cost in social
856 prestige. *Behavioral and Brain Sciences*, 27(04), 570-571.

857 Zahavi, A. 1977. Reliability in communication systems and the evolution of altruism. In:
858 Stonehouse, B., & Perrins, C. (Eds.), *Evolutionary Ecology*, (pp. 253-259). London:
859 Macmillan Press.

860

861 **Supporting Information**

862

863 **Fig. 1. Apparatus to test Capybaras' prosociality.**

864 **Table 1. Consequences attributed to each lever during the prosociality experiment.**

865 **Table 2. Capybaras' identity, hierarchical rank, and level of participation in the**
866 **experiment.**

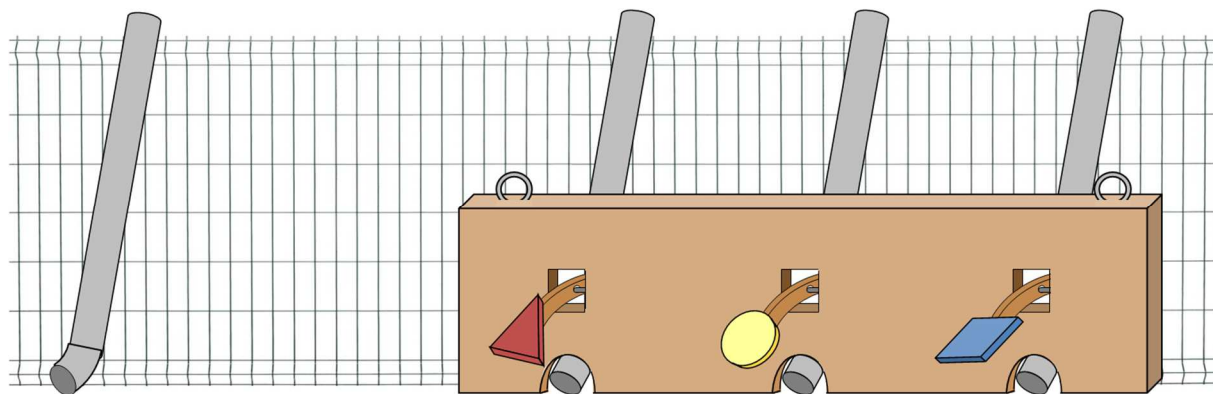
867 **Fig. 2. Capybaras' mean percentage of prosocial choices according to the hierarchical**
868 **status of the recipient individual.**

869 **Fig. 3. Capybaras' mean percentage of prosocial choices according to the number of**
870 **recipient individuals.**

871

872 **Figures**

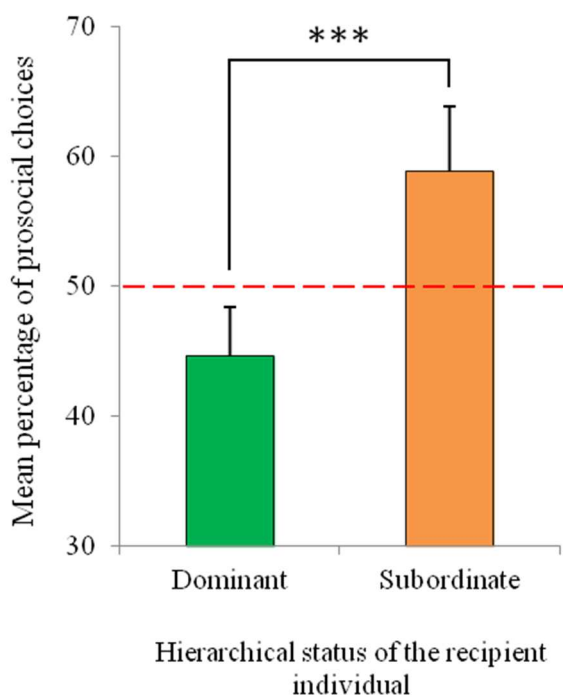
873



874

875 **Figure 1: Apparatus to test Capybaras' prosociality.** The wooden board offered three
876 options: pushing the blue square (prosocial item), pushing the red triangle (selfish item), or
877 pushing the yellow disk (null item). The food reward was distributed through the
878 corresponding pipe, which came out under the chosen item (except when the null item was
879 chosen). When the subject chose to press the prosocial lever, the same (in amount and in
880 nature) food reward was delivered to the subject and to the recipient (through the "recipient
881 pipe") simultaneously.

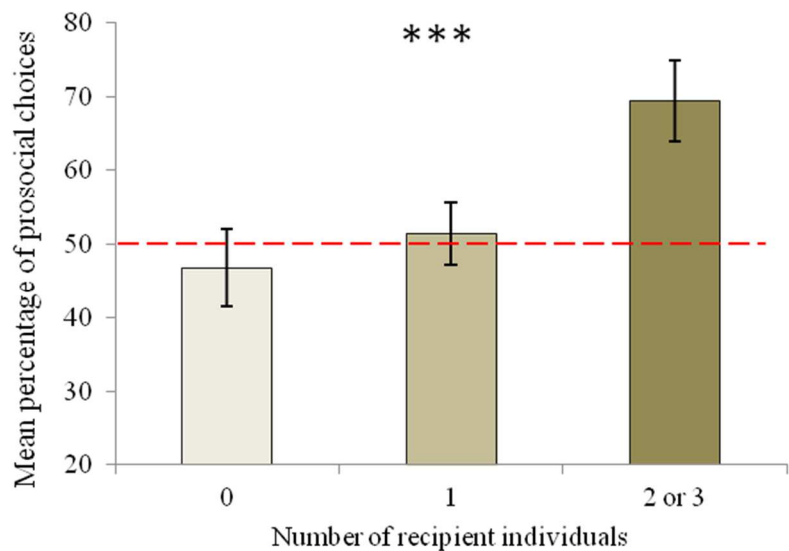
882



883

884 **Figure 2: Capybaras' mean percentage of prosocial choices according to the hierarchical**
885 **status of the recipient individual.** Error bars represent one standard error of the mean
886 (S.E.M.). (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

887





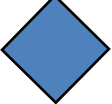
888

889 **Figure 3: Capybaras' mean percentage of prosocial choices according to the number of**
890 **recipient individuals.** Error bars represent one standard error of the mean (S.E.M.). (* $p <$
891 0.05 , ** $p < 0.01$, *** $p < 0.001$)

892

893 **Tables**

894

Token value		Food reward <i>(portion of fresh fruit)</i>	
		Tested individual	Recipient individual
	Null	0	0
	Selfish	1	0
	Prosocial	1	1

895

896 **Table 1. Consequences attributed to each lever during the prosociality experiment**

897

898

Individual	Sex	Age	David's Score	Number of Sessions as Subject	Number of Sessions as Recipient
MA6175	Male	7 years old	5.25	51	55
MA7234	Female	5 years old	2.19	53	55
MB0047	Female	3.5 years old	-2.29	38	55
MA9156	Male	3 years old	-5.15	50	55

899

900 **Table 2. Capybaras' identity, hierarchical rank** (represented by individual's David's
901 **score), and level of participation in the experiment.**

902