

1 TITLE: Lack of prosociality in great apes, capuchin monkeys and spider monkeys: convergent
2 evidence from two different food distribution tasks.

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14 SUMMARY

15

16 Prosociality can be defined as any behaviour performed to alleviate the needs of others or to
17 improve their welfare. Prosociality has probably played an essential role in the evolution of
18 cooperative behaviour and several studies have already investigated it in primates to understand
19 the evolutionary origins of human prosociality. Two main tasks have been used to test
20 prosociality in a food context. In the Platforms task, subjects can prosocially provide food to a
21 partner by selecting a prosocial platform over a selfish one. In the Tokens task, subjects can
22 prosocially provide food to a partner by selecting a prosocial token over a selfish one. As these
23 tasks have provided mixed results, we used both tasks to test prosociality in great apes, capuchin
24 monkeys, and spider monkeys. Our results provided no compelling evidence of prosociality in a
25 food context in any of the species tested. Additionally, our study revealed serious limitations of
26 the Tokens task as it has been previously used. These results highlight the importance of
27 controlling for confounding variables and of using multiple tasks to address inconsistencies
28 present in the literature.

29

30 KEY INDEX WORDS: prosocial behaviour, primates, other-regarding preferences, apes,
31 monkeys

32 INTRODUCTION

33 Prosociality can be defined as any behaviour performed by one individual to alleviate the
34 needs of other individuals or to improve their welfare, without the actor necessarily incurring in
35 extra costs to provide these benefits [1]. In evolutionary terms, prosociality might have played an
36 essential role in the evolution of mutually beneficial cooperative behaviour by providing
37 individuals with the psychological predisposition to be concerned for the welfare of others (e.g.
38 [2-4]; but see [5]). Although prosocial behaviour is well-documented among primates in feeding
39 and agonistic contexts [e.g. 6-8], pinpointing the precise motivations underlying this behaviour
40 has been difficult. Whereas several studies have reported chimpanzees helping others to obtain
41 objects (including tools) in both mutualistic and altruistic settings [9-13], studies involving food
42 distribution have produced mixed results [14-29].

43 Two types of task (Platforms and Tokens) have commonly been used to measure
44 primates' prosocial tendency to give food to partners. In the Platforms task, subjects are
45 presented with sliding platforms and two options (e.g. [14]). The subject always obtains the same
46 amount of food regardless of the option chosen, but one of the options also provides food to the
47 partner. By choosing this option the subject can therefore benefit a partner without incurring in
48 any extra cost. Versions of this task have been used with several primate species. Chimpanzees
49 (*Pan troglodytes*), for example, generally failed to give food to their partners [14-17]. In contrast,
50 dominant long-tailed macaques (*Macaca fascicularis*) behaved prosocially toward subordinates
51 [18]. However, the experimental set-up used in this last study makes the interpretation of the
52 results not entirely straightforward because making a prosocial choice required the subject to sit
53 closer to the partner, while making a non-prosocial choice required the subject to sit next to an
54 empty room. It is conceivable that dominants might have preferred to sit next to the subordinate

55 (to elicit grooming), while subordinates might have avoided the dominant's proximity (to avoid
56 aggression). Further studies would be necessary to rule out this alternative interpretation.

57 Tufted capuchin monkeys (*Sapajus apella*) also gave food to their partners in two
58 independent studies [19-20]. Similarly, common marmosets (*Callithrix jacchus*) prosocially and
59 altruistically gave food to their partners [21]. Interestingly, cotton-top tamarins (*Saguinus*
60 *oedipus*), despite also being a cooperative breeding species, did not prosocially provide food to
61 other group members in two different studies [22-23]. Additionally, in a new version of this task,
62 subjects could pull a platform to provide food rewards to all the other group members [24].
63 Capuchin monkeys and Japanese macaques (*Macaca fuscata*) failed to be prosocial, but
64 marmosets, again, gave food to their group members [24]. In general, subjects in the studies
65 above did not make more prosocial choices when the partner showed interest in the food reward,
66 by for example reaching out for it (chimpanzees [16], cotton-top tamarins [22], common
67 marmosets [21]; see [25]), suggesting that subjects may not have been responding to the needs of
68 their partner. Despite its frequent use, the Platforms task has been criticised, firstly for being too
69 complex from a technical and a social perspective, and secondly for the presence of visible food
70 rewards which may elicit selfish and competitive behaviour rather than prosocial attitudes ([26-
71 27]; but see [16, 25])

72 In the Tokens task, subjects learn to associate different stimuli with different food
73 distribution outcomes (e.g., food for the partner *versus* food for nobody, food for both *versus*
74 food for the subject). Then subjects have the opportunity to choose between stimuli, thus
75 determining who will receive food. Chang and colleagues [28] trained rhesus macaques (*Macaca*
76 *mulatta*) to associate unique visual cues with specific food distributions, and found that
77 macaques preferred the prosocial visual stimulus (providing food to the partner) over the selfish

78 one (in this case, providing food to nobody). However, this preference did not hold when
79 subjects also received food rewards (i.e. they did not prefer the stimulus providing food to the
80 partner and the subject over the one providing food to the subject). These results do not allow us
81 to draw definitive conclusions, as the number of subjects was too small. More importantly, this
82 study cannot rule out that subjects were not behaving prosocially, but were simply preferring the
83 prosocial option when receiving no food reward, as the prosocial option was the only one
84 associated with food. De Waal and colleagues [29] trained female capuchin monkeys to
85 discriminate between tokens providing food only to the subject and tokens providing food also to
86 their partners. Subjects significantly preferred the prosocial token over the selfish one. Also
87 female chimpanzees preferred the prosocial token when tested with a similar set-up [27]. These
88 studies, however, are problematic because they failed to rule out alternative explanations. In the
89 study by de Waal and colleagues [29], for example, there were no control conditions
90 investigating the behaviour of capuchin monkeys when subjects were provided with the same
91 two tokens, without a partner present in the adjacent cage. Without this control condition, it is
92 impossible to know whether subjects' choice reflected a prosocial tendency to give food to their
93 partners, or a general preference for the choice associated with an overall higher amount of food
94 rewards. Horner and colleagues [27] introduced no-partner control conditions, but they were
95 always conducted after the experimental condition with the partner, and used different pairs of
96 tokens to prevent subjects from learning that all tokens produced the same outcome. Therefore, it
97 is impossible to rule out the possibility that the order in which conditions were administered and
98 the type of tokens used affected the results. Moreover, both studies [27, 29] failed to test whether
99 subjects understood the task. Only recently, Suchak and de Waal [30] introduced a condition to
100 test subjects' understanding of the task, as well as a no-partner control condition, but

101 unfortunately the no-partner control always took place after the experimental condition with the
102 partner to try to avoid the expectation of receiving both rewards. Therefore, no definitive
103 conclusions can be drawn from these studies.

104 The main aim of this study was to use both the Platforms and the Tokens tasks to test
105 prosociality in six primate species: chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*),
106 gorillas (*Gorilla gorilla*), orangutans (*Pongo abelii*), tufted capuchin monkeys and Geoffroy's
107 spider monkeys (*Ateles geoffroyi*). Although prosociality has already been tested in some of
108 these species, as far as we know, no previous study has investigated multiple species of monkeys
109 and apes with the two most frequently used food providing prosociality tests. In the Platforms
110 task, subjects could choose the prosocial platform over the selfish one to provide food to their
111 partners, and in the Tokens task they could select a prosocial token over a selfish one to provide
112 food to their partners. If the use of both tasks (with appropriate controls) on the same population
113 leads to the same outcome, then results become more compelling. All the species included are
114 good candidates for prosociality owing to their complex cognitive skills (great apes: [31]), high
115 levels of allo-maternal care (capuchin monkeys, which might thus show enhanced motivation to
116 be prosocial: [32-33]), and high levels of social tolerance (*Pan*, *Pongo* and spider monkeys:
117 [34]).

118

119 METHODS

120 *Subjects.* We tested 7 spider monkeys (combined in 26 pairs) at the Animaya Zoo in
121 Merida, Mexico, 10 tufted capuchin monkeys (combined in 18 pairs) at the ISTC-CNR Primate
122 Centre in Rome, Italy, and 12 chimpanzees (combined in 34 pairs), 9 bonobos (combined in 26

123 pairs), 5 orangutans (combined in 18 pairs) and 7 gorillas (combined in 22 pairs) at the Wolfgang
124 Koehler Primate Research Center in the Leipzig Zoo, Germany. Subjects were of both sexes and
125 various age classes (adults, subadults and juveniles, according to [35-36]). They were all born in
126 captivity, except for one gorilla (Bebe) and all the spider monkeys, who were born in the wild
127 but were raised as pets before being rescued and brought to the zoo.

128 Subjects were all housed in groups with their group members, in enclosures with outdoor
129 and indoor areas, and they were never deprived of food or water before or during the experiment.
130 All of them were used to being temporarily isolated in testing rooms (with their infant if present)
131 and were tested by the same familiar experimenter only after they were comfortable with the set-
132 up and the testing room. All subjects had previously participated in experimental tasks, but they
133 had not been previously tested in the same tasks administered in this study, with the exception of
134 six chimpanzees tested by Jensen and colleagues [15] with a task similar to the Platforms task
135 (also see Table S1 in Electronic Supplementary Information). For different reasons, not all dyads
136 could be tested with both tasks. Some subjects were moved to/from different facilities during the
137 study, other subjects were not motivated to exchange tokens, or could not be paired with the
138 same partner when the second experiment started because the quality of their relationship
139 worsened for no reason the experimenters could discern. Importantly, only pairs with a good
140 quality of relationship were included in this study, consequently enhancing the possibility to
141 detect prosocial behaviour (see [1]). Quality of relationship was assessed by the keepers working
142 at the different facilities, excluding pairs that would have shown distress if being tested in two
143 adjacent rooms. Finally, spider monkeys were only tested with the Platforms task. They were the
144 only species with no previous experience at exchanging tokens (see Table S1 in Electronic
145 Supplementary Information) and time constraints meant that training was not possible.

146

147 *PLATFORMS TASK.*

148 *Materials and procedure.* In this task, the subject was located in the testing room and
149 faced an apparatus consisting of a table with three sliding platforms baited with different food
150 rewards (Figure 1). Food rewards were out of the subject's reach, but the subject could use
151 handles to pull in two of the three platforms (the prosocial one, or P, and the selfish one, or S).
152 After selecting either S or P by pulling the corresponding handle, the subject could reach the
153 food on the chosen platform, while the other platform moved back, out of the subject's reach.
154 The third platform could be pulled by neither the subject nor the partner, but it was connected to
155 P: if the subject pulled P, the third platform moved toward the adjacent room, where the food
156 could be retrieved by the partner. If the subject selected S the third platform moved further away
157 from the partner, who then received no food. In contrast to other studies [e.g. 14, 21], we did not
158 use stacked platforms, and the third platform was physically separated from P and S. Each dyad
159 received one training condition and three experimental conditions: Equal, Unequal and
160 Equidistant (with three corresponding control conditions).

161 In the Training condition the subject was tested alone. Sessions were alternated so that
162 the subject had access exclusively to her testing room (and thus S and P), or also to the adjacent
163 room (and thus also to the third platform). Each session was composed of 6 trials, in which only
164 one of the 3 platforms was baited (randomising the order and baiting each platform twice in each
165 session). Once the platforms were baited, the subject had 30 seconds to make a selection.
166 Subjects were considered to have knowledge of the set-up and could therefore move to the
167 following condition if (i) they always pulled S when S was baited and always pulled P when P

168 was baited in two consecutive sessions in which they had only access to S and P, and if (ii) they
169 always pulled S when S was baited and P when P or the third platform were baited in two
170 consecutive sessions in which they had access to all three platforms. Subjects required a mean of
171 3.4 sessions (with 2 sessions being the minimal number of sessions required to master the
172 Training condition) to advance to the next condition.

173 In the Equal condition, the subject was in the testing room and the partner in the adjacent
174 room. In full view of the subject, the Experimenter (E) baited all three platforms with an equal
175 food reward (a slice of banana, a raisin or a pellet, depending on the subject's preference). As
176 soon as the last platform was positioned and baited, the subject had 30 seconds to select one of
177 the two platforms (the prosocial one, P, or the selfish one, S) by pulling it and retrieving the
178 food. In this condition, subjects had therefore to get closer to their partner to make the prosocial
179 choice, something that we controlled for in the Equidistant condition (see below). In the
180 corresponding control condition, the subject was in the testing room and the partner in a room
181 other than the adjacent one, which was empty and visible to the subject. E followed exactly the
182 same procedure as before, but when the subject pulled P, E retrieved the food on the third
183 platform and put it back in the food bucket.

184 In the Unequal and Equidistant conditions, E followed exactly the same procedure as the
185 Equal condition, with the exception that (i) in the Unequal condition the third platform was
186 baited with 3 food rewards instead of one, and (ii) in the Equidistant condition the handles of S
187 and P did not point straight to the subject, but 45 degrees toward each other, so that the subject
188 did not have to get closer to the partner's adjacent room in order to pull P. The Unequal
189 condition allowed us to understand whether prosocial choices were facilitated by an
190 equal/unequal food distribution between subject and partner. The Equidistant condition, instead,

191 allowed us to control whether prosocial/selfish choices depended on whether the subject
192 preferred to approach or to avoid the side of the partner's room. The corresponding control
193 conditions were identical, but the partner was in a room other than the adjacent one, which was
194 empty and visible to the subject, and E retrieved the food on the third platform and put it back in
195 the food bucket in case the subject chose P.

196 After mastering the Training, dyads were administered the Equal condition (randomising
197 the order in which the three experimental and the three control sessions were administered),
198 followed by the Unequal condition (randomizing the order of the three experimental and control
199 sessions), and by the Equidistant condition (with half of the subjects starting with the
200 experimental and half with the control session). In all conditions, sessions consisted of 12 trials.
201 The inclusion of the three conditions allowed us to explore the potential effects of food
202 inequality and inter-individual distance when making choices.

203

204 *TOKENS TASK.*

205 *Materials and procedure.* Each subject was tested with up to three partners, and with
206 each partner a different pair of tokens was used (see Table S1 in Electronic Supplementary
207 Information). Great apes were tested with the same three pairs of tokens, while capuchin
208 monkeys were tested with three different pairs of tokens, to ensure that no species was tested
209 with tokens similar to those already used in the past. Tokens were little Plexiglas cylinders or
210 cuboids (approximately 4-6 cm in size) painted in different colours. If subjects were paired with
211 more than one partner, a different pair of tokens was used for each of the partners. Following
212 Horner and colleagues [27], subjects were tested with a second partner only after all the

213 conditions with the first partner had been run, and only after subject and partner had also
214 switched their roles (if this dyad was also planned). For each dyad, we administered five
215 conditions.

216 Unless otherwise stated, we followed the procedure by Horner and colleagues [27]. In the
217 Preference condition, we tested whether subjects preferred one of the two tokens, in each pair
218 they had been assigned. Subjects were tested alone and underwent one session of 10 trials. In
219 each trial, subjects were presented with the two different tokens and could choose one of the two
220 by pointing or trying to reach for it. The position of the tokens (right/left) was randomized and
221 counterbalanced across trials. Regardless of the choice made, subjects were rewarded with one
222 pellet wrapped in paper. In this task, food rewards were always wrapped in paper so that subjects
223 were not distracted by visible food and could rely on both sound and sight to know whether the
224 partner had been rewarded, as unwrapping the paper made noise and attracted the subject's
225 attention (see [27]). Subjects were considered to have a token preference when one of the two
226 tokens was selected in $\geq 80\%$ of the trials. As this only happened in 4 out of 55 dyads, and in
227 each case the preferred token was a different one, we did not change any pair of tokens, as done
228 in [27, 29].

229 In the Training condition, one of the two tokens within each pair was considered the
230 prosocial token (P) and the other one the selfish token (S). For each species, the same token was
231 considered to be P in approximately half of the dyads tested with that pair of tokens, and it was
232 considered to be S in the other half of the dyads, to avoid that our results were affected by any
233 intrinsic token properties. The Training condition consisted of one session of 10 trials. In this
234 condition, the subject was in the testing room and the partner in an adjacent room. In each trial,
235 the Experimenter (E) placed one of the two tokens in a bin hanging in the subject's room. The

236 tokens were randomized and counterbalanced across trials, so that the same token was not given
237 more than three times in a row. After the token was placed in the bin, E asked the subject to give
238 it back. The subject had 4 minutes to hand it back to E, who then placed it in a visible position
239 between the subject and the partner. If E received P, E took two food rewards from a bucket,
240 held them up briefly, one in each hand, to make them visible to the subject and partner, and then
241 gave one food reward to the subject and then one to the partner. If E received S, E took one food
242 reward from the bucket, held it briefly in one hand to make it visible to the subject and partner,
243 and then only rewarded the subject. Food rewards were always wrapped in paper. By the end of
244 this condition, subjects and partners had experienced 5 trials with a selfish outcome and 5 trials
245 with a prosocial one.

246 In the Experimental condition, as in the Training, the subject was in the testing room and
247 the partner in an adjacent room. This condition consisted of one session of 30 trials. At the
248 beginning of the session, E placed 15 S and 15 P tokens in the bin and then asked the subject to
249 hand one back within 4 minutes. E placed the returned token in a visible place between the
250 subject and the partner, before rewarding them with wrapped food rewards like in the Training
251 condition. At the end of the trial, E placed back the token in the bin and started another trial. If
252 subjects did not give back any token, the session was interrupted and continued on the next
253 possible day. If subjects selected more than one token from the bin, each returned token was
254 considered as a choice, tokens were rewarded sequentially, with each token displayed only as the
255 appropriate reward was offered, and all the tokens were placed back together in the bin.

256 In the Control condition, the subject was in the testing room but the partner was in
257 another non-adjacent room (so that the adjacent room was visibly empty to the subject). E
258 followed exactly the same procedure of the Experimental condition, but when she was given the

259 prosocial token P, E rewarded the subject and then pretended to reward a partner in the adjacent
260 testing room, which was empty, by pretending to put the wrapped food reward through the mesh,
261 hiding it in the hand and eventually placing it back in the bucket out of the subject's view (see
262 [27]). In contrast to the study from Horner and colleagues [27], dyads were tested with the same
263 pair of tokens as in the Experimental condition, in order to rule out the possibility that different
264 performance across conditions might depend on the different pair of tokens used. Also differing
265 from Horner and colleagues [27], subjects did not always run the Control condition after the
266 Experimental condition. After completing the Preference and Training conditions, instead, half
267 of the subjects underwent the Experimental before the Control condition, and half of the subjects
268 underwent the Control condition before the Experimental one (see Table S1 in Electronic
269 Supplementary Information). In this way, we ensured that the order in which conditions were
270 administered could not account for any differences in performance between the two conditions.

271 In the Solitary condition, the subject was in the testing room but also had access to the
272 adjacent room. E followed the same procedure of the Experimental condition, but when the
273 subject gave her P back, E placed the second wrapped food reward in the adjacent testing room,
274 so that the subject could obtain it by simply moving to that room. If subjects had knowledge of
275 the set-up, they should select P significantly more than chance to obtain double the amount of
276 food. This condition was always administered after the Experimental and Control conditions, to
277 avoid subjects expecting both rewards in all conditions and thus fostering competitive attitudes
278 and hindering prosocial behaviour in the Experimental condition [27].

279 *Scoring and data analysis.* In each condition of the two tasks, E coded live whether
280 subjects selected the prosocial (P) or the selfish (S) platform or token. We videotaped all the
281 trials (1.7% of the trials were not recorded due to technical problems) and later checked the live-

282 scored behaviour against the videotapes for accuracy. The videos are digitally archived at the
283 Max Planck Institute for Evolutionary Anthropology in Leipzig and are available on request. A
284 second observer coded 19% of all the trials performed (3589/18984 trials in the Platforms task,
285 and 983/4950 trials in the Tokens task) to assess the inter-observer reliability, which was very
286 good (Cohen's $k = 0.94$ in both cases).

287 In both tasks, our dependent variable was the percentage of P choices. Non-parametric
288 Wilcoxon tests were used to compare performance between conditions (for all species and for
289 each species separately). In the Tokens task, we repeated our analyses only including those dyads
290 in which the Experimental condition was performed before the Control condition (as in [27]), in
291 order to assess the impact of condition order on the subjects' performance. Additionally, we used
292 binomial tests to investigate subjects' knowledge of the set-up, by analysing whether subjects
293 selected P significantly more than chance in the Solitary condition, for each dyad separately.
294 When this was the case, Wilcoxon tests for each dyad were run to compare performance between
295 Experimental and Control conditions. No analyses were done for the Training condition in the
296 Platforms task, as almost all subjects immediately mastered the task and could move to the
297 following condition. All tests were exact and two-tailed, and α level was set at .05. However,
298 when analyses were conducted separately for each dyad, Bonferroni-Holm corrections were
299 added to control for multiple comparisons. Finally, to control that our conclusions were robust
300 to different forms of analyses, we also repeated our analyses using linear mixed models, which
301 provided the same results (see Electronic Supplementary Information).

302

303 RESULTS

304 *PLATFORMS TASK*

305 Overall subjects did not choose the prosocial platform (P) significantly more often in the
306 Experimental than in the Control sessions. In fact, they selected P more often in the Control than
307 in the Experimental sessions in the Equal condition ($n = 52$, $T = 2915$, $p = 0.031$; P choices in
308 Experimental: 27.0%) and in the Unequal condition ($n = 62$, $T = 2881$, $p = 0.004$; P choices in
309 Experimental: 24.0%), but showed no significant preference in the Equidistant condition ($n = 37$,
310 $T = 1195$, $p = 0.201$; P choices in Experimental: 22.9%).

311 Analysing each species separately in the Equal condition revealed that orangutans,
312 capuchin monkeys and spider monkeys selected P more often in the Control than in the
313 Experimental sessions (orangutans: $n = 11$, $T = 95.5$, $p = 0.043$; capuchin monkeys: $n = 10$, $T =$
314 96.5 , $p = 0.037$; spider monkeys: $n = 16$, $T = 224$, $p = 0.033$; Figure 2a). In contrast, gorillas
315 selected P more often in Experimental than Control sessions ($n = 10$, $T = 55.5$, $p = 0.048$).
316 Neither chimpanzees nor bonobos showed a significant difference between conditions
317 (chimpanzees: $n = 10$, $T = 120$, $p = 0.326$; bonobos: $n = 8$, $T = 52$, $p = 0.334$).

318 In the Unequal condition, chimpanzees and spider monkeys selected P more often in the
319 Control than in the Experimental sessions (chimpanzees: $n = 15$, $T = 176$, $p = 0.006$; spider
320 monkeys: $n = 19$, $T = 262.5$, $p = 0.006$). All other species showed no significant difference
321 between conditions in their choice of P (bonobos: $n = 9$, $T = 70$, $p = 0.094$; gorillas: $n = 9$, $T =$
322 59 , $p = 0.124$; orangutans: $n = 7$, $T = 29$, $p = 0.117$; capuchin monkeys: $n = 8$, $T = 66$, $p = 0.419$;
323 Figure 2b).

324 Finally, in the Equidistant condition no species selected P more often in one condition
325 than the other (chimpanzees: $n = 7$, $T = 56$, $p = 0.480$; bonobos: $n = 4$, $T = 11$, $p = 0.375$;

326 gorillas: $n = 8$, $T = 48$, $p = 0.194$; orangutans: $n = 4$, $T = 14$, $p = 0.563$; capuchin monkeys: $n = 6$,
327 $T = 40$, $p = 0.571$; spider monkeys: $n = 13$, $T = 106$, $p = 0.165$; Figure 2c). Bonobos were the
328 only species that selected P more often in the Experimental than in the Control sessions, in all
329 conditions, but this difference was never significant.

330

331 *TOKENS TASK*

332 Overall subjects did not choose the prosocial token (P) significantly more often in the
333 Experimental over the Control condition ($n = 26$, $T = 564$, $p = 0.801$; P choices in Experimental:
334 49.5%). This was true also when analysing each species separately (chimpanzees: $n = 8$, $T = 74$,
335 $p = 0.445$; bonobos: $n = 7$, $T = 29.5$, $p = 0.422$; gorillas: $n = 6$, $T = 23$, $p = 0.156$; orangutans: $n =$
336 4 , $T = 15$, $p = 0.953$; capuchin monkeys: $n = 6$, $T = 24.5$, $p = 0.414$; Figure 3).

337 However, subjects that received the Experimental before the Control condition selected P
338 significantly more often in the Experimental over the Control condition ($n = 16$, $T = 187.5$, $p =$
339 0.046 ; P choices in Experimental: 56.2%).

340 Crucially, subjects selected P at chance levels in the Solitary condition ($n = 31$, $T =$
341 803.5 , $p = 0.300$; P choices in Solitary: 43.8%). This was also true when analysing each species
342 separately (chimpanzees: $n = 10$, $T = 106.5$, $p = 0.374$; bonobos: $n = 6$, $T = 41$, $p = 0.894$;
343 gorillas: $n = 6$, $T = 30.5$, $p = 0.094$; orangutans: $n = 5$, $T = 16$, $p = 0.313$; capuchin monkeys: $n =$
344 6 , $T = 31$, $p = 0.086$; Figure 3). When separately analysing each of the 55 dyads, however, 10
345 subjects chose P significantly more often than expected by chance in the Solitary condition.
346 Within these dyads, however, none of the subjects chose P significantly more in the
347 Experimental than in the Control condition (Table 1).

348

349 DISCUSSION

350 Overall, our results provided no compelling evidence of prosocial behaviour in any of the
351 primate species tested with the two different tasks. None of the species, regardless of their socio-
352 ecological characteristics and cognitive capacities, showed a consistent preference for selecting
353 the prosocial option when a partner was present (Experimental sessions) compared to when the
354 partner was absent (Control condition). In the Equal condition of the Platforms task, no species
355 but gorillas chose the prosocial option significantly more in the Experimental than in the Control
356 condition. However, gorillas' preference for the prosocial option in the presence of conspecifics
357 was not replicated in any other condition. It is therefore difficult to conclude that gorillas were
358 behaving prosocially towards their conspecifics. In the Unequal condition, no species showed
359 evidence of prosocial behaviour, although the lack of prosocial behaviour might have been a
360 consequence of an aversion to disadvantageous inequity (e.g. [37-38]; but see [19]). Finally, no
361 species showed prosocial behaviour in the Equidistant condition. These results are consistent
362 with previous studies that failed to detect prosocial behaviour in chimpanzees using a similar
363 task [14-17].

364 Our results contrast with studies showing prosocial behaviour in capuchin monkeys
365 tested with the Platforms task [19-20]. One reason why results may differ for capuchin monkeys
366 is that a high variability might exist across populations in terms of prosociality and other
367 behaviours potentially linked to prosociality, like social tolerance. One might speculate that the
368 capuchin monkeys tested in our study were less socially tolerant than other capuchin monkey
369 populations [e.g. 39], and might therefore fail to behave prosocially towards each other (see [34])

370 for a test of social tolerance including some of the same individuals). This explanation, however,
371 is weakened by the fact that in our study we only tested tolerant dyads (see material and
372 methods). Moreover, even species showing high social tolerance levels in [34] showed no
373 evidence of prosociality in the present study. Unfortunately, no data are currently available
374 comparing the levels of social tolerance across different populations of capuchin monkeys. This
375 means that explaining our findings in terms of a lack of social tolerance in the tested populations
376 is conceivable, but it awaits empirical verification.

377 Our results extend previous findings on chimpanzees to other primate species, suggesting
378 that prosocial behaviour as assessed with food tasks may not be a robust phenomenon, although
379 groups and/or populations might differ in their levels of prosociality, as mentioned above. One
380 surprising finding was that some species were not simply indifferent to the partner in the
381 Platforms task, but made even fewer prosocial choices when the partner was present. In the
382 Equal condition, orangutans, capuchin monkeys, and spider monkeys preferred the prosocial
383 option less often when their partner was present than when absent, and the same was true for
384 chimpanzees and spider monkeys in the Unequal condition. Although these differences were not
385 fully consistent across conditions and not present for each species, one could argue that some
386 species behaved antisocially towards their group members. Alternatively, these species might
387 simply be more reluctant to approach the partner in the testing situation. Recall that in both the
388 Equal and Unequal conditions, subjects had to get closer to the partner to make the prosocial
389 choice. In these conditions, therefore, subjects might have failed to behave prosocially simply to
390 avoid approaching the partner. In line with this interpretation, all species ceased being antisocial
391 in the Equidistant condition (i.e. they became indifferent), when subjects did not need to get
392 closer to the partner to select the prosocial option. Therefore partner's proximity is an important

393 factor to consider not only when studying prosociality, but also in social competition tasks [e.g.
394 40]. Consequently, the stacked platforms set-up [e.g. 14, 21, 41] seems a better option to study
395 food-distribution-based prosociality than the side-by-side set-up used in our study. Note,
396 however, that even in the Equidistant condition, no species was prosocial, which means that lack
397 of prosociality in our Platforms task cannot be entirely ascribed to our set-up.

398 Prosocial behaviour was not elicited by the Tokens task either. In contrast to previous
399 studies highlighting the advantages of this procedure [27, 29, 30], our study revealed several
400 important limitations, at least in the way that this procedure has been used so far. The most
401 important limitation was that the vast majority of the subjects failed to understand the
402 contingencies governing the task, in contrast to what happened in the Platforms task, where
403 subjects mastered the procedure after a mean of only 3.4 sessions. This was clearly evidenced by
404 the fact that 45 out of 55 dyads having access to both testing rooms (Solitary condition) failed to
405 select the prosocial token significantly above chance level, thus missing the opportunity to
406 double the amount of food obtained. Moreover, none of the subjects of these remaining 10 dyads
407 that selected the prosocial token significantly more often than chance in the Solitary condition
408 chose the prosocial option significantly more often when the partner was present. In short, most
409 of the subjects did not understand the task, and those who did showed no evidence of prosocial
410 behaviour. Note that exchanging objects for food *per se* was not the problem here. Following
411 previous studies [27, 29, 30], we did not train subjects to reach a criterion. However, most of the
412 subjects and species included in our study had already exchanged objects for food in previous
413 studies [e.g., 42-46] and all subjects readily exchanged tokens in the current study (see Table S1
414 in Electronic Supplementary Information). In retrospect, our results highlight the importance of

415 assessing whether the subjects understand the task before drawing conclusions from the resulting
416 data.

417 Our study also demonstrated that the order in which conditions are administered
418 significantly affects the results. Although subjects did not select the prosocial token more often
419 when a partner was present as opposed to absent, such a preference was detected when analysing
420 only the dyads in which the Experimental condition (partner present) was administered before
421 the Control condition (partner absent). Randomizing the order of conditions is therefore essential
422 to obtain unbiased data on prosocial behaviour, something that previous studies did not fully
423 achieve.

424 Our results based on two tasks contrast with those previously reported for capuchin
425 monkeys [29, 30] and chimpanzees [27]. However, the caveats that we have identified above
426 require that those results are interpreted with great caution. In particular, we still failed to obtain
427 consistent evidence of prosocial behaviour in the tested species, despite our best attempts of
428 eliciting prosocial behaviour, for instance by following Horner and colleagues' [27] procedure
429 and ensuring the inclusion of all their procedural improvements (e.g. use of wrapped food
430 rewards not to distract subjects with visible food, use of transparent panels or mesh between
431 subject and partner to allow communication, avoidance of competitive attitudes by always
432 allowing them access to the partner's room in the Solitary condition only after administering the
433 Experimental condition).

434 Finally, since de Waal and colleagues [29] and Horner and colleagues [27] only tested
435 females, one could argue that sex differences could explain the discrepancies between the current
436 and previous studies. However, none of the females who responded appropriately in the Solitary

437 condition of the Tokens task behaved prosocially towards their partners. This means that the
438 inclusion of males in our sample cannot explain the differences with previous studies. Although
439 our findings with the Tokens task contrast with those in the three studies that have so far been
440 done with the same task, our results are quite consistent with the data from the Platforms task.

441 In conclusion, the results of both the Platforms and the Tokens tasks (with their
442 respective control conditions) did not provide compelling evidence of prosocial behaviour for
443 any of the six primate species tested. When food distribution was involved, great apes, spider
444 monkeys, and capuchin monkeys failed to show prosocial behaviour toward group members,
445 despite being paired with different partners and having the chance to provide them with food at
446 no extra cost to themselves. These results highlight the importance of implementing tasks that
447 control for confounding variables and of using different experimental paradigms when previous
448 results contradict one another. Although it is still possible that other populations perform
449 differently when tested with the same task (because of differences in diet quality, housing, or
450 personality, for example [47]), administering multiple tasks (with control conditions) is
451 necessary to demonstrate prosociality. Finally, it is important to stress that our conclusions are
452 limited to prosocial behaviour in an *active* food distribution context and do not allow us to
453 generalise our findings to other contexts, like helping behaviour [e.g. 9-13] or passive food
454 transfers [e.g. 7-8], as prosocial behaviour might be restricted to specific contexts and not
455 generalize to active food-sharing [10].

456

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466

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578

579 TABLE AND FIGURE CAPTIONS

580

581 TABLE 1. For each species, list of the dyads in which the subject chose the prosocial token
582 significantly more than chance in the Solitary condition of the Tokens task (Binomial test), with
583 the percentage of prosocial choices made, the P values for the Binomial test, and the results for
584 the Wilcoxon test when comparing the subject's percentage of prosocial choices in the
585 Experimental and Control conditions.

586

587 FIGURE 1. Set-up in the three conditions of the Platforms task.

588

589 FIGURE 2. Mean percentage of prosocial choices (+SE) in the (a) Equal condition, (b) Unequal
590 condition and (c) Equidistant condition of the Platforms task, as a function of species. Only
591 gorillas made the prosocial choice significantly more in the Experimental than in the Control
592 Equal condition ($p = 0.048$). The black line represents chance performance (at 50%).

593

594 FIGURE 3. Mean percentage of prosocial choices (+SE) in the Experimental, Control and
595 Solitary conditions of the Tokens task, as a function of species. The black line represents chance
596 performance (at 50%).