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Marmoset monkeys overcome dyadic social dilemmas while avoiding mutual defection

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1 Marmoset monkeys overcome dyadic social dilemmas while avoiding mutual defection

3 Abstract

4 Social primates constantly face situations in which their preferences collide and they need to
5 engineer strategies to overcome conflicts of interest. Studies with chimpanzees have found
6 that they use competitive strategies to overcome social dilemmas, maximizing their own
7 benefits while minimizing the loss of rewards. However, little is known about how other
8 primates that rely more on cooperation would overcome similar dilemmas. We therefore
9 presented male-female pairs of common marmosets (cooperative breeders) with two
10 experiments of an action-based paradigm that creates a conflict of interest over access to an
11 unequal reward distribution. Rather than engaging in mutual defection, marmosets were able
12 to overcome this social dilemma over time, by developing a mix of strategic behaviors
13 (predominantly by females) and tolerance to disadvantageous reward distributions
14 (predominantly by males). This mix of behavioral strategies yielded more and better rewards
15 for the females. Importantly, such a net outcome is consistent with the natural history of this
16 species where females, who carry a high energetic burden of reproduction, tend to be less
17 prosocial and are receivers, rather than donors, in food sharing events among adults.

18 Introduction

19 Social primates engage in a wide range of cooperative behaviors to reap the benefits of group
20 living (Kappeler & Van Schaik, 2006; Silk, 2005), including coalition formation (Newton-Fisher,
21 2006; Nishida & Hosaka, 1996), border patrols (Gilby et al., 2013; Muller & Mitani, 2005;
22 Wilson et al., 2001), group hunts (Boesch, 1994, 2002; Gilby et al., 2006, 2008, 2015; Gilby &
23 Wrangham, 2007), territorial advertisement and defense against outsiders (Kitchen, 2004;
24 Willems & van Schaik, 2015), food sharing (Guerreiro Martins et al., 2019; Jaeggi & Van Schaik,
25 2011; Liebal & Rossano, 2017; Wittig et al., 2014), communicating about food resources and
26 potential dangers (Crockford et al., 2012) and helping to raise others' offspring in cooperatively
27 breeding primates (Digby, 1995; Finkenwirth et al., 2016; Tardif et al., 1986). According to
28 Melis & Semmann (Melis & Semmann, 2010), these cooperative behaviors can be divided in
29 two types, depending on whether there is a delay between the benefits accrued by the parties
30 involved. When both individuals act together, mutual benefits tend to be immediate for both
31 cooperators and thus, cooperative partners have no conflict of interest or reasons to exploit
32 each other's behavior. In contrast, when one cooperator invests in the welfare of another
33 individual, there is typically a delay in time until the latter contributes back the initial
34 investment (see (Schino & Aureli, 2017; Schweinfurth & Call, 2019) for a review on primates'
35 cooperation through investments). This can result in a highly demanding endeavor for the
36 cooperation partners because individual interests collide, and exploiting the cooperative
37 attitudes of the partner through deception turns into a highly attractive immediate alternative.
38 In such situations of conflicts of interest between group members, individuals face social
39 dilemmas between acting selfishly or cooperatively.

40 Recent studies have begun to use game theory models to investigate how primates navigate
41 social dilemmas when their interests compete with those of their partners, i.e. when mutual
42 cooperation is not the best option from the individual perspective (Brosnan et al., 2017; Hall et
43 al., 2019; Sánchez-Amaro et al., 2016, 2017, 2019; Vale et al., 2019). On the one hand, some of
44 these studies have tackled primates' resolution of conflicts through the use of token-exchange
45 or computerized tasks with no prior training of the payoff structure of the game ((Brosnan et

46 al., 2017; Hall et al., 2019; Vale et al., 2019) but see (Watzek et al., 2018) for a review of this
47 approach). These studies have found that some primate species including rhesus macaques
48 and capuchin monkeys are able to reach Nash equilibrium over trials (i.e. an optimal outcome
49 from an interaction given the strategy of your partner) although it remains unclear whether
50 they converge on these equilibria strategically. On the other hand, others have established
51 action-based tasks with more obvious payoff structures for participants (Grueneisen et al.,
52 2017; Melis et al., 2016; Sánchez-Amaro et al., 2016, 2017; 2019). An action-based task can be
53 defined as a situation in which participants need to take decisions between different physical
54 actions to fulfill a certain goal (e.g. to obtain a food reward (Wunderlich et al., 2009)).

55 In an action-based scenario aimed to investigate how primates solve social dilemmas, Sánchez-
56 Amaro and colleagues (Sánchez-Amaro et al., 2017) presented pairs of chimpanzees, bonobos
57 and 5-year-old children with an unequal reward distribution (i.e. a high and a low value
58 reward), where choosing one reward would leave the partner with the other. In the social
59 dilemma condition, both partners had potential access to the low value reward. The high value
60 reward could therefore only be obtained if individuals would wait for their partners to act
61 before them (strategic waiting). However, if both individuals waited for each other to choose,
62 the rewards were removed and both would lose (mutual defection). This social dilemma
63 condition was contrasted with a competitive condition in which both partners had potential
64 access to the high value reward. Now, the partner who pulled faster would obtain the high
65 value reward and the other one the low value reward. In this and similar studies (Sánchez-
66 Amaro et al., 2016, 2019) chimpanzees used competitive strategies to maximize their goals
67 while minimizing the risks of losing rewards. That is, they distinguished between conditions by
68 waiting longer for their partner to act in the social dilemma situation (Sánchez-Amaro et al.,
69 2016, 2017, 2019) or ceased cooperation once the partner had started to collaborate to
70 maximize their likelihood to obtain rewards (Sánchez-Amaro et al., 2019). In addition, great
71 apes employed these competitive strategies regardless of whether the social dilemma and the
72 competitive conditions were randomly intermixed within sessions (Sánchez-Amaro et al., 2017)
73 or were presented separately (Sánchez-Amaro et al., 2019), further suggesting that great apes
74 competed with each other to obtain the best rewards (Melis et al., 2016; Sánchez-Amaro et al.,
75 2019). In contrast, 5-year-old children engaged in turn-taking as a cooperative strategy which
76 results in an equal division of rewards between pair members (Grueneisen & Tomasello, 2017;
77 Melis et al., 2016; Sánchez-Amaro et al., 2019) but see (Zeidler et al., 2016) for cultural
78 differences in the way children divide rewards). However, when social dilemma trials were
79 randomly intermixed with competitive trials, 5-year-old children behaved more similarly to
80 chimpanzees and bonobos by showing more signs of strategic decision-making by using verbal
81 communication to influence their partners decisions (Sánchez-Amaro et al., 2017).

82 In general, the results of these studies support the idea that chimpanzees' cooperation is
83 rooted in their competitive social system (Muller & Mitani, 2005; Tomasello, 2018). In contrast
84 to chimpanzees, cooperative breeding primates such as marmosets and tamarins rely more
85 heavily on cooperation in their everyday lives (Snowdon & Cronin, 2007; Yamamoto et al.,
86 2010). Their cooperation is supported by other-regarding preferences or proactive prosociality
87 (Burkart et al., 2007, 2014; Burkart & van Schaik, 2013). In prosocial species, individuals are
88 more resilient toward unequal outcomes that benefit the partner (Cronin & Snowdon, 2008).
89 The trade-offs of social dilemmas between acting selfishly vs cooperatively should therefore be
90 shifted toward more cooperative behaviors.

91 Among marmosets and tamarins, many group members help raising offspring. They proactively
92 offer food to immatures at high rates (Guerreiro-Martins et al., 2019; Martins & Burkart, 2013;
93 Moura et al., 2010; Price & Feistner, 1993; Rapaport & Brown, 2008), and they are particularly
94 likely to offer food when they are alone with the immatures (Brügger et al., 2018). In
95 prosociality tasks among adult marmosets, individuals also readily make food available to each
96 other (Burkart et al., 2007, 2014; Burkart & van Schaik, 2013), even for out-group strangers
97 (Burkart et al., 2007). Tamarins also show prosocial tendencies that allows them to maintain
98 high rates of mutual cooperation even when only one individual is rewarded at a time (Cronin
99 & Snowdon, 2008). Overall, converging evidence suggests that marmosets have some
100 intentional control over their prosocial behaviors (Burkart & Schaik, 2020). Among adults,
101 males tend to be more prosocial (Burkart et al., 2007): they provision more in experimental
102 prosociality tasks and in naturalistic food sharing between adults, food is almost exclusively
103 shared from males to females (Guerreiro Martins et al., 2019). Similar results have been found
104 in tamarins where adults helpers might prefer to transfer food to breeding females (Rapaport,
105 2001). Additionally, it has been reported that marmoset males groom females more than vice
106 versa among breeding-pairs (Lazaro-Perea, 2001). This is consistent with the natural history of
107 these animals (Yamamoto et al., 2010). Females bear high reproductive costs by producing
108 twins twice a year and can thus be simultaneously gestating and lactating (French, 1983; Tardif
109 et al., 2003). Moreover, they tend to be more motivated and skilled at finding food rewards
110 during foraging tasks (Box et al., 1999; Michels, 1998; Schubiger et al., 2015; Yamamoto et al.,
111 2004) despite the lack of sexual dimorphism in the Callitrichinae subfamily (Ford, 1994;
112 Plavcan & Van Schaik, 1997). Together, this suggests that in marmoset dyads the shift toward
113 more cooperative behavior is stronger in males than in females.

114 Our goal was to examine how common marmoset male-female dyads would solve a social
115 dilemma. Like children and chimpanzees (Sánchez-Amaro et al., 2017), we expected them to
116 behave strategically and wait longer before acting in the social dilemma than in the
117 competitive conditions. We hypothesized that this would be particularly the case for females.
118 As a result, the females should obtain more and better food rewards in the social dilemma
119 condition.

120 Given the high levels of cooperation in nature, marmosets could also be expected to engage in
121 cooperative strategies, in particular the males, similar to the 5-year-old children of the
122 previous studies (Sánchez-Amaro et al., 2017, 2019) who engaged in turn-taking to navigate
123 iterated social dilemma situations. Primates often engage in vocal turn-taking (Pika et al.,
124 2018) or in the care of infants (Snowdon & Ziegler, 2007). Note, however, that turn-taking
125 strategies to divide rewards equally are notoriously difficult and cognitively demanding for
126 nonhuman primates (Schino & Aureli, 2010; Stevens et al., 2005). The establishment of such
127 strategy presupposes that marmosets understand that both individuals have a joint goal and
128 that each individual should be equally rewarded to sustain cooperation over prolonged periods
129 of time (Melis et al., 2016). Furthermore, individuals should inhibit themselves from free riding
130 and obtaining the best rewards when repeated competitive conditions are presented.

131 To facilitate comparisons with human children and great apes we built on a previous study by
132 Sánchez-Amaro and colleagues (Sánchez-Amaro et al., 2017). We presented pairs of
133 marmosets with two studies. In study 1 we followed the original design and presented
134 monkeys with social dilemma trials randomly intermixed with competition trials. In study 2 we
135 alternated conditions between sessions (see (Sánchez-Amaro, Altinok, et al., 2019)) to
136 facilitate the marmosets' understanding of the game contingencies and to evaluate whether

137 they would develop different strategies (e.g. cooperative strategies such as turn-taking) when
138 conditions were presented separately. Furthermore, we introduced non-social control
139 sessions. The hypothesis was that, if marmosets behaved strategically, their latencies to act
140 would vary significantly more between social dilemma and competitive trials in the test
141 situation compared to the control situation. This is expected because waiting in social dilemma
142 trials during controls does not lead to better rewards—there is no partner present on the
143 opposite side of the apparatus.

144 We hypothesized that common marmosets would show signatures of strategic decision-
145 making similar to great apes and children in related tasks. That is, waiting longer to act in social
146 dilemma trials compared to competitive trials during test sessions. We also predicted that
147 females would be especially willing to maximize rewards by waiting longer than males to act in
148 social dilemma trials, and that these differences would increase during study 2 given the
149 repeated presentation of the same conditions within sessions.

150

151 **Methods**

152

153 **Participants**

154 We tested ten marmosets (five different pairs) in study 1. Eight of these marmosets (four pairs)
155 participated in study 2. The dropped pair that participated in our first study suffered the loss
156 of one of their group members due to old age by the end of study 1. We decided not to include
157 them in study 2 to facilitate the development of a new group dynamic (See ESM Table S1). All
158 individuals were housed as pairs or family groups (2 to 4 individuals per group) and had access
159 to indoor and outdoor areas (each 1.8 m * 2.7 m * 2.4 m) provided with shelter and different
160 environmental enrichments. Primates could also access an additional test room where the
161 experiments were conducted. Marmosets were never food or water deprived during the
162 experiments.

163

164 **Materials (apparatus)**

165 We presented marmosets with a smaller replica of a design used by Sánchez-Amaro and
166 colleagues (Sánchez-Amaro et al., 2017). The apparatus consisted of a rotating tray attached to
167 a square platform. The rotating tray could spin 360 degrees in either direction. Depending on
168 the study phase, either one or two ropes could be attached to the ends of the rotating tray.
169 Food could be baited on transparent plastic dishes located at the ends of the rotating tray (see
170 Figure 1).

171 In addition, we also built two plexiglass walls that served as separators between the test
172 compartments where the marmosets were tested, and the test booth where the apparatus
173 sat. In addition, we placed a transparent plexiglass square platform some centimeters above
174 the apparatus. The plexiglass walls had two openings. The higher opening served as a door to
175 let the marmosets access the transparent platform on the top of the apparatus. From there
176 marmosets could move between test compartments. The lower opening served as a door to
177 let the marmosets grab the rope and obtain the food rewards.

178

179 **Experimental design**

180 Phase 1: familiarization with the apparatus and test room

181 Phase 1 was divided in group familiarization sessions and individual familiarization sessions.
182 Each group or pair participated in two sessions of each type on alternate days. In the
183 familiarization phases we did not impose any strict criteria to advance to phase 2. The aim of
184 these familiarization phases was to simply present them with the apparatus and to make them
185 feel comfortable in the presence of the main experimenter and in the test room.

186 Group familiarization sessions.

187 In group familiarization sessions the monkeys interacted with the study apparatus through the
188 mesh of their home enclosures. The marmosets could access the apparatus for 30 minutes or
189 after completing 36 trials in the case of groups of four individuals or 18 trials in the case of
190 pairs. The purpose of these familiarization sessions was to present the monkeys with the
191 apparatus for the first time and with the way the rewards were delivered. In these sessions,
192 the marmosets could access a rope connected to one side of the rotating tray baited with food
193 rewards. We used a mixture of food rewards including pieces of banana, apple and
194 mealworms. The type of food randomly varied between trials and the monkeys could only
195 obtain one piece of food per trial (see Figure 1a).

196

197 Individual familiarization sessions.

198 In these sessions pairs and groups of marmosets had to travel from their enclosures to the test
199 room through semi-transparent tubes connecting both locations. Once there, the marmosets
200 could access two test compartments (50 cm * 50 cm * 60 cm) on each side of an empty test
201 booth. The marmosets could move between test compartments by accessing a transparent
202 plexiglass platform placed over the test booth, at approximately 10 cm from the ground (as in
203 Figure 1c but without the apparatus). To access the platform the marmosets had to jump
204 through an opening on the plexiglass walls separating the test compartments and the test
205 booth. To motivate and incentivize individuals to cross the booth we always placed rewards on
206 the opposite test compartment. This also confirms that they could pay attention to food
207 located across the test booth—where their partners would be located during test trials. We
208 presented them with the same food rewards as in the group familiarization sessions.
209 Individuals participated in a maximum of 12 trials per session, alternating their starting
210 location (right or left test compartments), as well as the bowl that was baited, between trials.
211 Eight of the ten individuals performed 12 trials per session. Two other individuals performed
212 12 and 4 trials, and 9 and 6 trials per session.

213

214 Phase 2: Individual training

215 After individuals participated in the familiarization phase, we trained them with the standard
216 setup by placing the apparatus used during group familiarization sessions in the test booth
217 between the test compartments (as in Figure 1c but without partner). In this phase monkeys
218 were trained alone to pull and obtain the rewards from both sides of the rotating tray. On a
219 given trial, they had to pull the rope connected to the interior end of tray to access the baited
220 rewards from that side. After that, we opened the access to the plexiglass platform and let

221 them access the opposite test compartment—as in the individual familiarization sessions.
222 Once they arrived to the opposite test compartment, we closed again the access to the
223 platform. Marmosets could then retrieve the rewards baited on the free end of the rotating
224 tray. We used the same type of food rewards we previously used during the familiarization
225 phase (for 9 individuals we had to introduce other types of food such as crickets or small
226 cookies to incentivize their participation during individual training sessions). Each marmoset
227 participated in an open-ended number of 8-trial sessions ranging from two to seven (with only
228 one marmoset participating in seven sessions). A trial would be considered successful if the
229 participants accessed both sides of the rotating tray. We alternated the starting location (right
230 or left test compartments) between trials. Participants had to succeed in at least 80% of the
231 trials in two consecutive training sessions to advance to the next phase.

232 Phase 3: food preference sessions

233 The marmosets participated in two 8-trial session to determine their food preferences for
234 future tests. Thus, marmosets were confronted with a choice between crickets or small
235 cookies with a small piece of solid gum (*a priori* high reward) and slices of apple (*a priori* low
236 reward). One individual participated in three sessions because we changed the food rewards
237 after the first session. In food preference sessions we placed the apparatus in front of their
238 test compartment—during phase 2 the apparatus was located on the test booth next to their
239 compartment. On a given trial a marmoset could decide to pull one of two ropes, each
240 connected to one side of the rotating tray while in the previous phase marmosets could only
241 access one rope attached to the interior end of the tray. Each side of the tray was baited with a
242 different type of food (see Figure 1b). Within sessions, the location of the rewards was pseudo
243 randomly counterbalanced, i.e. the same food constellation could not be repeated for more
244 than two consecutive trials. To facilitate the assessment of their food preferences, two
245 marmosets were tested without apparatus. We placed the food rewards on the surface in
246 front of their test compartments. All marmosets preferred the crickets or the cookies over the
247 slices of apple in a majority of trials. At the group level the marmosets chose their preferred
248 food in 81% of trials and only one subject chose his preferred food in 60% of trials.

249

250 Phase 4: Dyadic training

251 Finally, pairs of marmosets were trained together for at least two 8-trial sessions. As in
252 individual training sessions, the apparatus was located in the test booth between the test
253 compartments. Each marmoset was in one of the compartments. In this training phase we
254 connected two ropes to the interior end of the rotating tray but only one was accessible to a
255 marmoset at a time (as in Figure 1c but only one rope accessible to a marmoset). Furthermore,
256 the location of the food rewards was pseudo randomly counterbalanced so that the same food
257 constellation could not be repeated for more than two consecutive trials. By manipulating the
258 access to the rope and the location of the food rewards, we exposed marmosets to the four
259 potential outcomes they could experience during test trials. That is, trials in which they could
260 directly obtain the high food reward by pulling (high reward baited on the interior end of the
261 tray), trials in which they could directly obtain the low food reward by pulling, trials in which
262 they could only obtain the high food reward after their partner had pulled her rope (high
263 reward baited on the free end of the tray) and trials in which they could only obtain the low
264 food reward after their partner had pull her rope. In contrast to the individual training in Phase
265 2, marmosets remained on the same test compartment on a given session and only changed

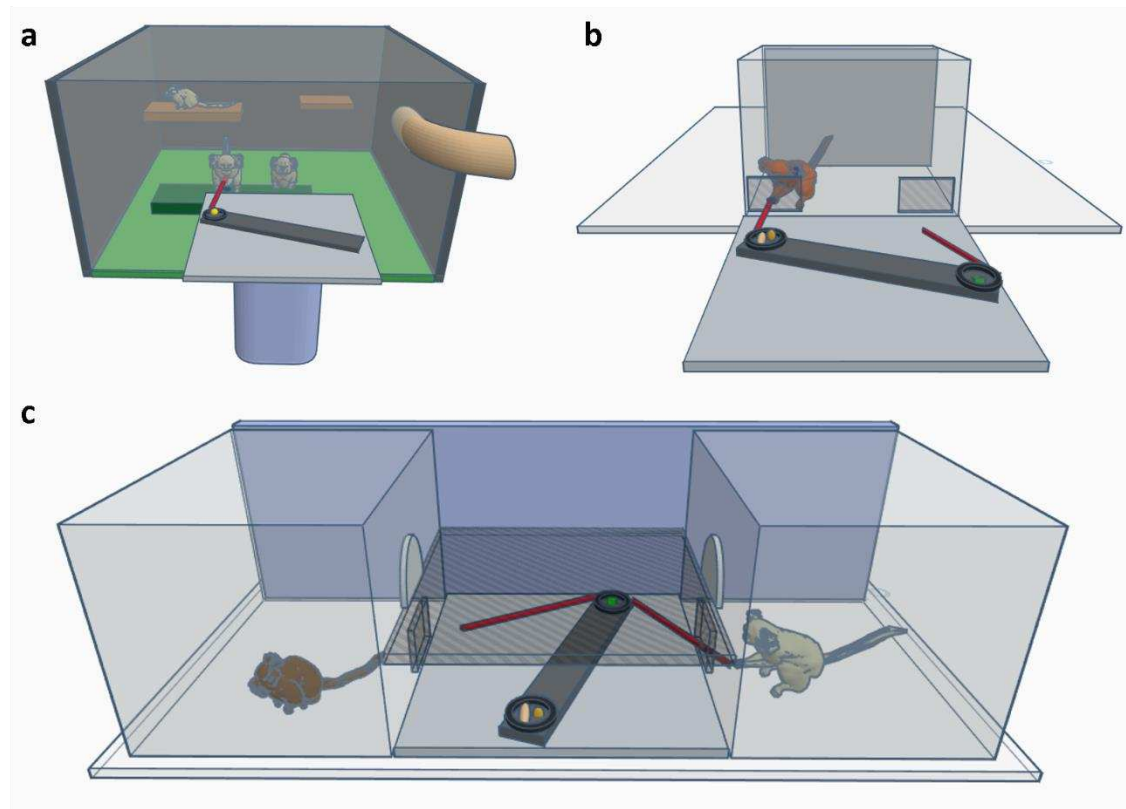
266 compartments between sessions. Therefore, the access to the platform communicating both
267 compartments was close. The passing criteria was the same as in Phase 2 and all pairs reached
268 the criteria within two sessions.

269

270 Test and control sessions for studies 1 and 2

271 On every study, each pair participated in 8 test sessions. Furthermore, each individual
272 participated in 8 control sessions per study. In test sessions, participants were located on
273 opposite test compartments while in control sessions individuals were tested alone.
274 Marmosets could access the rewards during 35 seconds before the trial was over. In addition,
275 the only difference between test and previous dyadic training sessions was that in the former
276 both marmosets could access a rope at the same time, i.e. two ropes were attached to the
277 interior ends of the tray with each rope end being accessible to one marmoset (see Figure 1c).
278 Marmosets changed sides between sessions. We alternated between test and control sessions
279 so that each pair of marmosets experienced the same type of session every second day of
280 tests. Half of the pairs started with test sessions and the other half with control sessions.

281 In the first study we pseudo randomly counterbalanced the presentation order of the food
282 rewards within sessions (social dilemma and competitive trials). Food constellations could not
283 be repeated for more than two trials in a row (see (Sánchez-Amaro et al., 2017)). The pseudo
284 random counterbalancing of the two conditions might have prevented great apes and children
285 to come up with cooperative strategies to divide rewards equally. Thus, to facilitate the
286 development of cooperative strategies between pair members and to reduce the cognitive
287 demands of the first task (e.g. due to the unpredictable switch between conditions within
288 sessions), in the second study we blocked the order presentation of social dilemma and
289 competitive trials. That is, we alternated these two conditions between sessions. On a single
290 session, high value food rewards could be directly accessible after pulling (baited on the
291 interior end of the tray; competitive trials) or after the partner pulled (baited on the free end
292 of the tray; social dilemma trials). We counterbalanced food locations between test and
293 control sessions.



294

295 Figure 1: Representation of the study setup during a) group familiarization sessions, b) food
 296 preference sessions and c) test trials.

297 Coding

298 We scored two main dependent measures on both studies: whether marmosets pulled their
 299 rope to access rewards and their latencies to pull. In addition, we also scored their attempts to
 300 pull and their latencies to attempt those pulls (see ESM for details).

301 A pulling act is defined as the first movement (to the left or to the right) of the roped end of
 302 the tray—the visible result from pulling the end of the rope. A latency to pull is defined as the
 303 elapsed time between the experimenter opening the access to both ropes and the pulling act.

304 We scored the presence of the first pulling acts during control and test trials. In test trials, we
 305 only scored the first pull act even when both monkeys pulled. We calculated the latencies for
 306 the first pulling acts from the moment we let the marmosets access the ropes until the actions
 307 occurred on a frame by frame analysis.

308 Finally, following the definitions used by Sánchez-Amaro and colleagues (Sánchez-Amaro et al.,
 309 2017) we scored the proportion of strategic choices for each individual during test sessions. In
 310 competitive trials the strategic choice was to pull while in social dilemma trials the strategic
 311 choice was to not pull. Thus, in both conditions we scored the proportion of trials in which
 312 marmosets pulled (and did not pull). Then, we divided marmosets into three categories:
 313 “pullers” (marmosets that pulled in more than 75% of times in both conditions), “non-pullers”
 314 (marmosets that pulled in less than 25% of times in both conditions) and “strategizers”
 315 (marmosets that acted significantly more in competitive trials over social dilemma trials). As in
 316 Sánchez-Amaro and colleagues (Sánchez-Amaro et al., 2017), in this analysis we counted

317 whether a marmoset pulled on a given trial regardless of whether the partner had previously
318 pulled in that same trial.

319

320 The analyses were conducted using Linear Mixed Models and Generalized Linear Mixed
321 Models. All analyses were conducted with R statistics (version 3.4.4). We ran all LMM with
322 Gaussian error structure and identity link function. Variables were z-transformed and log-
323 transformed when required.

324 All full models were compared to a null model excluding the test variables. When the
325 comparison between the full and the null model was significant, we further investigated the
326 significance of the test variables. We used the drop1 function of the lme4 package (Bates,
327 2010) to test each variable's significance including interactions between test predictors. Non-
328 significant interactions were removed and a new reduced model was produced. A likelihood
329 ratio test with significance set at $p < 0.05$ was used to compare models and to test the
330 significance of the individual fixed effects. We ruled out collinearity by checking Variance
331 Inflation Factors (VIF). All VIF values were closer to 1 (maximum VIF value = 1.01). For every
332 model we assessed its stability by comparing the estimates derived by a model based on all
333 data with those obtained from models with the levels of the random effects excluded one at a
334 time. All models were stable. In addition, we ran binomial tests at the individual level to
335 determine whether marmosets were acting strategically and whether they were maximizing
336 the best food rewards over chance levels.

337 The interobserver reliability was excellent based on the 15% of the data that was coded by a
338 second rater: occurrence of pulls in control sessions of study 1 (Cohen's Kappa = 0.8), control
339 sessions of study 2 (Cohen's Kappa = 0.9), test sessions of study 1 and 2 (Cohen's Kappa =
340 0.96). The interobserver reliability on the marmosets' latencies to pull was also very high:
341 latency to pull in control sessions of study 1 (Pearson's $r = 0.99$), latency to pull in control
342 sessions of study 2 (Pearson's $r = 0.98$), latencies to pull in test sessions of studies 1 and 2
343 (Pearson's $r = 0.98$).

344

345 **Results**

346 **Study 1**

347 In the test trials, marmosets participated in 97.8% of trials (average latency to pull = 1.83
348 seconds). That is, one of the two pair members accessed the rope and pulled. Marmoset dyads
349 refused to participate in 7 social dilemma trials (2.2%) and never in competitive trials. We
350 found a main effect of session suggesting that marmosets hesitated less to pull across sessions
351 (LMM: $\chi^2 = 4.12$, $df = 1$, $p = 0.04$, $N = 313$). In addition, we found a non-significant trend
352 suggesting that marmosets pulled faster in competitive trials compared to test trials (LMM: χ^2
353 $= 3.5$, $df = 1$, $p = 0.06$, $N = 313$; Figure S1 and model details in the ESM).

354 In the control trials, we found that marmosets participated in 93% of trials (average latency to
355 pull = 3.5 seconds). They refused to participate in 31 control social dilemma trials (4.8%) and
356 14 control competitive trials (2.2%). When they participated, we found that marmosets
357 latencies to pull were significantly affected by the condition presented. Marmosets pulled

358 significantly faster in control competitive trials compared to control social dilemma trials
359 (LMM: $\chi^2 = 5.87$, $df = 1$, $p = 0.015$, $N = 595$; Figure S2 and model details in the ESM).

360 Besides their latencies, we analyzed whether their decisions to pull or not were strategic. That
361 is, whether they would pull in competitive trials but not in social dilemma trials. We found that
362 only one male marmoset was classified as “puller” after acting in more than 75% of trials
363 across conditions. Furthermore, two marmosets (one male and one female) were classified as
364 “strategizers” after pulling significantly more often in competitive trials than in social dilemma
365 trials (binomial test, $p < 0.05$; Figure S3). The rest of marmosets were unclassified.

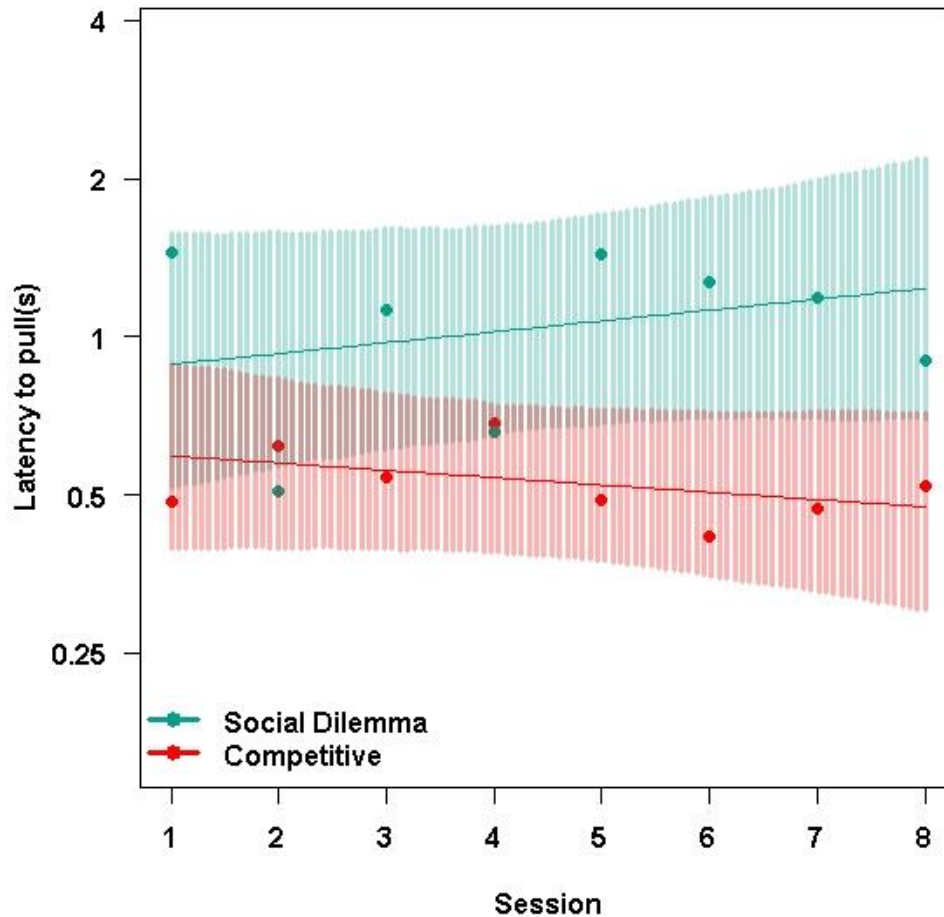
366 Finally, we also analyzed the proportion of best food rewards obtained across conditions (i.e.
367 to obtain the food baited on the roped end of the apparatus during competitive trials and to
368 obtain the food baited on the free end of the apparatus during social dilemma trials) for each
369 individual. We found that no marmoset obtained the best rewards significantly above chance
370 when we considered both conditions together (binomial test, $p > 0.05$; Figure S4).

371

372 **Study 2**

373

374 In the test trials, marmoset dyads participated in all but one trial (99.6%; average latency to
375 pull = 1.14 seconds). We found a main significant two-way interaction between condition and
376 session suggesting that marmosets became more strategic across sessions. Marmosets
377 increased their latencies to pull during social dilemma sessions and decreased their latencies
378 to pull during competitive sessions (LMM: $\chi^2 = 5.03$, $df = 1$, $p = 0.025$, $N = 255$; Figure 2). For
379 the sake of comparison with study 1 we also represented individuals' latencies in boxplots
380 separated by condition and sex (Figure S5).



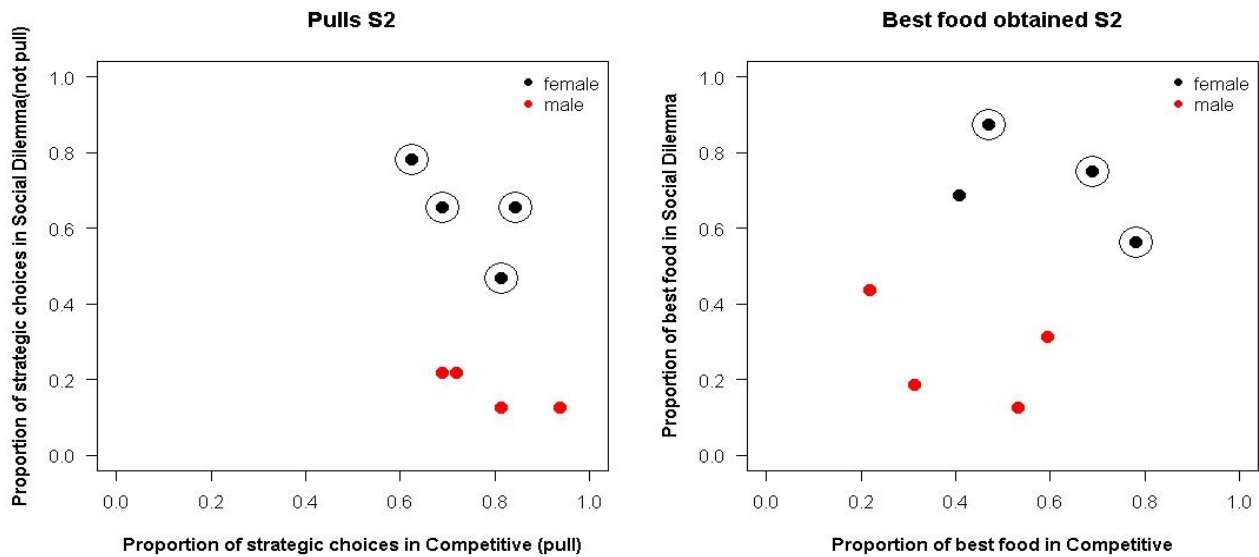
381

382 Figure 2. Latency to pull across social dilemma and competitive sessions in study 2. Data points
 383 represent the mean average latencies across sessions. The solid line represents the fitted
 384 model and the shaded areas the confidence intervals at 95%. Latencies in seconds are
 385 represented in a logarithmic scale.

386 In the control trials, we found that marmosets participated in 92.7% of all trials (average
 387 latency to pull = 2.54 seconds). They refused to participate in 30 control social dilemma trials
 388 (5.9%) and 7 control competitive trials (1.4%). When they participated, we found that
 389 marmosets' latencies to pull were significantly affected by an interaction between condition
 390 and sex (LMM: $\chi^2 = 4.68$, $df = 1$, $p = 0.03$, $N = 474$). That is, marmosets acted faster in control
 391 competitive trials compared to control social dilemma trials but females hesitated more than
 392 males to pull during control social dilemma trials during control sessions (Figure S6).

393 As in study 1, we also analyzed whether their decisions to pull or not were strategic. We found
 394 that only two male marmosets were classified as "pullers" after acting in more than 75% of
 395 trials across conditions. In addition, all four females were classified as strategic after pulling
 396 significantly more often in competitive than in social dilemma trials (binomial test, $p < 0.05$;
 397 Figure 3 left panel). The two other marmosets were unclassified. Finally, we analyzed the
 398 proportion of best food rewards obtained across conditions for each individual. We found that
 399 three females obtained the best rewards significantly above chance when we considered both
 400 conditions together (binomial test, $p < 0.05$; Figure 3 right panel).

401



411

412 Figure 3. Left panel: Proportion of strategic choices in social dilemma and competitive trials for
 413 each individual. Circle dots indicate marmosets that were classified as *strategizers*. Right panel:
 414 Proportion of best food obtained in social dilemma and competitive trials per individual.
 415 Circled dots indicate marmosets that obtained the high value rewards significantly over chance
 416 levels.

417

418 **Discussion**

419 The results of the two studies demonstrate that marmosets possess the abilities to solve a
 420 conflict of interest in which only one pair member can access a high value food reward while
 421 the partner accesses a lower value food reward. Similar to chimpanzees, bonobos and 5-year-
 422 old children in a previous version of the task (Sánchez-Amaro et al., 2017), marmosets avoided
 423 food losses and solved the conflict of interest in a majority of trials.

424 Marmosets waited longer to act in the social dilemma condition compared to the competitive
 425 condition. These results are in line with previous findings suggesting that great apes also wait
 426 longer to act when they can benefit from their partners' cooperative behavior in similar social
 427 dilemma scenarios (Sánchez-Amaro et al., 2016, 2017, 2019). However, even though common
 428 marmosets showed signatures of strategic decision-making during test sessions, they also
 429 waited longer to pull in social dilemma trials than competitive trials in control sessions.

430 These results may suggest that marmosets did not fully understand the contingencies of both
 431 studies. However, in study 2 the marmosets seemed to learn over time when to wait for their
 432 partners to pull. That is, the marmosets increased their latencies to pull across social dilemma
 433 sessions while they decreased their latencies to pull across competitive sessions. Most likely,
 434 the iterated presentation of the study conditions facilitated the marmosets' implementation
 435 and reinforcement of strategies aimed at maximizing access to the high value rewards. In
 436 contrast, when the marmosets were randomly presented with competitive and social dilemma
 437 trials within sessions, they did not seem to show any behavioral pattern suggesting that they
 438 improved their strategies over time. Our results are thus in line with studies showing how the
 439 blocked presentation of the same cooperative condition improved cotton-top tamarins'
 440 coordination abilities to pull together for mutual rewards (Cronin et al., 2005; Cronin &
 441 Snowden, 2008). These findings also relate to developmental studies showing that 5-year-old

442 children are more likely to engage in cooperative strategies such as turn taking to overcome
443 conflicts of interest, similar to the one presented to marmosets, only when the same social
444 dilemma situations are repeatedly presented (Grueneisen & Tomasello, 2017; Melis et al.,
445 2016; Sánchez-Amaro et al., 2017, 2019). In other words, when they can predict the next
446 scenario, children establish collaborative strategies to avoid conflict and divide rewards
447 equally.

448 The question is then, why did marmosets wait differently between conditions during control
449 trials? One possibility is that common marmosets felt frustrated during control social dilemma
450 trials because they were not able to obtain the highest value reward. This frustration would
451 have been especially salient among females during study 2 (when the access to high-value
452 rewards was not possible for the entire session) since they are generally more motivated to
453 find high value food compared to males (Box et al., 1999; Michels, 1998; Schubiger et al., 2015;
454 Yamamoto et al., 2004; see Box et al., 1995 for similar findings in tamarins). However,
455 marmosets did not lose their motivation to participate in the study. They pulled from their
456 rope in a majority of trials regardless of the condition presented.

457 Related, marmosets hesitated more to act in control compared to test trials regardless of the
458 condition presented. One explanation for this difference is social facilitation, the phenomenon
459 by which the presence of another individual facilitates an actors' likelihood to perform a
460 behavior (Whiten & Ham, 1992; Zajonc, 1965). This is unlikely, however, because social
461 facilitation would have acted on both sexes equally whereas we did find clear sex differences
462 in study 2. In line with previous work suggesting that female marmosets are more motivated at
463 finding food rewards (Box et al., 1999; Yamamoto et al., 2004), we found that in study 2 all
464 females, but none of the males, adopted strategies to maximize access to the high value food
465 rewards. That is, they waited for their male partners to pull in social dilemma trials while they
466 still pulled their end of the rope to access rewards in competitive trials. Those strategies
467 resulted in three of four females obtaining the best rewards significantly above chance during
468 the test phase of our second study.

469 Another possibility is that males actively tried to provide food for their female partners by
470 pulling before them in social dilemma trials. This would be in line with findings showing that
471 food transfers between adult common marmosets are almost exclusively directed from males
472 to females (Guerreiro Martins et al., 2019). This possibility appears to contrast with the fact
473 that males did not hesitate or even refuse to pull in competitive test trials. It is important to
474 note, however, that the two situations differ in that in competitive trials, the high value food
475 can become available through individual effort to both partners. In social dilemma trials, on
476 the other hand, this is not the case, and the high value food can never be obtained through
477 individual effort. In other contexts, prosocial provisioning has likewise been observed to be
478 higher when partners cannot obtain the food through individual effort, both in food sharing
479 contexts (Dell'Mour et al., 2009; Moura et al., 2010), and in experimental prosociality tasks
480 (Burkart et al., 2007, 2014). It may well be that the marmosets reacted to this difference in
481 competitive versus social dilemma trials and prosocial responses by males were more
482 prevalent in the situation where the females could not obtain the high-quality reward through
483 individual effort.

484 These results suggest that marmosets, in particular females, understood the contingency of
485 the task in the second study, i.e. that they could obtain the highest reward if their partners
486 acted before them. Importantly, this outcome did not result from females generally avoiding
487 the low value rewards since they pulled in the great majority of social dilemma trials during

488 control sessions (in over 85% of trials across studies). A more plausible explanation is that
489 females were more motivated to obtain the high value food rewards compared to males. This
490 predisposition together with the iterated presentation of social dilemma conditions allowed
491 females to behave strategically in study 2.

492 Overall, while both sexes became more strategic during our second study, most likely
493 facilitated by the separate presentation of the study conditions between sessions, only
494 females took advantage of it by refusing to pull in some social dilemma trials of study 2 while
495 their male partners continued to participate in those trials. Most strikingly, the combination of
496 male and females' behavioral strategies results in a meaningful net outcome that fits the
497 natural history of the species (Yamamoto et al., 2010). The results make additional sense if we
498 consider common marmosets' other regarding preferences (Burkart & van Schaik, 2020),
499 where common marmoset males are usually more willing to provide females access to food
500 rewards and share food with them (Burkart et al., 2007; Guerreiro Martins et al., 2019). It is
501 possible that, despite males not seeming to actively try to benefit females (e.g. they did not
502 refuse to pull in competitive trials), their prosocial nature could explain certain tolerance
503 towards disadvantageous inequity in favor of their female partners (Brosnan et al., 2010;
504 Cronin & Snowdon, 2008; de Waal & Suchak, 2010).

505 Future studies should investigate in more detail to what degree marmosets and other
506 cooperatively breeding primates are able to sustain inequity when they solve conflicts of
507 interest (see Cronin & Snowdon, 2008 for results showing how tamarins sustain inequity in a
508 mutual cooperation task), under which conditions they will procure benefits for the self or
509 others and how these strategies may differ between sexes as in our study. For instance, future
510 work should focus on whether marmosets would refuse to engage in a cooperative dilemma if
511 they can access an alternative secure reward (Sánchez-Amaro et al., 2017). Nevertheless,
512 comparative work on how different primates solve social dilemmas should include species
513 other than cooperative breeders and great apes. For instance, it would be very interesting to
514 shed light on the strategies that cooperative monkeys such as capuchins (Boinski, 1988; Rose,
515 1997) would employ in these scenarios given their participation in a number of experimental
516 studies on cooperation (Brosnan, 2011) and even on a recent computerized task including
517 various social dilemmas (Smith et al., 2019). Finally, it would be intriguing to extend these
518 dyadic scenarios to group level social dilemmas with the aim to shed light on the diversity of
519 individual and group factors underlying cooperation when primates' personal preferences are
520 in conflict.

521 **Ethical Statement:** The experiments have been licensed by the Kantonales Veterinäramt
522 Zürich, license number ZH223/16. Marmosets were not used to travel from their home
523 enclosure to the test room and to remain in the test room to participate in experimental
524 studies. To create a comfortable space for them we often provided them with their first meal
525 in the test room. This way marmosets got used to move between their home enclosure and
526 the test room. The experimental task did not create any stress to the participants. The
527 simplistic design of the apparatus has been proven effective to test pairs of children, great
528 apes and marmoset monkeys.

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