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1   **Chimpanzees, bonobos and children successfully coordinate in conflict situations**

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8   Social animals need to coordinate with others to reap the benefits of group-living even when individuals'
9   interests are misaligned. We compare how chimpanzees, bonobos and children coordinate their actions
10   with a conspecific in a Snowdrift game, which provides a model for understanding how organisms
11   coordinate and make decisions under conflict. In study 1, we presented pairs of chimpanzees, bonobos
12   and children with an unequal reward distribution. In the critical condition the preferred reward could only
13   be obtained by waiting for the partner to act, with the risk that if no one acted, both would lose the
14   rewards. Apes and children successfully coordinated to obtain the rewards. Children used a "both-
15   partner-pull" strategy and communicated during the task while some apes relied on an "only-one-partner-
16   pulls" strategy to solve the task although there were also signs of strategic behavior as they waited for
17   their partner to pull when that strategy led to the preferred reward. In study 2, we presented pairs of
18   chimpanzees and bonobos with the same setup as in study 1 with the addition of a non-social option that
19   provided them with a secure reward. In this situation, apes had to actively decide between the unequal
20   distribution or the alternative. In this setup, apes maximized their rewards by taking their partners'
21   potential actions into account. In conclusion, children and apes showed clear instances of strategic
22   decision-making to maximize their own rewards while maintaining successful coordination.

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Introduction

Many animal species regularly face situations in which individuals need to coordinate to overcome conflicts of interest. Most research has focused on how groups decide on the direction of travel when individuals have differing preferences [1-2] but, as with humans, there are many other contexts involving a conflict of interest. For instance, lions [3] during inter-group encounters or chimpanzees [4] that lag behind in cooperative hunting events waiting for others to start the chase may avoid fighting, injuries and energy expenditure [5]. But if everyone waits, no hunt will ensue. Recent evidence suggests that some chimpanzees solve the coordination problem by starting the hunt and thus paying the initiation costs (acting as "impact-hunters") [6]. However, it remains unclear whether the benefits that "impact-hunters" obtain from the hunt outweigh the initiation costs. In other words, it is unclear whether these subjects strategically take into account the potential costs and benefits of the hunt when they initiate it.

Situations of the type described above can be understood as collective-action problems [7, 8], or at the dyadic level, as Snowdrift dilemmas (SD) [9-12]. The SD occurs when an individual (A) would prefer another individual (B) to carry out a costly action that benefits both A and B. However, if B does not act, it is better for A to act alone rather than not act at all. Therefore the preference for A would be 1st) to wait for B to act, 2nd) divide the cost by acting together and 3rd) pay all the cost of the action. One crucial difference between the SD and other classical games such as the Prisoners Dilemma (PD) [13] is that the worst case scenario in the SD occurs when both partners defect while in the PD occurs when the individual cooperates but the partner defects. Consistent with the idea that cooperation is less risky in a SD than in PD, both agent-based simulations [14] and human behavioural experiments [15, 16] have found higher and more stable levels of cooperation in SD than PD.

In general, models in which mutual defection is the worst-case scenario offer a better explanatory model of the emergence of cooperation and helping in natural conditions [17]. Although models like the Stag Hunt game [18] –a situation in which each individual can decide between an individual option that provides a secure but less preferred reward or a social option in which participants need to collaborate to obtain a highly preferred reward– show crucial differences between the way chimpanzees and humans manage the challenge of coordinating actions and maintaining high levels of cooperation [19, 20], SD models seem a better fit for situations in which chimpanzees need to coordinate actions towards common goals [21-24], especially as soon as there is conflict of interest. Recently, two studies have investigated how chimpanzees [25] and five-year-old children [26] coordinate their actions in SD dilemmas. Chimpanzee dyads were presented with a task in which they could access food by pulling a weighted tray. Individuals could pull together and split the costs or they could pull alone and do all the work. However, if after a certain period of time neither individual had pulled, the experimenters removed the rewards. Chimpanzees solved the dilemma, cooperating on an average of 70% of trials. However, in situations where the tray was very heavy (and thus more difficult to pull) chimpanzees waited longer before pulling. Additionally, the difference between the weight pulled by the individual pulling first and pulling second increased across sessions. The authors concluded that the chimpanzees may have tried to avoid being the first one pulling to reduce the risk of pulling alone, while still maintaining successful coordination. In another study, Grueneisen and Tomasello [26] presented pairs of five-year-old children with a different version of a SD: two toy trains with rewards in the cargo. Each child controlled one train which had to

73   arrive at its own station positioned behind the partners train to retrieve the rewards. However, if both
74   trains continued along the track they were on, they would crash into each other before arriving to their
75   stations and all rewards would be lost. Thus, one child needed to swerve onto a side track at the cost of
76   some cargo. Therefore, it was in each child's interest to wait for the partner to swerve. Children rarely
77   crashed the trains by taking turns swerving.

78   Although these two studies demonstrated that both species can solve SD dilemmas, they are not directly
79   comparable because chimpanzee dyads had the option to cooperate and share costs within trials [25],
80   whereas children did not [26]. Consequently, the current study presented children and two nonhuman
81   great ape (henceforth ape) species, chimpanzees and bonobos, with the same SD dilemma paying special
82   attention to any indication of strategic decision-making (i.e., waiting to pull). Although bonobos have not
83   been studied in SD dilemmas, previous studies on cooperation indicate that they performed better than
84   chimpanzees under some conditions that required higher tolerance towards conspecifics [27]. Study 1
85   investigated subjects' decisions in a SD and a competitive condition (COM). The best strategy in the SD
86   condition was to wait for a partner to pull and thus obtain the higher of two rewards. However, as in the
87   classical SD situation, it was better to pull if no-one pulled. We compared SD to COM, which required
88   subjects to pull faster than the partner to obtain the higher reward. If subjects behaved strategically, we
89   expected a higher latency to pull in the SD than COM and a higher frequency of both individuals pulling in
90   COM than SD. Finally, based on a recent study [20], we expected communication to play a role in
91   children's coordination but not in chimpanzees or bonobos. We conducted a follow-up study with apes
92   (Study 2) because some individuals in Study 1 had shown indications of strategic decision making by
93   waiting to pull in the SD condition. We used the same apparatus (and conditions) as in Study 1a except
94   that we added an alternative option for each individual. We hypothesized that this would allow subjects
95   to better manage the risk by choosing the alternative option depending on the options available in the
96   apparatus and their partner's preferences.

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98   **Study 1a: Chimpanzees and Bonobos Snowdrift**

99   Subjects

100 We tested 10 captive chimpanzees (5 females; M_{age}= 20.5 years) and 6 captive bonobos (5 females;
101 M_{age}=13.7 years) housed at the Wolfgang Kohler Primate Research Center in Leipzig zoo (see Table 1 in
102 the electronic supplementary materials, henceforth ESM, for more information about the apes in study
103 1a and 2). During the first phase of the study, the chimpanzees made up 5 unique pairs and the bonobos
104 made up 3 unique pairs. In the second phase pairs were reshuffled to create 5 new chimpanzee pairs and
105 3 new bonobo pairs.

106 Materials

107 We presented ape dyads with a rotating blade (10x91 cm) (Figure 1a) attached to a platform (88.5x96.5
108 cm) placed between two rooms. Each end of the rotating blade was baited by different amounts of fruit
109 (banana slices for chimpanzees and half grapes for bonobos). Subjects faced each other across the

110 platform, each with access to one side of the apparatus. Two identical ropes (76 cm) were attached to the
111 interior end of the blade with Velcro (see Figure 1a) and fed into each subjects' room. Subjects could
112 access the apparatus via a small window on either side of the platform; the experimenter opened these
113 windows at the start of a trial but the windows remained closed between trials. Apes could only access
114 the interior or the exterior end of the blade by pulling the rope towards them or by waiting for the partner
115 to pull from the other side, respectively. Thus, when a subject pulled its rope, the roped end of the blade
116 rotated towards her while the free end rotated towards her partner.

117 Figure 1. Experimental set-up of study 1a (Figure 1a), study 1b (Figure 1b) and study 2 (Figure 1c).

118 Design and procedure

119 We used a within-subjects design with two conditions (SD & COM). In the SD condition, one piece of fruit
120 was placed on the roped end of the blade and four pieces on the free end, thus creating a SD dilemma
121 because the subject's best choice was to wait for the partner to pull and bring the free end within her
122 reach. In the COM condition, the four pieces of fruit were placed on the roped end while the free end was
123 baited with one piece. In this condition subjects should pull earlier than their partner to obtain the higher
124 reward.

125 At the start of a trial, two experimenters allowed subjects access to their respective ropes by opening the
126 windows. The subjects then had 30 seconds to pull the rope and get the rewards placed on the rotating
127 blade or wait for the partner to pull. If no ape pulled after the 30 seconds, the experimenter removed all
128 rewards and ended the trial. In case both individuals pulled simultaneously, one or both ropes
129 disconnected from the blade resulting in a random movement and a possible loss of all rewards.

130 Training phases

131 Prior to the test phase all subjects completed two training phases (see ESM for more details of the training
132 phases).

133 Phase 1. Individual training

134 This training phase served to expose the subjects to the task's main contingencies including how to access
135 the rewards. Subjects were required to pull the blade to retrieve food. After pulling the rope subjects
136 could access both rooms and retrieve the food from both sides of the apparatus.

137 Phase 2. Dyadic training

138 This training served to demonstrate that, depending on the condition, subjects could get either high or
139 low rewards by either pulling themselves or by waiting for a partner to pull.

140 Test sessions

141 After completing the training phases each dyad received eight 8-trial test sessions (4 SD and 4 COM trials
142 in a randomised order). Subjects only received one session per day and switched sides between sessions.
143 Test sessions were identical to the dyadic training sessions except that both subjects had access to their

144 own rope. After completing eight sessions with their first partner (phase 1) each subject was paired with
145 another one for another eight sessions (phase 2).

146 Coding

147 Our measure of coordination success was the percentage of trials in which dyads succeeded, defined as
148 trials in which at least one member obtained a reward. We scored three further dependent variables:
149 subjects' latencies to pull, their pulling rate (derived in three different measures) and communication (see
150 ESM for details of interobserver reliability measures for all studies). We defined the latency to pull as the
151 elapsed time between the opening of the doors and the first pulling action). We defined a pulling action
152 as either the first instance of blade movement towards a subject or the first instance of tension between
153 the ropes of both subjects, which occurred when both subjects pulled simultaneously. Communication
154 was defined as any vocal or gestural communicative acts directed towards the partner or the partner´s
155 actions, such as attention-getters (see ESM for details). It is possible, though, that we may have missed
156 more subtle cues of communication.

157 We calculated three measures derived from the subject's pulling rate. First, we considered whether apes
158 behaved strategically by comparing the number of strategic choices (i.e., proportion of pulls in the COM
159 condition plus the proportion of non-pull decisions in the SD condition) to the levels expected by chance.
160 With this information we also classified subjects as pullers (pulling ≥ 75% of trials in both conditions), non-
161 pullers *(*pulls ≤ 25% of trials in both conditions) and strategisers (COM pulling > SD pulling resulting in a
162 food intake significantly above chance in both conditions). Second, we scored conflict trials defined as
163 both subjects pulling simultaneously and investigated whether their likelihood of occurrence increased by
164 the occurrence of a conflict in the previous trial. Finally, we investigated subjects' flexibility defined as the
165 change in pulling behaviour shown between subjects (see the ESM for details).

166 Statistical analysis

167 All analyses were conducted using linear mixed models (LMM) or generalized linear mixed models
168 (GLMM). In all models significance was set at P < 0.05 (see ESM for full details of the statistical analysis).

169

170 **Results and discussion**

171 Overall, dyads obtained the rewards in 98% of trials. Subjects waited longer to pull during SD than COM
172 trials (Model 1, LMM: χ^2_1 = 9.181, N = 1019, P = 0.002, CI [0.057, 0.483]). From their pulling rates, we
173 classified four subjects as "pullers", three as "non-pullers" and two as "strategisers". The remaining seven
174 subjects were unclassified. The two "strategisers" (one male chimpanzee and one female bonobo) pulled
175 in COM trials and not in SD trials (binomial test, p < 0.005), a behavior that resulted in a maximization of
176 their payoffs (see Table 1 in ESM). However, when we considered strategies at the dyadic level a different
177 picture emerged. In nine of 16 dyads one subject pulled in most of trials (>75%) while the other almost
178 never pulled (<25%). Thus, a high proportion of dyads displayed a strategy based on only one subject
179 pulling in both conditions. Pulling rates also indicated that apes were more likely to pull simultaneously in

180 COM than SD trials (Model 2, GLMM: χ^2_1 = 6.607, N = 895, P = 0.01). Previous conflict trials had no effect

181 on their subsequent response (Model 2, GLMM: χ^2_1 = 5.286, N = 895, P = 0.071) (see ESM for detailed

182 information of Model 1 and 2). We found that subjects' behavior changed between partners: 31% of

183 subjects modified their behavior (varying their pulling rates by more than 50% between partners; see

184 Figure 2 in ESM). Finally, we found that apes almost never communicated with their partner to solve the

185 task (individuals protested on 0.01 % trials).

186 In sum, chimpanzees and bonobos came up with an efficient, simple solution to coordinate in this task,

187 the "only-one-partner-pulls" strategy. Although this strategy prevented subjects from maximizing their

188 own payoffs, the randomized presentation of the rewards led to an almost equal division of rewards

189 between partners. Moreover, two subjects behaved strategically although it was unclear why so few did

190 so (2 out of 16 individuals) and what strategic level their decisions entailed. Next we presented 5-year-old

191 children with the same basic task to compare their strategies to those of apes (study 1a) and subsequently

192 probed ape strategic behavior further by varying potential payoffs for the subject and the partner in study

193 2.

194

195 **Study 1b: Children Snowdrift**

196 Subjects

197 We tested 20 pairs of- 5- to 5.5-year-old children (10 pairs of girls and 10 pairs of boys) in kindergartens

198 in the Leipzig area. All participants were recruited from a database of children whose parents had provided

199 written consent to take part in child development and comparative studies. The children in each pair were

200 from the same kindergarten.

201 Materials

202 In general, dyads were presented with the same task as chimpanzees and bonobos (Figure 1b). The

203 apparatus was a wooden box with a lid that prevented children from directly accessing the rewards. We

204 made a few minor changes to accommodate the apparatus for children (see ESM for differences between

205 study 1a and study 1b).

206 Design and Procedure

207 The procedure the same as the one used in study 1a except for three differences. First, children were only

208 tested with one partner. Second, we used tokens (wooden blocks during training and more valuable

209 plastic marbles ("jewels") during test sessions) as rewards, which children had to collect during the study.

210 Third, children received three sessions (24 trials in total) compared to 16 sessions (128 trials) for the apes

211 (see ESM for other minor differences between study 1a and study 1b design and procedure).

212 Test sessions

213   After the training, each dyad performed three test sessions on two consecutive days. The first session
214   was conducted after the training and the second and third sessions were conducted on a second day. Each
215   session consisted of eight trials and children swapped sides after completing trial four. Children received
216   two COM and two SD trials in a randomised order from each side of the apparatus. At the beginning of
217   each trial, Experimenter 1 showed the reward locations to the children before allowing them to access to
218   the ropes. In the test sessions, children collected their rewards and kept them in their own plastic tubes
219   previously provided by the experimenters (see ESM for details of the test sessions).

220   Coding

221   We analysed the same dependent measures as in study 1a, excluding flexibility because children only
222   played with one partner. Additionally, we adjusted our coding to include verbal communication (see ESM
223   for communication coding details). We only analysed verbal communication related to the task by
224   focussing on the five following types: *imperative*: deontic verbs used to direct their partners' actions (e.g.
225   "You should pull"), *protests:* statements of disapproval and objection about a partner action's or intention
226   (e.g. "No, I also wanted"), *informative:* acts aimed at informing partners about a child's current or
227   impending actions or intentions (e.g. "I am going to pull now"), *turn-taking:* stating previous or future
228   actions aimed at influence others' decisions. This type of communication could be coupled with either
229   *imperative, protests or informative* (e.g. "I pull because you pulled before"; "Next time you pull") and
230   *deception:* acts aimed at explicitly cheating their partners.

231

232   **Results and discussion**

233   Overall, dyads obtained the rewards in almost all trials (99%). Children increased their latency to pull
234   across sessions in SD trials and decreased it in COM trials (Model 3, LMM: χ^2_1 = 4.913, N = 478, P = 0.027,
235   CI [-0.023, 0.223]; Figure 2) indicating that like apes, they distinguished the conditions. Based on their
236   pulling rates, we classified most children as "pullers" (24 of 40) and one child was classified as a "non-
237   puller". Three children made strategic decisions significantly above chance (binomial test, p < 0.005) by
238   pulling in COM trials and not pulling in SD trials (see ESM for a detailed comparison between children' and
239   apes' strategies). At the dyadic level, only one dyad followed the "only-one-partner-pulls" strategy
240   described for apes. Instead, most child dyads followed a "both-partners-pull" strategy regardless of the
241   condition. In contrast to apes, children both pulled equally often in COM (53 % of times together)
242   compared to SD trials (43 % of times together) (Model 4, GLMM: χ^2_4 = 5.305, N = 420, P = 0.257). Finally,
243   we found that children communicated more often in SD than COM trials (Model 5, GLMM: χ^2_1 = 4.72, N =
244   480 P = 0.03, CI [-0.219, 2.464]). Communication occurred in 33% of the trials (in 96 SD and 56 COM trials
245   out of 240 trials per condition). Although we could not analyze statistically the distribution of children
246   communicative types, we found that imperative utterances (e.g. "you should pull") were mostly used in
247   situations in which they needed a partner to act against the partners' self-interest (58% of 96
248   communicative acts in SD trials). In contrast, no communicative type predominated in competitive
249   situations (see ESM for detailed information of Models 3, 4, 5 and Figure 4 in ESM).

Figure 2. Latency of the 1st puller to pull the rope in SD and COM trials across the three test sessions. The dotted line represents the fitted model and the shadowed areas represent the CI at 95%. Latencies in seconds are presented in a logarithmic scale. Data from children in study 1b.

In summary, children were as successful as apes and made a similar proportion of strategic choices compared to apes (53% of strategic choices in children, 51% in chimpanzees and 54% in bonobos). However, they did so with much less experience with the task -24 compared to 128 trials suggesting that, in contrast to apes, they learned faster the contingencies of the task. Unlike apes, we found that most children followed a "both-partners-pull" strategy regardless of the condition, which may not be that different in terms of complexity to the apes' "only-one-partner-pulls" strategy. However, children showed more signs of strategic decision-making than apes: they used communication to influence their partner decisions and learned to distinguish both conditions after only three sessions (Figure 2).

Study 2: Chimpanzees and bonobos Snowdrift with alternative option

In the previous study, although a majority of ape dyads engaged in the "only-one-partner-pulls" strategy, some apes showed indications of strategic decision making. To further investigate individuals´ decision-making strategies in conflict situations, we used the same apparatus of Study 1a with the addition of an alternative option for each individual.

Subjects

We tested 8 captive chimpanzees (3 females; M_{age}= 13.5 years) and 4 captive bonobos (3 females; M_{age}= 13.5 years) housed at the Wolfgang Kohler Primate Research Center in Leipzig zoo. Seven chimpanzees and all bonobos had taken part in study 1a. Each individual was tested with three partners. During the first phase of the study, the chimpanzees made up four unique pairs and the bonobos made up two unique pairs. In the second and third phase, pairs were shuffled to create another four new chimpanzee pairs and two new bonobos' pairs per phase.

Materials

We presented pairs of individuals with the same apparatus used in study 1a with two main additions. In this new setup, subjects needed to move a sliding door either to the left or the right side to access the apparatus. If they moved the sliding door to the right side they could access the ropes as in the original apparatus. However, if they slid the door towards the left they could directly access an alternative option (Figure 1c). The alternative option consisted of a fixed platform (10X10 cm) attached to the Plexiglas frame located approximately 5 cm above the apparatus to not interfere with the rotation of the blade. When the sliding door was opened to one side, another locking mechanism prevented it from being moved back to its original position. Therefore, subjects could only make one choice per trial (see ESM for details of the materials).

Design and procedure

285 Subjects were tested in a within-subjects design in the same two conditions as study 1a (SD and COM). In
286 this set-up the rotating blade was baited with one and five food pieces. The alternative platforms could
287 be baited with either zero, one, three or five food pieces depending on the condition presented (non-
288 social condition levels). Both alternative platforms were baited with the same food quantity on a given
289 trial. Chimpanzees and bonobos received the same kind of food as in study 1a.

290 At the beginning of a trial, two experimenters simultaneously removed the pin that had prevented
291 choosing between options and apes had 10 seconds to make their choices. When a subject opened the
292 window to the alternative platform, they could immediately access the reward. When a subject opened
293 the door to the blade they could either wait for the partner to pull the rope or pull themselves (as in study
294 1a). We defined an apes' choice for the rotating blade as the "social option" and the alternative platform
295 as the "non-social option".

296 Test sessions

297 After completing the training phases (see ESM for details of the training phases), every dyad performed
298 eight test sessions. Each session contained four SD and four COM trials presented in a randomized order.
299 In the alternative platform, the levels of the non-social condition (0, 1, 3 or 5) were randomly presented
300 between sessions, each level was presented in two sessions. In the test sessions, both subjects had access
301 to either the rope attached to the rotating tray or the alternative option. Subjects switched sides between
302 sessions. After the eight sessions with their first partner (phase 1) each subject was paired with two
303 further partners for another two blocks of eight sessions (phase 2 and 3).

304 Coding

305 We measured the percentage of successful trials (defined as in study 1). Additionally, to study how
306 chimpanzees and bonobos solved this new version of the game, we focused on two main dependent
307 variables: choices and latencies (further divided in two latency measures). Choices were defined as the
308 proportion of trials in which each subject chose the social or the non-social option. The first latency
309 measure consisted of the elapsed time between the pins' removal and the sliding of the door halfway to
310 one side (at which point they could not change direction). The second latency measure was the elapsed
311 time between accessing the social option and pulling the rope (defined as in study 1a). These latencies
312 allowed us to assess whether the 2nd actors made strategic decisions contingent on the previous action of
313 the 1st actors during the same trial.

314 To determine who acted in 1st and 2nd position (by acting we mean the initial decisions to slide the door
315 to access either the social or non-social option), we only considered those trials in which both individuals
316 acted at different times (at least $\frac{1}{25}$ of a second). The average time between 1st and 2nd actors was less
317 than 2 seconds. Then, for each combination of social and non-social conditions (8 combinations) we
318 categorized the strategic choices of the 2nd actors. Moreover, we took into account those instances where
319 the 2nd actors could maximize their rewards by taking into account the previous action of 1st actors (see
320 the two combinations of non-social option 3 in Table 1). In other words, in these two combinations 2nd

321 actors strategic choices differed depending on 1st actors actions. Finally, we calculated the proportion of
322 strategic choices for each of the 8 combinations and we compared them to chance levels.

323 Table 1. Rational choices dependent on the combination of social and non-social options.

Social option	Non-social option	Strategic choice
SD and COM	0	Social option
SD and COM	1	Social option
SD	3	Same action of 1st actor
COM	3	Opposite action to 1st actor
SD and COM	5	Non-social option

324

325

Results and discussion

327 Overall, ape dyads obtained the rewards in 92% of trials. Both ape species behaved rationally by choosing
328 the social option when there were no rewards available in the non-social alternative (93% of trials). As
329 expected, the proportion of choices towards the non-social option relative to the social option also
330 increased as the rewards in the alternative platform increased. This change was not driven solely by the
331 number of rewards in the alternative option but also by the social condition: the switch in preference
332 from the social to the non-social option was steeper in SD trials compared to COM trials (Model 6, GLMM:
333 χ^2_1 = 9.572, P = 0.002, N = 2218, CI [0.284, 2.258], Figure 3).

334 Figure 3. Percentage of chimpanzees and bonobos' decisions towards the social choice as a function of
335 the number of food pieces in the non-social and the social option (SD and COM trials) in study 2.

336 Our first latency measure was the time taken to open the door to either platform. When there was no
337 reward in the non-social platform apes waited longer to open the doors in SD trials compared to COM
338 trials, replicating the findings from study 1a. However, as the rewards in the non-social platform increased,
339 apes tended to decrease their latency to decide, and the differences between SD and COM conditions
340 decreased. This decrease in latency occurred in conjunction with a change in their decisions, from the
341 social to the non-social option (see Figure 3) (Model 7, LMM: χ^2_1 = 6.62, N = 2216, P = 0.01, CI [-0.007,
342 0.295], see Figures 6 and 7 in the ESM). Overall, chimpanzees were faster than bonobos in both conditions
343 (Model 7, LMM: χ^2_1 = 8.06, N = 2216, P = 0.004, CI [-1.061, -0.099]) but there were no significant
344 interactions between species and conditions.

345 Our second latency measure focused on whether subjects waited further for their partner to pull in the
346 SD condition, or whether the decision to open the door always led to immediate pulling of the rope. We
347 found that both chimpanzees and bonobos did indeed wait longer to pull in SD trials compared to COM
348 trials. Additionally, as the rewards in the non-social option increased apes tended to wait longer to pull
349 (Model 8, LMM: χ^2_1 = 3.888, N = 773, P = 0.048, CI [-0.044, 0.37], see Figures 8 and 9 in the ESM), with a
350 more pronounced effect in bonobos. This was unexpected as at that point the content of the non-social

351 option was already inaccessible and thus should not play a role in their decision to wait. However, these
352 results should be interpreted cautiously as they are based on a small subset of trials (see Figure 3).

353 Overall, we found that the individuals acting second made strategic decisions on 85% of the trials.
354 Moreover, when they could respond to the decision that the first actor had made in that trial –in non-
355 social option 3, they made strategic choices on 75% of trials. However, they only chose significantly above
356 chance when there were 0 or 5 food rewards baited in the alternative platform (P < 0.02; see Model 9 for
357 detailed results of the pair-wise comparisons derived from the model and Figure 10 in ESM). Finally, we
358 also found that 2nd actors differed in their choices depending on the previous choices of the 1st actors and
359 the combination of social and non-social conditions presented (combinations Non-social option 1-SD,
360 Non-social option 3-COM and Non-social option 5-COM) (Model 10, GLMM: χ^2_2 = 12.53, N = 396, P =
361 0.002). Moreover, a further inspection of the model revealed that the probability of 2nd actors to choose
362 the social option increased when 1st actors chose the social option in Non-social option 1-SD (P = 0.02) but
363 the choice was not significantly affected in the other two combinations (Non-social option 3-COM: P =
364 0.22; Non-social option 5-COM: P = 0.4). See ESM for detailed information of Model 6-10.

365

366 In sum, results of study 2 substantially clarified those from study 1a by showing that when apes had access
367 to an alternative option, their decisions were clearly strategic. They understood the payoffs of the game
368 and acted rationally according to all the rewards involved by maximizing their benefits, as shown in
369 previous social dilemmas [28]. This may have simply been due to increased experience, as all individuals
370 completed study 1a before study 2. However, if this were the case, we would have expected changes
371 across sessions in study 1a. We suggest that one important factor is that the inhibitory demands of study
372 1a were higher. Subjects faced the decision to either act on the apparatus (pull) or not at all, but in study
373 2 apes could decide between the two actions (sliding the door left or right). Thus, one possible way to
374 interpret our results is that when apes had to actively decide between different alternatives, it may have
375 been easier for them to inhibit and compare their potential options and act appropriately according to
376 the payoffs of the game in order to maximize their rewards.

377

378 **General Discussion**

379 Using the Snowdrift dilemma to investigate how pairs of children, chimpanzees and bonobos coordinate
380 their actions to overcome conflicts of interest, we found that all three species coordinated their actions
381 effectively and succeeded in over 90% of the trials. All species showed clear indications of strategic
382 decision making, trying to maximize their own rewards while maintaining high levels of coordination. In
383 study 1, children's communicative acts revealed clear signs of strategic behavior but no such indication
384 was observed among apes. In study 2, in which apes had access to an alternative (non-social) option, their
385 decisions were clearly strategic even though communication between partners was still virtually
386 nonexistent.

387   Children are skilled at coordinating for mutual gain from a young age [20, 26, 29-31]. Even in situations
388   where the risk of coordination failure is increased, children are able to use communication and theory of
389   mind reasoning to avoid this risk [20, 26, 29 and 32]. However, the goals of partners in those studies were
390   aligned (i.e. there was no conflict of interest between partners). The current study showed that even
391   when facing with a potential conflict of interest, children's rate of coordination failure was very low.
392   Crucially, their success in the task cannot be attributed to a failure to appreciate the conflict of interest
393   because their communicative exchanges indicated that they encouraged their partners to pay the higher
394   cost to maximize their own rewards.

395   Our results are consistent with Grueneisen and Tomasello. [26] who also observed high levels of
396   coordination in five-year-old children playing a version of the SD game. Coordination in that study was
397   maintained by turn-taking, which also has been shown to enable resource sharing in a collaborative task
398   [33]. Note however, that children in those studies always depended on their partner to obtain either the
399   preferred reward [26] or all the rewards [33]. In contrast, our procedure eliminated a strict partner
400   dependency because SD trials were randomly intermixed with COM trials in which children competed to
401   obtain the preferred reward by pulling first, without the need of their partner's action. Besides preventing
402   partner dependency, mixing SD and COM trials may have made a turn-taking strategy much more
403   cognitively demanding than previous studies (and therefore useless) because it would have required
404   children to keep track of all their previous actions and outcomes to maximize efficiency. However, a
405   consequence of this strategy is that the coordination was maintained despite a skewed reward
406   distribution between partners (also observed in Grueneisen et al. [26]), perhaps because receiving some
407   reward was more important than the social comparison, but further research is needed to determine the
408   effects of resource inequality on coordination.

409   Apes also solved the SD dilemma successfully (coordination in 98% of the trials) but their behavior differed
410   from children's in two important ways: there was little communication between partners and only one
411   partner pulled in most dyads. This strategy produced an equal distribution of rewards between partners,
412   which may seem surprising given that apes behaved as rational maximizers in other studies [28, 34].
413   However, the observed equal distribution may have been a by-product of the one-partner-pulling strategy
414   combined with the counterbalancing of payoffs across multiple trials. Even when one of the partners was
415   a passive participant (always waiting) it does not necessarily mean that they were indifferent to the
416   outcomes. Apes experienced pulling in both conditions during the training and experimental sessions,
417   and there is evidence suggesting that subordinate chimpanzees wait to pull a rope to "negotiate" a better
418   reward distribution with a dominant individual [35]. Thus, it is conceivable that some apes preferred to
419   obtain lower rewards instead of competing for higher rewards to avoid conflict [21]. However, in our case
420   it is difficult to ascertain whether not pulling was a strategic decision, or some individuals were content
421   with the food received for not pulling at all.

422   Study 2 directly addressed this ambiguity by offering an alternative option to inaction. Based on their
423   change in preference from social to non-social choices (and their associated timing), apes generally
424   behaved more strategically in study 2 compared to study 1. However, apes not always maximized their
425   rewards in all conditions. For instance, when apes were confronted with the COM condition (five pieces
426   of food in the roped end) and the alternative option was baited with three pieces of food, they sometimes

427   preferred the lower but secure reward even when they pulled first (20% of times they chose the non-
428   social option). Perhaps an aversion to either risk or even competition with their partners led them to
429   select lower value (but secure) rewards in those cases. In the absence of risk, chimpanzees prefer to act
430   alone rather than to collaborate provided both actions yield the same rewards [34] but they switch to
431   collaborative options that result in better outcomes than acting alone [34, 36]). However, if social risks
432   increase, as in the current study or other tasks [20], they may prefer lower but more secure rewards, thus
433   managing a trade-off between competition and reward maximization.

434   Based on previous findings [37, 38], we expected bonobos to be more risk averse (preferring the secure
435   option) than chimpanzees but we found no clear inter-specific differences. A possible explanation for this
436   result is that most studies have focused on non-social risk effects. Interestingly, in a study in which
437   bonobos could choose between feeding alone or co-feeding with strangers, they preferred the social
438   option [39] despite the potential social risks involved. Thus, we need further studies comparing
439   chimpanzees and bonobos across different social and non-social risk tasks to fully understand possible
440   differences between these two species.

441   Finally, we investigated whether apes took advantage of situations in which they already had information
442   about their partner's decisions (i.e. when their partner acted before them) and whether they varied their
443   choices depending on their partner´s previous choices. Overall, individuals acting second chose
444   strategically. However, in those conditions where the strategic choice of second actors differed depending
445   on what their partner had chosen in that trial, they did not perform significantly above chance. Moreover,
446   in some combinations of social and non-social conditions, the decisions of individuals acting second were
447   affected by their partners' previous choice, suggesting that they were taking into account their partners
448   previous actions. Our results are consistent with previous studies in competitive contexts showing that
449   chimpanzees can adjust their strategies in anticipation of likely decisions of partners [40, 41] but we did
450   not see clear strategic responses to a partner's specific decision. The short time that apes had to respond
451   to their partner and the random presentation of conditions within sessions may have contributed to this
452   outcome. We found that apes anticipated their partner's likely behaviour when they faced a symmetrical
453   conflict of interest in which both participants started with the same probabilities to maximize their pay-
454   offs. However, to explore in more detail whether apes act strategically in response to their partners'
455   decisions, future research could focus on how apes solve conflicts of interest when only one individual
456   has bargaining leverage (i.e. only one member of the pair has access to an alternative option).

457   In conclusion, using a Snowdrift game to model situations such as group hunting or agonistic intergroup
458   encounters in which individuals need to overcome a conflict of interest to coordinate with others, we
459   found that pairs of children, chimpanzees and bonobos successfully solved this social dilemma. However,
460   they did so in different ways. Whereas both partners pulled and communicated in children, one of the
461   partners did most of the pulling in apes with virtually no communication. Nevertheless, an additional
462   study that included an additional secure option revealed that apes behaved strategically by choosing
463   options that maximized their own payoffs, which in some cases included delaying (or accelerating) their
464   choices to net the largest reward available.

465

Ethical Statement

The study was ethically approved by an internal committee at the Max Planck Institute for Evolutionary Anthropology. Animal husbandry and research comply with the 'EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria', the 'WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums' and the ASAB/ABS 'Guidelines for the Treatment of Animals in Behavioural Research and Teaching'.

Children studies were carried out with the written informed consent of the participants, and in accordance with all applicable laws and rules governing psychological research in Germany.

Data accessibility

Data available from the Dryad digital depository: http://datadryad.org/review?doi=doi:10.5061/dryad.8638h

Authors' contributions

A.S, S.D, J.C and M.T conceived the study. A.S conducted the research, A.S coded and analysed the data, A.S, S.D, J.C and M.T wrote and revised the paper.

Competing interests

Authors declare no competing interests.

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