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<https://orcid.org/0000-0003-4844-0673>, Wyman, Emily, Bullinger, Anke F., Herfurth, Katharina and Tomasello, Michael (2014) Coordination strategies of chimpanzees and human children in a Stag Hunt game. *Proceedings of the Royal Society B: Biological Sciences*, 281 (1796).

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Coordination Strategies of Chimpanzees and Human Children  
in a Stag Hunt Game

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### **Abstract**

Much of human cooperation takes place in mutualistic contexts in which the main challenge for individuals is how to coordinate decisions. In the current studies we compared the abilities of chimpanzees and young children to coordinate with a partner in two versions of a Stag Hunt game. When risks were low (the hare was of low value) and information was cheap (the partner's behaviour was readily observable) partners of both species were able to successfully coordinate on the higher value stag more than 90% of the time. In contrast, when the risks were raised and observing the partner was more difficult, the chimpanzees became less successful, whereas the children compensated, and so remained highly successful, by communicating more often and more specifically. This pattern of results is consistent with the hypothesis that humans evolved unique skills of coordination and communication in the context of especially risky coordination problems.

## Introduction

Human cooperation is most often studied in the framework of ‘social dilemmas’ such as the Prisoner’s Dilemma and the Public Goods Game in which the individual must pay a cost to cooperate e.g. [1];[2];[3]. But much of human cooperation is mutualistic and so better described by coordination games in which cooperation benefits all, and there is no temptation to defect [4]; [5]. A particularly realistic game is the Stag Hunt [6]. In this game two hunters may each safely pursue their own low-value prey (hare) or they may coordinate to pursue a higher value prey (stag). They both know that they need a partner to capture the stag so that pursuing it alone means losing both options. To solve this problem the hunters need to be able to coordinate their decisions and subsequent actions so that both either go for the stag (the risky, payoff dominant solution) or both go for hare (the safe, risk dominant solution). The most straightforward way for humans to coordinate on the stag, in particular, is to communicate with each other [7].

Humans’ closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), both engage in the group hunting of small mammals, mostly monkeys. The typical situation for chimpanzees (the species about whom much more is known) is that several males coordinate their behaviours to surround and capture the prey [8] [9]. In going for the monkey, individuals forsake time and energy that they could have spent foraging for other, lower value, food sources. Chimpanzee group hunting could thus be modelled as a Stag Hunt game. In two recent studies, Brosnan and colleagues gave pairs of primate conspecifics (capuchin monkeys, Rhesus macaques, chimpanzees, and human adults) a choice between two types of tokens (or symbols on a computer screen) in a Stag Hunt game: one represented the stag option and the other the hare option [10, 11]. In order to standardise procedures across species minimal instructions or training was provided, and so none of the participants were aware of the pay-off structure prior to testing. Under these conditions, all species struggled to coordinate on the high pay-off stag option (humans became successful when they were allowed to communicate with each other).

60           The results from these two studies suggest that coordination in the Stag Hunt  
61 game is challenging for all primates. However, chimpanzees have also demonstrated the  
62 ability to coordinate actions with a partner to solve cooperative tasks in a number of  
63 experimental settings e.g. [12-15]. This raises the question of whether their performance  
64 would be different in a Stag Hunt game in which, unlike the studies of Brosnan et al., the  
65 pay-off structure is clear to subjects. Bullinger et al. [16] presented pairs of chimpanzees  
66 with a Stag Hunt game using a foraging task. Subjects were given the choice between  
67 collecting a completely safe low value food (hare) individually or cooperating with a  
68 partner to acquire higher value food (stag). Importantly, they received training to ensure  
69 they understood that if they attempted to acquire the high value reward alone, they would  
70 not only fail but also lose access to the low value food. Therefore, to be maximally  
71 successful subjects needed to take a risk and coordinate their decisions with one another  
72 on the stag.

73           The chimpanzees were highly successful in coordinating to acquire the stag, doing  
74 so in 91% of trials. However, they did so with very little communication or visual  
75 monitoring of their partner (communication only occurred after a subject was at the stag  
76 exhorting their partner to join). Bullinger et al. [16] suggest that subjects were using a  
77 simple ‘leader-follower’ strategy. Once one individual takes the risk and goes for stag, the  
78 best decision for the second individual is to follow so that they are successful on the stag.  
79 This strategy is employed by a wide range of species encountering coordination problems.  
80 A common example is deciding on travel direction for species that travel in large groups  
81 (e.g. pigeons) in which case some individuals (leaders) have disproportionate influences  
82 on the chosen direction according to factors such as their motivation or knowledge (see  
83 [17] for a review). While the reason for the follower to abandon the hare is clear, the  
84 mechanism of leadership in the Stag Hunt game is more difficult to discern, since leaders  
85 would seem to be taking on all the risk. Theorists such as Schelling [18] and Lewis [19]  
86 have argued that the solution is mutual knowledge. If both hunters know that each of them  
87 would prefer the stag and that they need a partner to succeed (i.e. they both know that they

88 both understand the game and pay-off structure) then, once mutual knowledge of the  
89 presence of the stag is established both hunters should abandon their hare in pursuit of the  
90 stag. This can be accomplished by communication prior to decision-making.

91         Our aim was to directly compare coordination strategies used by chimpanzees and  
92 humans in solving an evolutionary relevant coordination problem (the Stag Hunt). In  
93 Experiment 1 we presented pairs of 4-year-old children (who conceivably have less  
94 experience and less conventionalised solutions to such problems than adults would) with  
95 the Stag Hunt game of Bullinger et al. [16]. In a previous study, using a different Stag  
96 Hunt game, 4 year olds had to decide between hare and stag without knowledge of their  
97 partner's decision and without any verbal or gestural communication. However, in one  
98 condition the partner (as adult experimenter) made eye contact with and smiled at the child  
99 prior to the decision being made, and this minimal communication was enough to increase  
100 cooperation, presumably because it established mutual knowledge about the arrival of the  
101 stag [20]. We were interested in whether 4 year old children would solve our version of  
102 the Stag Hunt problem by actively establishing mutual knowledge to coordinate their  
103 decisions. If this were the case we would expect that they would do so by communicating  
104 with their partner prior to going for the stag. Alternatively, it may be that, in this low risk  
105 situation, children would employ a leader-follower strategy, similar to chimpanzees.

106         In Experiments 2a and 2b we investigated how pairs of chimpanzees and pairs of  
107 children, respectively, coordinated in a higher risk Stag Hunt game. Risk was increased in  
108 two ways: (1) by increasing the value of the hare in relation to the stag, so that there were  
109 greater losses incurred through a failed attempt to cooperate; and (2) by reducing the  
110 auditory and visual information participants have about their partner's decision, thus  
111 rendering the leader-follower strategy ineffective. In this high risk Stag Hunt we would  
112 expect individuals of both species to mitigate the risk through increases in communication  
113 and visual monitoring before going for the stag. If they are unable to do so, then we would  
114 expect them to be less likely to take the risk of going for the stag.

115

### 116 **Experiment 1: Low Risk Stag Hunt with Children**

117 In this experiment, pairs of 4 year old children participated in a low risk Stag Hunt  
118 game based on Bullinger et al. [16]. During the game, children began by collecting a low  
119 value food reward (hare) alone. While they were doing this a high value food reward  
120 (stag) appeared, which they knew required cooperation with a partner to acquire. Children  
121 therefore had to decide either to continue collecting their low-value reward, or to try to  
122 obtain the high value option. The latter choice entailed the risk that if their partner did not  
123 also try to cooperate, they would then lose both rewards. We recorded children's decisions  
124 and their communication, with a particular focus on the use of communication prior to  
125 making a decision.

126

### 127 **Material and Methods**

#### 128 *Subjects*

129 Forty children (20 girls, mean age: 50 months, range 45-56 months) were included  
130 in the final sample. An additional seven children took part, but were excluded from the  
131 analysis either because they failed pre-tests (see below,  $N = 3$ ), or because their motivation  
132 wavered during testing ( $N = 4$ ). Children were paired into 20 same-sex dyads, which  
133 belonged to the same kindergarten group, or were known to play together. All testing took  
134 place at kindergartens.

135

#### 136 *Materials*

137 **Hare boxes.** Each child was assigned their own hare box (denoted by colour and  
138 location), containing low value food (sweet rice puffs) which they could retrieve alone, but  
139 that required some time to do so. The front face of the box could be accessed by opening a  
140 transparent door, behind which were six tubes (6cm deep) containing the hare reward. An  
141 elastic hinge ensured that the door would close automatically when let go, and once the  
142 door closed a magnet held it shut so children were unable to re-open it until it was re-set  
143 by the experimenter.

144           **Stag box.** The stag box contained the high value food (gummibears) and required  
145 both children to work together to acquire the reward. The apparatus consisted of a large  
146 wooden box (approx. 100x70x30cm) containing a sliding tray that could be set to three  
147 positions (operated surreptitiously by E3, who pretended to read). When released to the  
148 mid-way position the contents of the tray could be seen by the children. In this position, a  
149 loud ticker sounded for 15 seconds, during which children could pull simultaneously on  
150 ropes at either side of the box to release the tray to the final position and retrieve one  
151 reward each. A bell sounded at the end of the 15 seconds, if the dyad had not retrieved the  
152 rewards, and the tray was fully retracted to the start position. The hare and stag boxes were  
153 positioned at opposite ends of the testing room (approx. 300cm apart, see Figure 1).

154           **Barrier.** An opaque curtain (150x150cm) was positioned between the hare boxes  
155 for barrier test trials. This barrier meant that children could not see each other while they  
156 were both at hare, although they could look around the barrier if they repositioned  
157 themselves, as well as see their partner if one was waiting at the stag box already.

158

#### 159 *Design and Procedure*

160           Dyads participated in two conditions (within subjects). In *no-barrier trials*,  
161 partners were able to see each other throughout the trial. In *barrier trials*, visual  
162 monitoring was restricted by the barrier so that partners could not see each other whilst  
163 were both at hare (unless they repositioned themselves). Each dyad received one block of  
164 3 no-barrier trials and one block of 3 barrier trials (with order counterbalanced across  
165 dyads).

166           **Training and pre-tests.** Children were trained individually by the first  
167 experimenter (E1) so that they understood the apparatuses and the relationships between  
168 them. They never experienced the full test set-up prior to test trials with their partner (for  
169 full details of the training see ESM). Each child then received two types of pre-test. The  
170 *social pre-test* trials ensured that children were motivated to coordinate when a willing  
171 partner was available, and children could see this (i.e. they preferred the stag over the hare



172 reward). The child started collecting the hare and E1 waited beside the stag box, so that  
173 when the stag appeared, the child had to decide whether to continue collecting hare, or  
174 abandon it and attempt to get to the stag together with E1. To pass the social pre-test  
175 children were required to go for the stag. The *non-social pre-test* was designed to ensure  
176 that children did not attempt to retrieve the stag payoff indiscriminately, and that they  
177 valued the hare enough to collect it when the stag was unavailable. Once the child had  
178 begun to collect the hare, E1 made an excuse to leave the room. The stag then appeared,  
179 and in order to pass the children had to stay at the hare. Pre-tests were presented in a block  
180 of 6 alternating trials, which was repeated if they did not pass the first block. To pass,  
181 children needed to respond correctly in at least 2 out of 3 trials for each trial type.

182       **Test trials.** The dyad now played together for the first time. Each was guided to  
183 her respective hare box by E1, who then left the room. The trials began when the children  
184 had opened the door to their hare boxes and the stag appeared (accompanied by an  
185 exclamation of “Oh, wow” by E3 and the onset of the ticking sound). At this point the  
186 children had 15 seconds to decide whether to stay on their hares or try to retrieve the stag.  
187 The trial ended once the stag had been acquired, or, if unsuccessful, until the stag was  
188 removed. If they were still collecting hare at the end of the trial the children were allowed  
189 to continue until they had emptied their hare box. Both children left the room with E1  
190 while E3 re-set the apparatuses for the next trial.

191

### 192 *Coding*

193       Based on the coding in Bullinger et al. (2011), we coded several aspects of participants’  
194 behaviour in order to determine a) how likely individuals were to decide to go for the stag;  
195 b) how well these decisions were coordinated with their partner’s decisions; and c) the role  
196 of communication and visual monitoring of partners in successful coordination. All testing  
197 sessions were video recorded and the following variables were coded from the tapes. We  
198 coded:

199       **Decisions to leave hare.** For each individual on every trial we coded whether or not

200 individuals left their hare to go for stag during the trial.

201       **Coordination success.** Trials were coded as successful coordination when both  
202 partners left hare to go for stag, as a measure of whether dyads coordinated their decisions.

203       **Communication.** Each individual on every trial was given a communication score (1  
204 or 0) for the two phases of a trial a) while still at hare, and b) after leaving hare, to denote  
205 whether or not they communicated during each of these phases. Communication was  
206 defined as: verbal communication related to the objects, actions, or players in the game,  
207 directed towards their partner (as indicated by either looking towards them while talking,  
208 addressing them directly, or otherwise indicated by the context of the utterance).

209       **Visual monitoring.** Each individual on each trial was given a visual monitoring score  
210 (1 or 0) for each of the two phases of a test trial a) while still at hare, and b) after leaving  
211 hare, to denote whether they looked in the direction of their partner's face during these  
212 phases.

213       **Reliability.** An independent observer who was blind to the hypotheses of the study  
214 coded a random sample of 20% of children (4 pairs) for reliability. As some of the  
215 behaviours coded occurred infrequently we used Prevalence-Adjusted Bias-Adjusted  
216 Kappa (PABAK, [21]) to determine reliability (this was the measure used for all  
217 subsequent calculations of inter-rater reliability). Agreement on whether dyads acquired  
218 the stag was 100% ( $K = 1.00$ ); whether individuals went for stag 99% ( $K = 0.96$ );  
219 communication at hare 96% ( $K = 0.91$ ); communication after leaving hare 88% ( $K = 0.71$ );  
220 monitoring at hare was 90% ( $K = 0.77$ ); monitoring after leaving hare was 85% ( $K = 0.62$ ).

221

222

## Results

223       All of the following analyses (including analysis for Experiments 2a and 2b) used  
224 Generalized Linear Mixed Models (GLMM; [22]), with significant set at  $p < 0.05$ . See  
225 ESM for details of model construction and results.

226       Children overwhelmingly decided to go for stag, with no effect of condition (no-  
227 barrier condition: 96.7% of decisions; barrier condition: 98.3%;  $\chi^2 = 3.284$ ,  $df = 4$ ,  $p = 0.51$ ,

228  $N=240$ ). This corresponded to high levels of successful coordination in both conditions  
229 (no-barrier condition: 95.0% trials; barrier condition: 96.7%;  $\chi^2=2.27$ ,  $df=3$ ,  $p=0.52$ ,  
230  $N=120$ ).

231 These high levels of coordination were achieved with very little verbal  
232 communication prior to making their decisions (i.e. before leaving hare), with no effect of  
233 condition or order (no-barrier condition: 7.5% trials; barrier condition: 4.2%;  $\chi^2=5.81$ ,  
234  $df=7$ ,  $p=0.56$ ,  $N=240$ ). Most verbal communication occurred after leaving hare, when  
235 children were running for the stag or waiting for their partners to join them, and also did  
236 not differ between conditions (no-barrier condition: 32.8% trials; barrier condition: 38.1%;  
237  $\chi^2=4.26$ ,  $df=3$ ,  $p=0.23$ ,  $N=234$ ).

238 Visual monitoring of the partner showed a pattern similar to that of verbal  
239 communication. There was some monitoring while individuals were still at hare, with no  
240 effect of condition (no-barrier condition: 13.3% trials; barrier condition: 11.7%;  $\chi^2=2.63$ ,  
241  $df=3$ ,  $p=0.45$ ,  $N=240$ ); but there was more after leaving the hare, again with no effect of  
242 condition (no-barrier condition: 72.4% trials; barrier condition: 66.9%;  $\chi^2=6.821$ ,  $df=4$ ,  
243  $p=0.146$ ,  $N=234$ ).

244

## 245 Discussion

246 Four year-old children achieved high rates of successful coordination, directly  
247 comparable to those of the chimpanzees in Bullinger et al. [16], with coordination in both  
248 species at or above 90% of the trials. Communication and monitoring also showed a  
249 largely similar pattern between species: like the chimpanzees, the children in our study  
250 produced little pre-decision communication and monitoring, especially compared to their  
251 post-decision production. Thus, under these particular conditions, the coordination of  
252 young children - and the strategies they used to achieve this - appears quite similar to that  
253 seen in chimpanzees under similar conditions.

254 These results are consistent with children also using a 'leader-follower strategy'.  
255 They could use this strategy in the current experimental set-up because (i) leaders could

256 rely on followers hearing their hare door closing and see them once they reached the stag,  
257 and (ii) the hare was of such low value that leaving it was no real risk.

258           Alternatively, the value of the hare was not high enough for its loss in a failed  
259 coordination attempt to present a real cost. However, children were motivated to collect  
260 the hare when there was no partner available, indicating that the rewards were of some  
261 value to them. A richer alternative is that children assumed mutual knowledge of the stag.  
262 The stag was accompanied by auditory signals, the salience of which might have been  
263 enough for children to not only assume that their partner was also aware of the stag but  
264 was making the same assumptions of them. Thus, if the cues were removed, we would  
265 expect the children to use other means to actively establish mutual knowledge of the stag.

266           To test these potential explanations Experiments 2a and 2b presented chimpanzees  
267 and children with a modified version of the Stag Hunt game used in Experiment 1 and  
268 Bullinger et al. (2011). We increased the value of the hare, which increased the risk of  
269 pursuing the stag. We also eliminated auditory cues associated with the stag and visual  
270 cues (by extending the barrier all the way up to the stag), which meant that the leader-  
271 follower strategy was no longer viable (without something like blind faith). Under these  
272 conditions, if either species attempted to continue using a leader-follower strategy, we  
273 would expect them mostly to fail – unless they compensated with some pre-decision  
274 communication.

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## 277           **Experiment 2a: High Risk Stag Hunt with Chimpanzees**

278

### 279                           **Material and Methods**

#### 280           *Subjects*

281           Ten chimpanzees (*Pan troglodytes*) (eight of which took part in Bullinger et al.);  
282 four males and six females were included in the final sample (mean age=20.1 years, range:  
283 7 -35 years, see ESM for full subject table). Three additional subjects did not complete the

284 training or pre-tests and thus did not take part in the test trials. Subjects could choose to  
285 stop participating at any time. They were never food deprived and water was available ad  
286 libitum throughout testing. Animal husbandry and research comply with the EAZA  
287 Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria  
288 and the WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and  
289 Aquarium.

290

### 291 *Materials*

292 The materials were adapted from Bullinger et al. [16] and had the same properties  
293 as in Experiment 1, with minor exceptions. First, the hare boxes contained a drinking  
294 bottle with a weak mixture of fruit syrup and water. Secondly, the stag apparatus consisted  
295 of a platform and rope spanning a booth between two cages. When two individuals pulled  
296 simultaneously on ends of the rope, the platform lifted and the stag rewards (6cm of  
297 banana for each) became accessible. In Bullinger et al. sounds cued the arrival of the stag  
298 and the time it was available; these cues were removed and a sound that mimicked the  
299 closing of hare box door played throughout pre-tests and test trials. Thus this cue could not  
300 be used as a reliable indicator of their partner's decision. Finally, the barrier (several  
301 plastic panels) was positioned so that dyads could see each other only when they were  
302 both at the stag apparatus.

303 Subjects were tested in two adjacent cages (8.05m<sup>2</sup> and 6.75 m<sup>2</sup>) separated by wire  
304 mesh. Each had a hare box in their own cage and the stag apparatus was situated between  
305 the two cages, at the opposite end to the hares (see Figure 2).

306

### 307 *Design and Procedure*

308 Subjects were divided into two groups of five; balanced for sex and age and to  
309 maximise the number of dyads that were not previously paired together in Bullinger et al.  
310 (see subject table in ESM for details). Individuals were paired with all other members of  
311 the group (10 pairs per group) in a within subjects design with two conditions. In the *no-*

312 *barrier condition* subjects were able to visually monitor their partner throughout the trial.  
313 In the *barrier condition* the barrier was placed such that subjects had no visual access to  
314 their partners (and thus their partner's decisions) until both were already at stag. Each pair  
315 had 12 trials per condition, conducted across 2-3 testing days. Each subject completed one  
316 condition with all of their partners before moving on to the next condition (order  
317 counterbalanced across groups).

318 **Training and pre-tests.** As in Experiment 1 and Bullinger et al., subjects  
319 completed several training phases and pre-tests (see ESM for full details of all training  
320 phases and attainment). After training, subjects were also given *social* and *non-social pre-*  
321 *tests* (though in this case E1 was replaced by a conspecific stooge) before each new testing  
322 session. A set of pre-tests consisted of one social and one non-social pre-test trial. Subjects  
323 could only participate in test trials if they responded correctly to both trial types in a set. If  
324 they did so in either the first or the second set, subjects could go on to test. If not, a third  
325 set was presented as training and testing was discontinued for that day. Subjects were  
326 given another opportunity to pass pre-test in the following session.

327 **Test trials.** Test trials were the first time subjects were paired together. The trial  
328 started when both subjects opened their own hare boxes, and the stag reward was placed  
329 on the stag apparatus. The trial ended when the stag was retrieved. If the stag was not  
330 retrieved within 20 seconds, E1 pulled a rope from outside the room to cause the stag to  
331 fall out of reach of the subjects and end the trial. If a subject was still at hare at this point  
332 they were allowed to finish the contents.

333

#### 334 *Coding*

335 The coding scheme was identical to that used in Exp. 1 with the following  
336 modifications: communication was defined as gestural attention-getters (e.g. clapping) and  
337 vocalisations. Visual monitoring includes 'checking back' from the hare to either the stag,  
338 or their partner's cage.

339 **Reliability.** A second coder, unaware of the hypotheses coded one randomly

340 selected trial per condition per dyad (8.33% of total trials). Agreement on whether dyads  
341 acquired the stag, and whether they left hare before the stag disappeared was 100% ( $K$   
342 =1.00); checking back at hare was 91% ( $K$  =0.81); there was also 100% agreement that  
343 there was no communication at hare ( $K$  =1.00), and 98% ( $K$  =0.97) on communication  
344 after leaving hare.

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### Results

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We directly compared the behaviour of the chimpanzees in Experiment 2a with  
their behaviour in Bullinger et al. ([16], hereafter the low risk game). Our main aims were  
to compare how likely individuals were to take the risk to go for stag on a given trial; how  
well dyads coordinated their decisions; and the role of communication and visual  
monitoring in these interactions.

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Subjects responded to the game modifications in the high risk game by being less  
likely to leave hare than in the low risk game (low risk: 94.3% of decisions, high risk:  
69%), though this reduction was greatest in the barrier condition, when this was  
experienced after the no-barrier condition (3-way interaction between game, condition and  
condition order;  $\chi^2=5.79$ ,  $df=1$ ,  $p=0.02$ ,  $N=1536$ ). The reduced likelihood of going for stag  
in the high risk game was reflected in a reduction in successful coordination (low risk:  
91% both leaving hare, high risk: 53%; see Figure 3; 3-way interaction between game,  
condition and condition order  $\chi^2=6.63$ ,  $df=1$ ,  $p=0.01$ ,  $N=768$ ). Additionally, leaving hare  
and coordination were both more likely in later trials (leaving hare:  $\chi^2=8.02$ ,  $df=1$ ,  $p<0.01$ ,  
 $N=1536$ ; coordination:  $\chi^2=5.84$ ,  $df=1$ ,  $p=0.02$ ,  $N=768$ ).

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The reduction in successful coordination on stag in the high risk game could have  
been due to both individuals coordinating on hare, the safe, risk dominant option.  
However, even when we consider coordination failures to be trials in which one individual  
stayed at hare while their partner went for the stag (and therefore successful coordination  
to include trials in which both individuals stayed at hare or both went for stag),

368 coordination failures were generally more likely in the high risk game (low risk game:  
369 6.6% trials, high risk game: 31.7%; except in the no-barrier trials for the no-barrier first  
370 group, they were equally likely to fail to coordinate in the low and high risk games; 3-way  
371 interaction between game, condition and order:  $\chi^2=5.82$ ,  $df=1$ ,  $p=0.02$ ,  $N=768$ ). This  
372 supports our conclusion that pairs were worse at coordinating decisions in high risk  
373 contexts.

374         The overall pattern of communication did not differ between the low and high risk  
375 games. That is, there was no pre-decision communication in either game. However, in  
376 both games subjects did occasionally communicate while they were at stag waiting for  
377 their partner (low risk: on 7.9% of trials the leader communicated; high risk: 11.5%; no  
378 significant difference between games; see Figure 4); with leaders being more likely to  
379 communicate the longer they waited ( $\chi^2=34.96$ ,  $df=1$ ,  $p<0.01$ ,  $N=686$ ).

380         While subjects did not communicate at hare, they did visually monitor the situation  
381 ('check back' from their hare to either the stag or their partner's cage). They did so more  
382 often in the high risk game (31.7% of trials) than low risk game (5.7% of trials;  $\chi^2=4.79$ ,  
383  $df=1$ ,  $p<0.01$ ,  $N=1536$ ). However, subjects were no more likely to check back when they  
384 could get information about their partner (no-barrier condition) as when only information  
385 about the presence of the stag was available (barrier condition), suggesting that increased  
386 checking may not have been motivated by coordination with a partner but monitoring the  
387 presence of the stag.

388

389

### Discussion

390         These results suggest that chimpanzees did not adapt their coordination strategy to  
391 the new situation. As in the Bullinger et al. study, communication was rare overall (at the  
392 highest: 11% trials in the high risk game); did not differ in frequency between the two risk  
393 contexts; and never occurred pre-decision. This indicates that chimpanzees' use of  
394 communication for coordination purposes may be fairly inflexible and restricted to  
395 attempting to get the attention of their partners post-decision, once they have already made



396 their decision for the stag and time is running out. Bullinger et al. argued that a leader-  
397 follower strategy could best account for their findings. This account predicted  
398 coordination failure in the barrier condition of the high risk game. This was supported to a  
399 certain extent: a reduction in the barrier condition for those individuals that started with  
400 the no-barrier condition suggests that at least they may have been using a leader-follower  
401 strategy. Alternatively, subjects could have based their decisions on the predicted  
402 likelihood of a partner to go for stag (e.g. by projecting their own preferences as in [23])  
403 and thus the likelihood of success. This is consistent with sensitivity to risk in group  
404 hunting frequency observed in the wild: males are more likely to hunt during times of fruit  
405 abundance (reduced loss in unsuccessful attempts; [24-26]).

406 In sum, rather than mediating risk through pre-decision communication,  
407 chimpanzees responded by adjusting their likelihood to cooperate. In Experiment 2b we  
408 examine how young children respond to our high-risk Stag Hunt game.

409

## 410 **Experiment 2b: High Risk Stag Hunt with Children**

411

### 412 **Material and Methods**

#### 413 *Subjects*

414 Forty-eight children (24 girls, mean age: 54 months, range 46-58 months) were  
415 included in the analysis. Ten children were not tested because they either failed the pre-  
416 tests or were able to reach both sides of the stag-ropes. Children were paired into 24 same-  
417 sex dyads. All children were recruited from a database of middle-class children and  
418 brought by their parents to an institute for testing.

419

#### 420 *Materials*

421 The apparatuses from the low risk experiment were re-used with some alterations.  
422 The value of the hare was increased so that the hare boxes now contained larger chocolate  
423 cereal balls rather than rice puffs. In order to remove the sound cues associated with the

424 arrival of the stag the tray in the stag box started at the midway point and the gummibears  
425 were now inside red plastic balls, released by E3 via tubes at the back of the box. Also, the  
426 auditory cue indicating the approaching removal of the stag was removed. The length of  
427 the barrier was extended so that there was no visual access to their partner until both were  
428 at stag. Finally, music was played during pre-test and test trials to disguise the sound of  
429 the stag arriving, the closing of the hare box doors and children's movements.

430

#### 431 *Procedure*

432 The design and procedure was the same as the low risk game with the following  
433 modifications. First, some of the training trials were replaced with demonstrations by  
434 experimenters to reduce the number of trials. The pre-test structure was adjusted to more  
435 closely follow the procedure for the chimpanzees: children had blocks of up to three social  
436 or non-social practice pre-test trials before the actual pre-tests and were then presented  
437 with two sets of one social and one non-social pre-test. If they responded correctly to both  
438 trial types within either set they could go on to test. However, if children did not pass, they  
439 were given one more set of "instructed" pre-tests in which E1 indicated what the best  
440 solution to the trial was. In the social pre-test: "The gummibears are here. Come and pull  
441 with me." In the non-social pre-test: "I have to answer my phone. Stay at the chocopuffs  
442 until I get back." If they responded correctly to these trials they moved on to test (see ESM  
443 for full details).

444

#### 445 *Coding*

446 Coding was identical to Experiment 1, except that communication was divided into  
447 two categories: (1) **Attention-getters**: verbalisations that get their partner's attention but do  
448 not refer to objects or actions in the game (e.g. calling their partner's name); and (2)  
449 **Content**: verbalisations that referred to objects in the game (e.g. red balls, gummibears,  
450 chocopops, rope), or to actions in the game (e.g. pulling, running, looking for  
451 gummibears). Content communication was further subdivided into: *imperatives*

452 (instructions for their partner to perform an action related to the game, e.g. “come, pull  
453 with me”); *informatives* (reports to their partner about objects in the game or players’  
454 actions in the game, e.g. “the balls are there”). Each occurrence of communication was  
455 coded for the type of communication hierarchically: content communication and attention-  
456 getters in the same phase was coded as content. Within the content category imperatives  
457 were prioritised over informatives.

458 **Reliability.** A second coder, unaware of the hypotheses coded one randomly  
459 selected trial per condition per dyad (33% of total trials). Agreement on whether dyads  
460 acquired the stag was 100% ( $K = 1.00$ ); whether individuals went for stag 97% ( $K = 0.94$ );  
461 communication at hare 94% ( $K = 0.85$ ); communication after leaving hare 92% ( $K = 0.81$ );  
462 monitoring at hare was 95% ( $K = 0.89$ ); monitoring after leaving hare was 89% ( $K = 0.74$ );  
463 type of communication 91% ( $K = 0.84$ ).

464

465

466

## Results

467 As with the chimpanzees, we directly compared the behaviour of children in the  
468 low risk and high risk games (Exp. 1 and 2a).

469 Children continued to leave hare at a high rate in the high risk game, despite the  
470 changes in risk. Individuals left hare on 92.0 % trials in the no-barrier condition (low risk:  
471 96.7%, high risk: 88.2%) and 92.8% trials in the barrier condition (low risk: 98.3%, high  
472 risk: 88.2%), with no effects of game, condition or order ( $\chi^2 = 14.05$ ,  $df = 8$ ,  $p = 0.08$ ,  $N = 528$ ).  
473 Again, this resulted in high levels of coordination: 89.4% trials in the no-barrier condition  
474 (low risk: 95.0%, high risk: 84.7%, see Figure 1) and 90.2% trials in the barrier condition  
475 (low risk: 96.7%, high risk: 84.7%;  $\chi^2 = 12.87$ ,  $df = 8$ ,  $p = 0.12$ ,  $N = 264$ ).

476 Children responded to the increased risk of coordination failure by increasing their  
477 verbal communication prior to leaving the hare in the high risk game (low risk: 5.8%  
478 individual trials; high risk: 26%;  $\chi^2 = 24.70$ ,  $df = 1$ ,  $p < 0.01$ ,  $N = 528$ ). Strikingly, if we  
479 consider communication in terms of whether at least one of the partners communicated

480 while both were still at hare (i.e. trials in which partners communicated before either of  
481 them had made their decisions), communication occurred in 47.9% of trials in the high  
482 risk game compared to 4.2% of trials in the low risk game (main effect of game:  
483  $\chi^2=60.50$ ,  $df=1$ ,  $p<.01$ ,  $N=264$ , no effect of condition or order; see Figure 4). In the high  
484 risk game most pairs (87.5%) communicated prior to leaving hare on at least one out of six  
485 trials, compared to 15.0% in the low risk game.

486 Children were most likely to communicate after leaving the hare in the riskiest  
487 trials: barrier trials in the high risk game. However, this was specific to when the barrier  
488 condition came first such that the pairs had little experience cooperating with each other  
489 (3-way-interaction between game, condition and order:  $\chi^2=6.74$ ,  $df=1$ ,  $p=0.01$ ,  $N=488$ ).

490 Analysis of the type of verbal communication indicates how children were using it  
491 to reduce risk. Content communication was generally more prevalent than attention-getters  
492 (at hare: 80.7% trials with content communication, after leaving hare: 89.4%) and did not  
493 differ between high and low risk games, phase or condition ( $\chi^2=12.90$ ,  $df=8$ ,  $p=0.12$ ,  
494  $N=271$ ). However, when we looked more closely at the type of content communication we  
495 found that informatives (typically “the balls are there!”) were employed most frequently in  
496 pre-decision communication, particularly in the high risk game (68.7% of trials with  
497 content communication were informatives; in the low risk game only eight trials contained  
498 content communication and 50% of those were informatives. In contrast, imperatives  
499 (such as “Hurry up!”) were generally used after leaving hare in both games (low risk:  
500 90.0% of trials with content communication after leaving hare were imperatives, and high  
501 risk: 68%; main effect of phase  $\chi^2=29.96$ ,  $df=1$ ,  $p<0.01$ ,  $N=235$ ). Children were also more  
502 likely to use informatives in the high risk game and the barrier condition, consistent with  
503 the hypothesis that they are using informatives to reduce risk when coordination is more  
504 challenging (main effects of game:  $\chi^2=8.02$ ,  $df=1$ ,  $p<0.01$  and condition:  $\chi^2=5.26$ ,  $df=1$ ,  
505  $p=0.02$ ).

506 There was no possibility of visually monitoring a partner in the barrier condition in  
507 the high risk game while at hare, and reduced possibility after leaving hare due to the

508 extended barrier. Thus, we only compared monitoring in the no-barrier condition. The  
509 pattern of pre-decision visual monitoring of their partners reflected that found for verbal  
510 communication: increasing in the high risk game relative to the low risk game (low risk:  
511 13.3% trials, high risk: 29.1%; ( $\chi^2=6.52$ ,  $df=1$ ,  $p=0.01$ ,  $N=264$ ) and also decreasing across  
512 trials ( $\chi^2=7.33$ ,  $df=1$ ,  $p=0.01$ ). There was a decrease in post-decision visual monitoring in  
513 the high risk game (perhaps because it was unnecessary in addition to the verbal  
514 communication and pre-decision monitoring; low risk: 72.4% trials, high risk: 38.6%  
515 trials;  $\chi^2=21.69$ ,  $df=1$ ,  $p<0.01$ ,  $N=243$ ).

516

517

### Discussion

518 Increasing the difficulty of coordination in the high risk game had no effect on  
519 children's ability to achieve successful coordination, with children coordinating in more  
520 than 90% of trials in both the high and low risk versions. What differed was how they  
521 achieved coordination: in high risk conditions they increased their frequency of  
522 communication and visual monitoring before taking the risk of going for the stag, with  
523 verbal communication replacing much visual monitoring. The verbal communication was  
524 appropriate to the situation, as children's pre-decision communication was predominantly  
525 informative (e.g. "The gummibears are here.") – ensuring mutual knowledge of the stag's  
526 presence - whilst their post-decision communication was predominantly imperative (e.g.  
527 "Quick!"). Together these differences suggest a coordination strategy different from the  
528 cognitively simpler strategies such as the leader-follower: actively establishing mutual  
529 knowledge between partners in order to mediate the risk associated with coordination.

530

531

### General Discussion

532 By presenting children and chimpanzees with a comparative foraging task we are  
533 able to clearly demonstrate a divergence in the mechanisms underlying mutualistic  
534 cooperation in humans and chimpanzees. Under conditions of low risk chimpanzees and  
535 children were both highly successful with minimal communication. Under conditions of

536 high risk, however, the two species used different strategies. When chimpanzees were  
537 confronted with a more challenging Stag Hunt scenario in which the potential losses were  
538 higher and there were less cues to the appearance of the stag and a partner's decision, they  
539 were much less successful at coordinating, suggesting that there are limits to their  
540 coordination strategy. Individuals occasionally communicated while waiting for a partner  
541 at stag, but not prior to leaving hare. In contrast, children's coordination success remained  
542 high in the high risk game, and there was a marked increase in communication preceding  
543 their decision to leave hare. Children adjusted their strategy by using communication to  
544 establish mutual knowledge of the presence of the stag (e.g. by informing their partner  
545 "the balls are here!") and thus reducing the risk associated with leaving the hare to  
546 coordinate.

547 In comparison to Brosnan et al. [10, 11] we found humans, in this case 4 year olds,  
548 to be highly effective coordinators. This difference may be in large part due to differences  
549 in methodology. As the main aims of the current paper and Bullinger et al. [16] were to  
550 examine if and how the two species coordinated their decisions in the context of a Stag  
551 Hunt game, it was essential that the participants were aware of the contingencies of the  
552 game, particularly that their rewards were dependent upon the decision of their partner. In  
553 Brosnan et al. participants were not informed of the game structure, nor could it be  
554 inferred from the physical affordances of the task, as in the present study. Therefore it is  
555 unclear to what extent the level of coordination in the Brosnan et al. studies is due to a  
556 lack of understanding of the pay-off structure.

557 Our results are consistent with what is already understood about children's abilities  
558 to coordinate their actions: from 18 months can coordinate very simple actions in a  
559 cooperative activity with an adult or peer [27] [28]. Here we have shown that 4 year-olds  
560 are able to coordinate decisions, as well as actions, to cooperate successfully with a peer in  
561 a more complex coordination problem.

562 We have also extended findings on the role of communication in children's  
563 coordination. In Wyman et al. [20] non-verbal pre-decision communication from an adult

564 experimenter (eye contact) influenced their decision making in the Stag Hunt game. We  
565 show that by 4 years children are able to initiate appropriate communication to solve a  
566 coordination problem with a peer. Similarly, Warneken et al. [29] found that  
567 communication predicted correct choices in a collaborative planning task with 3 and 5  
568 year olds.

569         Several experimental studies have shown that dyads of chimpanzees can  
570 coordinate their actions to acquire a reward (e.g. [12, 14, 30]). In addition to this, the  
571 results from Bullinger et al. [16] and the current study show that they can successfully  
572 coordinate their decisions to forsake a safe, low value reward to acquire a higher value  
573 reward, although this is more limited in the high risk game. The pattern of communication  
574 seen here also reflects that of previous findings: when required to coordinate their actions  
575 to cooperate with conspecifics little communication is reported, even when the task  
576 demanded negotiation of conflicting preferences [15]. There is also little evidence from  
577 the wild that chimpanzees coordinate their decisions prior to the start of a hunt, though  
578 there is some recent evidence that chimpanzees vocalize to coordinate joint travel [31].  
579 Although these calls ('travel hoos') did occur prior to the onset of travel movement, these  
580 calls could be interpreted as requests for travel companions by individuals who have  
581 already decided to travel (since callers continue to travel even if the recruitment has been  
582 unsuccessful) and thus, as more similar to the post-decision attention-getters, rather than  
583 the pre-decision communication exhibited by the children.

584         The Interdependence Hypothesis of the evolution of human cooperation suggests  
585 that humans have unique cognitive skills for mutualistic cooperation, an important set of  
586 which concern cooperative communication, and further that the selective context for  
587 uniquely human skills of cooperation was social coordination in something like Stag Hunt  
588 foraging contexts [5, 32]. In the current studies these unique abilities did not manifest  
589 themselves in the low risk game: both chimpanzees and children were successful  
590 coordinators. However, when the costs of coordination failure increased and the  
591 information available about a partner's decision were reduced, the strategies available to

592 chimpanzees limited their ability to coordinate; but children simply began communicating  
593 to the partner to establish mutual knowledge. This pattern of results is thus consistent with  
594 the hypothesis that humans evolved unique skills of coordination and communication in  
595 the context of especially risky coordination problems.

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599

### Acknowledgements

600 We thank R.Piesek and M.Ulrich for building the apparatuses; J.Jurkat, E. Rossi,  
601 I.de Gaillande-Mustoe, E.Klonowski and the students at the WKPRC for help with  
602 recruiting children and data collection; T.Malmovoelgyi, S.Hunger and S.Peoples for  
603 reliability coding; and R.Mundry for statistical advice. Thank you to N.Raihani and two  
604 anonymous reviewers for their helpful comments on a previous draft. Finally we thank the  
605 kindergartens, parents, children, chimpanzees and the animal caretakers for their  
606 cooperation.

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- 693

694 *Figure 1:* The set-up for the children (Exp. 1 and 2b). Both children start at their hare  
695 boxes (top left and right), and then stag reward (red balls) becomes available. The barrier  
696 (between the two children) is present only in the barrier condition.

697

698 *Figure 2:* Test trial set-up for the chimpanzees (Exp. 2a) in the no-barrier condition. Each  
699 individual has their own hare box (top left and right). The stag reward is then placed  
700 between the two cages.

701

702 *Figure 3*: The mean likelihood to successfully coordinate for chimpanzees (left) and  
703 children (right) in the low and high risk games with 95% confidence intervals.

704

705 *Figure 4:* The mean likelihood for communicate to occur before either partner left hare  
706 (upper panels), and after at least one partner has gone for the stag (lower panels) for  
707 chimpanzees (left panels) and children (right panels) in the low and high risk games (with  
708 95% confidence intervals).

709