

1 **How chimpanzees decide in the face of social and nonsocial uncertainty**

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13 Accepted for publication at *Animal Behaviour* in October 2020

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25

Abstract

26 Uncertainty can arise in interactions with both social partners and nonliving objects.
27 Previous research has shown that humans display higher aversion to uncertainty arising
28 from social interactions than to uncertainty caused by interactions with objects such as
29 gambling machines, and that this difference may be mediated by betrayal aversion. We
30 investigated whether chimpanzees (*Pan troglodytes*) differentiate between social and
31 nonsocial forms of uncertainty. Subjects participated in two studies, each involving a social
32 and a nonsocial condition. In both studies, choosing the safe option resulted in immediate
33 access to low-value food. Choosing the uncertain option could result in access to high-
34 value food, but only if the partner (social condition) or a machine (nonsocial condition)
35 proved trustworthy. In Study 1, where chimpanzees had no prior information on
36 reciprocation rates (i.e., decided under uncertainty), chimpanzees were less likely to choose
37 the uncertain option when they interacted with a partner than with a machine. When they
38 did choose the uncertain option, chimpanzees also hesitated longer in the social condition.
39 In Study 2, where chimpanzees had learned the statistical probabilities on reciprocation
40 rates (i.e., decided under risk), they did not distinguish between social and nonsocial
41 situations and were generally risk averse. These results suggest that chimpanzees are more
42 averse to engaging in uncertain choices when the source of uncertainty is a conspecific than
43 when it is a machine; when confronted with risky choices, chimpanzees show no such
44 tendency.

45

46 **Keywords:** chimpanzees, decision making, risk, trust, uncertainty

47

48 In their natural habitat, chimpanzees face myriad situations that present substantial risks
49 and require choices. Should they enter situations of conflict and engage in intergroup
50 aggression (Wittig & Boesch, 2003)? Should they cross a potentially dangerous road
51 (Hockings, Anderson, & Matsuzawa, 2006)? How should the risks and benefits of hunting
52 and mating be traded off (Gilby, Eberly, Pintea, & Pusey, 2006)? With which conspecific
53 should one tackle a problem that requires collaboration (Melis, Hare, & Tomasello, 2006)?
54 Chimpanzees' behavioural decision making in such contexts exhibits important similarities
55 to human decision making (Rosati, 2017; Santos & Rosati, 2015). For instance, it has been
56 argued that chimpanzees, like humans, show systematic deviations from rational choice
57 theory, such as framing effects (Krupenye, Rosati, & Hare, 2015; but see Kanngiesser &
58 Woike, 2016), and endowment effects (Brosnan et al., 2007; but see Kanngiesser, Santos,
59 Hood, & Call, 2011).

60 One especially important condition for adaptive decision making is uncertainty (see
61 Kozyreva & Hertwig, 2019). Frequently, decision makers have no or very incomplete
62 knowledge with respect to the outcome and probability space of the consequences of their
63 decisions and actions. Knight (1921/1964; see also Keynes, 1936/1973, 1937)
64 distinguished the world of unmeasurable *uncertainty* from the world of measurable *risk*.
65 Using the classic terminology of Luce and Raiffa (1957/1989), in decision making under
66 risk, "each action leads to one of a set of possible specific outcomes, each outcome
67 occurring with a known probability. The probabilities are assumed to be known to the
68 decision maker" (p. 13). In contrast, the realm of decision making under uncertainty
69 encompasses situations in which "either action or both has as its consequence a set of
70 possible specific outcomes, but where the probabilities of these outcomes are completely

71 unknown or are not even meaningful” (p. 13). It is worth emphasizing that in Knight’s and
72 Keynes’s original notion of uncertainty, the state of the world or mind is characterized by
73 incomplete or lack of knowledge of possible outcomes. In humans, choices under risk and
74 uncertainty are commonly studied by giving participants a series of choices between
75 monetary lotteries. In line with Luce and Raiffa’s definition, probability information is
76 (sometimes partly) removed under uncertainty (in economics this situation is also referred
77 to as ambiguity; Ellsberg, 1961), whereas outcomes and probabilities are fully stated (either
78 visually or numerically) under risk. In the latter context, participants make *decisions from*
79 *description*: In choosing one option, they can rely on a priori communicated probabilities
80 (Hertwig, Barron, Weber, & Erev, 2004). As other animals do not base their
81 communication on symbols, all their decisions (e.g., about where to forage) are necessarily
82 *decisions from experience* (but see Heilbrunner & Hayden, 2016). When making decisions,
83 animals may rely on subjective estimates or intuitive statistics based on past experiences
84 (for a discussion on the description–experience gap in humans see Hau, Pleskac, &
85 Hertwig, 2010; Hertwig, 2015; Wulff, Mergenthaler-Canseco, & Hertwig, 2018).

86 In recent years, comparative researchers have begun to investigate the evolutionary
87 pathway of decision mechanisms under uncertainty and risk by adapting economic risk
88 paradigms for use with great apes (Rosati, 2017; Santos & Rosati, 2015). For instance,
89 Heilbrunner, Rosati, Stevens, Hare, and Hauser (2008) studied chimpanzees’ and bonobos’
90 behaviour in an economic risk-taking task. Subjects made a series of choices between a
91 safe option that granted four pieces of food and a risky option that granted either one piece
92 or seven pieces with equal probability. Although both options had the same expected value,
93 chimpanzees preferred the risky option (with risk defined as outcome variance, as is

94 common in economic choice theory). Moreover, chimpanzees were more risk-taking than
95 bonobos. Haun, Nawroth, and Call (2011) investigated risky choices in all four great ape
96 species: chimpanzees, bonobos, gorillas, and orangutans. Apes chose between a safe and a
97 risky reward with varying expected values. The size of the safe reward and the number of
98 cups under which the risky reward was potentially hidden were systematically manipulated.
99 Findings indicated a high overall rate of choosing the risky option in all four great apes.
100 Rosati and Hare (2010) investigated how uncertainty affects chimpanzees' and bonobos'
101 decision strategies. In one condition, subjects chose between a safe and a risky option with
102 known outcomes and probabilities; in another condition, subjects selected between a safe
103 and an uncertain option with unknown probabilities and outcomes of obtaining food.
104 Although the options' expected values in both conditions were identical, chimpanzees and
105 bonobos chose the risky option, relative to the safe option, more often than they chose the
106 uncertain option relative to the same option. Despite the fact that this effect diminished
107 with time, the results suggest that great apes were sensitive to different degrees of lack of
108 knowledge when making decisions. These findings converge in suggesting that
109 chimpanzees are generally risk seeking and thus appear to differ in their risk attitude from
110 humans' frequently observed risk aversion.

111 The studies reviewed above share a common feature: They investigated chimpanzees'
112 decision making under uncertainty and risk as a game against nature—that is, in the context
113 of an interaction with the physical environment. In these studies, the human experimenter
114 can be considered part of the physical environment, given that the experimenter draws
115 rewards randomly, without looking and acts like a 'nonsocial' chance generator (see Eckert
116 et al., 2018, showing that chimpanzees appear to assume random sampling by human

117 experimenters—an assumption that can be altered under specific circumstances). However,
118 individuals also make decisions under uncertainty and risk when interacting with the social
119 environment (see also Hertwig, Hoffrage, & the ABC Research Group, 2013). Several lines
120 of evidence suggest that humans process and view risk and uncertainty in social and
121 nonsocial settings differently (Blount, 1995; Bohnet & Zeckhauser, 2004; Fehr, 2009;
122 FeldmanHall & Shenhav, 2019; Li, Turmunkh, & Wakker, 2019; Rilling, King-Casas, &
123 Sanfey, 2008). For instance, in a series of experiments, Bohnet, Greig, Herrmann, and
124 Zeckhauser (2008) compared individuals' willingness to engage in two odds-and-payoffs
125 situations that differed only in terms of the possible outcome: in one, the possible outcome
126 was a function of a chance device in a dictator game and in the other, the possible outcome
127 was a function of the trustworthiness of another player in a trust game. Results from six
128 different cultures suggest that participants' stated minimum acceptable odds were higher
129 for the trust game than for the risky dictator game. Humans are thus more averse to risks
130 brought about by social partners than to risks brought about by random chance. One factor
131 that may explain this difference is betrayal aversion (Bohnet et al., 2008; Fehr, 2009):
132 Being duped by a social partner prompts stronger negative emotions than does being let
133 down by a nonsocial agent (e.g., nature or a machine).

134 Several primate species have been shown to be sensitive to the degree of uncertainty in
135 situations where payoffs vary as a function of a partner's choice (for a review, see Rosati,
136 2017). Specifically, chimpanzees display sensitivity to social uncertainty in competitive
137 interactions: They use their knowledge about what conspecifics can and cannot see to
138 devise effective social-cognitive strategies in food competition situations (Hare, Call,
139 Agnetta, & Tomasello, 2000). Similarly, many cooperative social interactions that have

140 been studied in chimpanzees are also characterized by a degree of uncertainty to the extent
141 that their outcome depends on the behaviour of another individual, as in the stag hunt game
142 (Bullinger, Wyman, Melis, & Tomasello, 2011; Duguid, Wyman, Bullinger, Herfurth-
143 Majstorovic, & Tomasello, 2014), the ultimatum game and other negotiation games
144 (Jensen, Call, & Tomasello, 2007a; Melis, Hare, & Tomasello, 2009), the trust game
145 (Engelmann, Herrmann, & Tomasello, 2015; Engelmann & Herrmann, 2016) and
146 interdependent, mutualistic scenarios (Melis, Hare, & Tomasello, 2006).

147 Previous research thus suggests that chimpanzees take uncertainty about their partner's
148 behaviour into account when making decisions in competitive and cooperative social
149 situations. But whether chimpanzees, like humans, distinguish between social and
150 nonsocial forms of uncertainty and risk is unclear. This question is of considerable interest
151 as chimpanzees are highly social animals and regularly make decisions in both social and
152 nonsocial contexts. Studying how chimpanzees respond to uncertainty and risk in social
153 and nonsocial situations will shed more light on how—and how differently—one of
154 humans' closest living relatives navigates these contexts. Most relevant to the current
155 investigation is the recent study by Calcutt, Proctor, Berman, and de Waal (2019), which
156 found that female chimpanzees are more averse to social than to nonsocial risk. However,
157 the authors did not differentiate between chimpanzees' behaviour in uncertain situations
158 and their behaviour in risky situations. In addition, their results are hard to interpret because
159 it is unclear whether chimpanzees fully understood the setup and its contingencies (see
160 Calcutt et al., 2019). We therefore conducted two studies to investigate whether
161 chimpanzees distinguish between social and nonsocial forms of uncertainty as well as risk.
162 To this end, we adapted a method that has previously been used with chimpanzees, the trust

163 game (Engelmann, Herrmann, & Tomasello, 2015; Engelmann, & Herrmann, 2016), and
164 we took the necessary steps to confirm chimpanzees' understanding of the task.
165 Chimpanzees were presented with a safe option, in which low-value food was reliably
166 provided, and an uncertain (or risky) option, in which high-value food was provided only
167 half of the time. In the social condition, the outcome of the uncertain (or risky) option
168 ostensibly depended on a conspecific's decision to send the food back to the subject; in the
169 nonsocial condition, it depended on a machine. In Study 1, the potential outcomes were
170 visible to the subject, but the reciprocation rates of the partner/machine were unknown; the
171 interaction thus involved uncertainty and provided us with a measure of chimpanzees'
172 behaviour in uncertain contexts. In Study 2, potential outcomes were visible and
173 probabilities were known (chimpanzees made decisions based on the statistical
174 probabilities experienced in Study 1). The interaction thus involved risk. In Study 1,
175 chimpanzees were exposed to the safe option and the uncertain option in separate trials;
176 they decided to pull or not pull (go/no-go) the rope leading to that option. This allowed us
177 to study their preferences towards both options separately and to familiarize them with the
178 payoff probabilities associated with each option. In Study 2, chimpanzees were exposed
179 to the safe and the risky option simultaneously and decided between the two options.

180 For Study 1, we predicted that chimpanzees pull the uncertain option less often in the
181 social than in the nonsocial condition (P1). This is based on findings demonstrating that in
182 decisions under uncertainty, humans are more averse to social than to nonsocial settings
183 (Bohnet et al., 2008; Fehr, 2009). Furthermore, we predicted that chimpanzees' decision to
184 pull the uncertain option takes longer in the social condition, that is, they hesitate longer
185 than in the nonsocial condition (P2). This prediction is based on findings showing that

186 under uncertainty an increase in response latency is a proxy of cognitive conflict in
187 nonhuman animals (Call, 2012). We predicted that the cognitive conflict is greater in
188 uncertain social compared to uncertain nonsocial situations (based on P1). Additionally,
189 we predicted that chimpanzees show more negative emotional reactions to the uncertain
190 option in the social condition than in the nonsocial condition (P3). This prediction is based
191 on findings suggesting that humans exhibit betrayal aversion in uncertain social situations
192 (Bohnet et al., 2008; Fehr, 2009). In nonhuman animals, affective responses are often
193 accompanied by changes in arousal level, as indicated by behavioural responses (see Baker
194 & Aureli, 1997; Call, 2012; Jensen, Call, & Tomasello, 2007b; Rosati & Hare, 2013).

195 For Study 2, we predicted that chimpanzees are more averse to choosing the risky
196 option in the social condition than in the nonsocial condition (P4). This prediction is based
197 on the finding that humans (Bohnet et al., 2008) and female chimpanzees are more averse
198 to social than to nonsocial risk (Calcutt et al., 2019). We also investigated whether subjects'
199 sex, age, and hierarchy position are possible predictors for chimpanzees' risk-taking
200 behaviour (P5). We refrained from stating a prediction as it is an open question whether
201 these properties of individuals, like in humans, influence risk-taking behaviour in
202 chimpanzees. Finally, we were interested in whether subjects' choice of the risky option
203 depended on whether the risky choice in the previous trial led to a reward (P6). Existing
204 results on this possible contingency have been mixed (see Calcutt et al., 2019; Melis et al.,
205 2006; Rosati & Hare, 2013).

206

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208

209 **METHODS**

210 *Participants*

211 Thirteen chimpanzees (eight females) ranging in age from 11 to 30 years ($M = 23$
212 years) participated in the two studies. Each subject was paired with a neutral partner (see
213 the Supplementary Material, SM, for details on how we determined neutral partners). One
214 additional male chimpanzee did not pass the apparatus understanding test and therefore
215 acted solely as a partner. Four of the subjects (two females) acted as partners after
216 participating in the studies themselves. For more information on subjects and their partners,
217 see Table A1 of the SM.

218 *Ethical Note*

219 Chimpanzees had access to a large outdoor enclosure during the day and received
220 regular daily feedings, daily enrichment sessions, and water ad libitum. Subjects
221 participated in the studies voluntarily and were never deprived of food or water. The
222 research was noninvasive and carried out in accordance with the guidelines of the Pan
223 African Sanctuary Alliance and the regulations of Sweetwaters Chimpanzee Sanctuary.

224 Most of the apes at Sweetwaters Chimpanzee Sanctuary were born in the wild and
225 came to the sanctuary after being confiscated at an early age (~2–3 years old) as a result of
226 the trade in apes for pets and bushmeat. Once the apes arrived at the sanctuary, they were
227 raised by humans together with peers until they were old enough to join a mixed-age social
228 group. Sweetwaters Chimpanzee Sanctuary hosts two groups of chimpanzees (17
229 individuals in group one, 10 females and 7 males, all between 4 and 31 years of age and 22
230 individuals in the second group, 10 females and 12 males, all between 1 and 39 years of
231 age). From group 1, thirteen chimpanzees participated in the two studies.

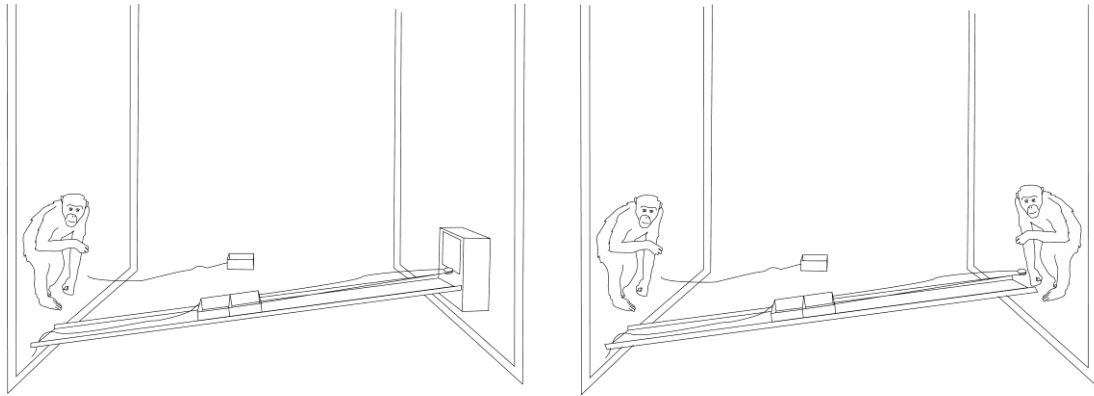
232 All chimpanzees live in social groups. During the day chimpanzees have access to
233 large tracts of outdoor enclosures, including trees, bushes, and climbing structures (group
234 1: 29.09 hectares; group 2: 35.31 hectares). In the evening, all individuals return from the
235 outdoor enclosures and stay in indoor enclosures overnight. Subjects are tested in familiar
236 rooms in their indoor enclosures and are never deprived of food or water for any reason;
237 they are fed a combination of fruits, vegetables, and other species-appropriate foods three
238 times daily.

239 The full procedure of the study was approved by the local ethics committee at the
240 Sanctuary (board members and veterinarian), the Kenya Wildlife Service, and the National
241 Council for Science and Technology, Kenya. A research permit was issued by the National
242 Council for Science and Technology, Kenya (NACOSTI/P/19/7557/27803;
243 NACOSTI/P/18/24055/20857).

244 All testing was strictly voluntary. During testing a subject could indicate their wish
245 to stop participating at any time (e.g., by leaving the test area and/or sitting by the door).
246 All chimpanzees were highly motivated to participate.

247 *Materials*

248 The same apparatuses (see Figure 1) were used for both studies. The safe option
249 consisted of a small vehicle loaded with low-value food (one piece of banana) on an 80 cm
250 long track. Pulling the rope for the safe option resulted in direct access to the food reward.
251 The uncertain/risky option consisted of a small vehicle loaded with high-value food (two
252 pieces of banana and ¼ apple) on a 300 cm track. Pulling the rope for the uncertain/risky
253 option resulted in the vehicle moving along the track to a partner (social condition) or a
254 machine (nonsocial condition).



255

256

257 **Figure 1.** Experimental setup. Nonsocial condition (left) and social condition (right). The subject is depicted
258 on the left and the machine (or partner) on the right side of the apparatus. The safe rope is on the left side of
259 the subject and the uncertain/risky rope on the right side. In Study 1 (decision making under uncertainty),
260 only one of the two ropes was present at a time. In Study 2 (decision making under risk), both ropes were
261 present and subjects could choose between the two options.

262

263 *Design*

264 In a within-subjects design, subjects participated in two studies: decision making
265 under uncertainty (Study 1) and decision making under risk (Study 2). Both studies
266 comprised two conditions: a social condition and a nonsocial condition. Half of the subjects
267 were first presented with both social conditions (Study 1 followed by Study 2), followed
268 by both nonsocial conditions (Study 1 followed by Study 2); the other half were first
269 presented with both nonsocial conditions, followed by both social conditions. Each
270 chimpanzee had the same partner in both studies and conditions. Subjects participated in
271 one test session per day.

272 Study 1, decision making under uncertainty, consisted of 48 decision-making trials
273 per condition (24 safe trials; 24 uncertain trials), presented across four sessions. Each

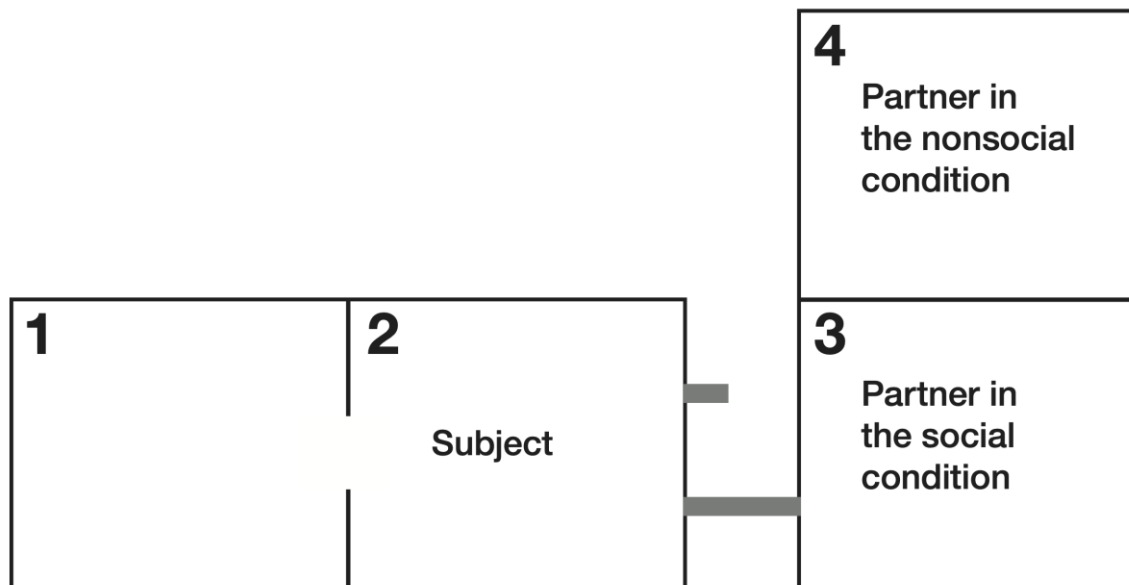
274 session consisted of six safe trials (i.e., only the safe option was present) and six uncertain
275 trials (i.e., only the uncertain option was present). The safe option guaranteed immediate
276 access to low-value food (100% rewarded); the uncertain option gave access to high-value
277 food, but only 50% of the time. Throughout Study 1, chimpanzees experienced the relative
278 frequencies (probabilities) and outcomes of the respective options. Our use of 24 trials per
279 option was based on reported learning effects of relative frequencies in apes (see Rosati &
280 Hare, 2010). Study 2, decision making under risk, consisted of 24 decision-making trials
281 per condition, presented across four sessions. In all trials, both the safe and the risky option
282 were available. Prior to each test session in Study 2, chimpanzees received four reminder
283 trials to remind them of the outcomes and probabilities of each option: two safe trials
284 resulting in immediate access to low-value food and two uncertain trials with a 50% chance
285 of obtaining high-value food.

286 *Familiarization Phase*

287 All subjects first completed a food preference test. They were then introduced to
288 the experimental setup and their understanding of the apparatus was tested. Those subjects
289 who passed the apparatus understanding test participated in the two studies.

290 *Food preference.* Each subject completed a food preference test comprising two
291 consecutive sessions of 10 trials each. Subjects chose between two food options: one the
292 same as the safe option (one piece of banana) and the other the same as the uncertain/risky
293 option (two pieces of banana and $\frac{1}{4}$ apple). For each trial, food pieces were placed on two
294 dishes on a sliding platform behind an occluder. The occluder was then removed and the
295 sliding platform was pushed toward the subject. The subject selected one of the two food
296 options and received the selected food. The nonselected option was removed and placed in

297 a food bucket. After each trial, the occluder was placed back on the platform, and
298 preparation for the next trial began. The location of the two food options (left or right side)
299 was randomized and evenly distributed over the 10 trials. The option selected in at least
300 80% of trials in the two consecutive sessions was categorized as high-value food. For all
301 subjects, this was two pieces of banana and ¼ apple.
302



303
304

305 **Figure 2.** Testing rooms with position of the chimpanzees (subject and partner) in Studies 1 and 2. The grey
306 bars between rooms 2 and 3 represent the safe option (small bar) and the uncertain/risky option (larger bar).
307

308 *Apparatus understanding.* In four consecutive steps, all subjects were then individually
309 introduced to the experimental setup and their understanding of the apparatus was tested.
310 Partners were not present. Individuals participated in one session per day.

311 In the first step, subjects were exposed to the safe rope and the uncertain/risky rope
312 separately. The criterion for apparatus understanding was that they successfully pulled the

313 respective rope within 60 seconds eight out of 10 times in one session. In the case of the
314 uncertain/risky rope, moreover, they had to pull the rope within 60 seconds (room 2), move
315 to the opposite room (room 3) via the overhead runway, eat the high-value food from the
316 second compartment, send the vehicle back, move back to room 2, and eat the high-value
317 food from the first compartment (see Figure 2). This procedure was implemented to ensure
318 that subjects learned to pull the vehicle all the way up to the other side, as the food in the
319 second compartment was accessible only once the vehicle was pulled to the top of the track.
320 In the test trials, only the compartment close to the subject was baited with food.

321 In the second step, both ropes were present but only one option was baited. The
322 criterion for apparatus understanding was that subjects chose the correct rope (the one
323 giving access to food) in at least eight out of 10 trials in two subsequent sessions. Once
324 subjects started pulling one rope, an experimenter removed the other rope. Chimpanzees
325 thus experienced that they could only pull one rope during each trial.

326 The third step was identical to the second, except that there was no food in the
327 second food compartment in the uncertain/risky option. The criterion for apparatus
328 understanding was that subjects chose the correct rope (the one giving access to food) in at
329 least eight out of 10 trials. Again, once subjects started pulling a rope, an experimenter
330 removed the other. Chimpanzees thus experienced that they could only pull one rope during
331 each trial and that their partner would not be able to access food on the other side (room 3)
332 if only the first food compartment was baited.

333 The fourth step exposed subjects to a setup closely matching that of the actual
334 studies: Both ropes were present and both options were baited (there was no food in the
335 second food compartment in the uncertain/risky option). The overhead runway between the

336 two rooms was open; chimpanzees could move between the rooms. Subjects participated
337 in two sessions of 10 trials each. Chimpanzees chose to pull the uncertain/risky rope in 72
338 % of the trials.

339 Importantly, chimpanzees were not in any way trained to pull the uncertain/risky or
340 safe rope. In steps 1, 2, and 3 they pulled each rope an equal proportion of times. In step 4,
341 they were rewarded for pulling either the uncertain/risky rope or the safe rope. Following
342 the familiarization phase, chimpanzees engaged in the two studies.

343 *Study 1: Social and Nonsocial Uncertainty*

344 In Study 1, chimpanzees were separately exposed to the safe option and the
345 uncertain option and decided to pull or not pull (go/no-go) the rope leading to that option
346 in both a social and a nonsocial condition. More specifically, chimpanzees entered room 2
347 at the beginning of each trial and only one option (i.e., the safe rope or the uncertain rope)
348 was present. Pulling the safe rope resulted in immediate access to low-value food for the
349 subject. Pulling the uncertain rope resulted in the vehicle moving along the track to the
350 partner (social condition) or machine (nonsocial condition). The partner or machine could
351 not access the high-value food but ostensibly sent, or did not send, the baited vehicle back
352 to the subject (see Figures 1 and 2). Choosing the uncertain option thus could result in
353 access to high-value food for the subject, but only if the partner or machine proved
354 trustworthy. To the subject, it looked as if the partner or machine had made the choice but
355 it was actually the experimenter, who covertly pulled a transparent fishing line to send the
356 vehicle back. In both conditions, the experimenter systematically manipulated the
357 reciprocation rate for the uncertain option, ensuring that subjects were rewarded 50% of
358 the times that they pulled the uncertain rope. The reciprocation rate was pseudo-

359 randomised, with a maximum of two consecutively rewarded (or not rewarded) trials in a
360 row. To ensure that the partner in the social condition was close to the rope for the uncertain
361 option when the decision to send the food back was made, the experimenter placed peanuts
362 in the partner's food tray (located directly under the compartment where the vehicle arrived
363 in room 3) before the actual trial started. In the nonsocial condition, partners were present
364 in room 4 (to control for the mere presence of another individual) and the experimenter
365 placed peanuts in room 4 to keep this feeding aspect constant across conditions (see Figure
366 2). The social and nonsocial test trials were thus identical, except that the nonsocial
367 condition involved a machine rather than a conspecific partner. Chimpanzees had 30
368 seconds to pull the rope. If chimpanzee subjects did not pull the rope within 30 seconds,
369 the experimenter pulled the rope after 30 seconds to ensure that all chimpanzees had the
370 same experience of the relative frequencies (in preparation for Study 2). To control for the
371 delay in receiving the reward in the uncertain option in both conditions, the food was sent
372 back 5 seconds after the vehicle reached the other side in rewarded trials. All rewarded
373 trials ended once subjects finished eating the food. If the uncertain trial was not rewarded,
374 it ended 30 seconds after the vehicle reached the other side. This was to ensure that the
375 duration of trials was identical, regardless of whether the subject's choice was rewarded or
376 not.

377 ***Coding and Reliability***

378 We were interested in whether and, if so, when chimpanzees pulled the uncertain
379 rope. If chimpanzees did not pull the uncertain rope within 30 seconds, we coded this as
380 aversion to pull. If chimpanzees did pull the rope, we measured the latency from
381 chimpanzees entering the room to starting to pull the rope. The latency for trials in which

382 chimpanzees did not pull the rope was set to 30 seconds. Finally, we coded whether
383 chimpanzees showed an affective response. The following behaviours were coded (see
384 Baker & Aureli, 1997; Jensen, Call, & Tomasello, 2007b; Rosati & Hare, 2013): (1)
385 negative emotional vocalizations, particularly screams; (2) scratching, particularly body or
386 head scratches with nails; (3) banging, particularly banging against the apparatus or the
387 mesh with hands or feet; (4) agitated movements, that is, restless behaviour such as walking
388 in circles or swinging. Coding of affective responses began as soon as chimpanzees entered
389 room 2 and ended when they received food (or 5 seconds after the food vehicle reached the
390 partner's side in trials where chimpanzees received no food).

391 All trials were videotaped with two cameras. The first author coded all trials live as
392 well as later from videotape. Due to camera failure, eight trials could not be coded. A
393 research assistant who was unaware of the study design and our predictions independently
394 coded 20% of all trials. Interrater agreement was calculated in R (R Core Team, 2019)
395 using the function kappa2 (Cohen's κ) for nominal-scaled data and kripp.alpha
396 (Krippendorff's α) for ratio-scaled data of the irr package (Gamer, Lemon, & Singh, 2019).
397 Interrater agreement was good to excellent for aversion to pull (Cohen's $\kappa = 1.00$), latency
398 to pull (Krippendorff's $\alpha = 0.95$), and negative affective responses (Cohen's $\kappa = 0.69$).

399 ***Study 2: Social and Nonsocial Risk***

400 In Study 2, chimpanzees were simultaneously confronted with a safe option and a
401 risky option in both a social and a nonsocial condition. They could decide to pull either
402 rope, and made their decisions based on the statistical probabilities and outcomes
403 experienced in Study 1. Subjects received four reminder trials about each option before
404 each test session (see Design). As in Study 1, only one option was present at a time in these

405 reminder trials. After completing the reminder trials, chimpanzees engaged in the actual
406 test trials. The setup and procedure was the same as in Study 1, with the only difference
407 that during each test trial both options—the safe rope and the risky rope—were present.
408 Chimpanzees had 60 seconds to make a choice. Once the subject had decided to pull one
409 rope, the experimenter removed the other rope.

410 Due to experimenter error, one chimpanzee (Kisa) participated in his last nonsocial
411 session of Study 2 after completing both social conditions (Study 1, followed by Study 2).

412 *Coding and Reliability*

413 We were interested in whether chimpanzees pulled the risky rope. Moreover, to
414 analyse whether the choice of the risky option was predicted by a rewarded or not rewarded
415 risky choice in the previous trial, we analysed all trials (from the second trial onwards) that
416 followed the choice of the risky rope. (By design, the first trial could not be influenced by
417 a previous reward.) Additionally, in an exploratory analysis, we investigated whether
418 chimpanzees waited longer before making a decision in the social condition than in the
419 nonsocial condition. Specifically, we coded the time between chimpanzees entering the
420 room and starting to pull either rope. Finally, we coded chimpanzees' affective responses
421 (for coding details see Study 1).

422 All trials were videotaped with two cameras. The first author coded all trials live as
423 well as later from videotape. Due to camera failure, 19 trials could not be coded. A research
424 assistant who was unaware of the study design and hypothesis independently coded 20%
425 of all trials. Interrater agreement was excellent for choice of the risky option (Cohen's $\kappa =$
426 1.00) and latency to pull (Krippendorff's $\alpha = 0.90$).

427

428 ANALYSIS

429 The predictions (P1–P6) and the analysis plan of this project were preregistered at
430 the [Open Science Foundation](#) (see Stevens, 2017, for a discussion of replicability and
431 reproducibility in comparative psychology). All models were fitted in R (R Core Team,
432 2019) using the function lmer (for linear mixed models) or glmer (for generalized linear
433 mixed models) of the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) with the
434 optimizer bobyqa. The general procedure for all analyses was as follows: We first
435 established the significance of the full model by running a full–null model comparison
436 using a likelihood ratio test (Dobson, 2002). We compared the full model with the
437 respective reduced model that lacked the effect to be tested but had the same random effect
438 structure (Forstmeier & Schielzeth, 2011). For the preregistered models in Study 1, we
439 included condition as a fixed effect. To control for the sequence of testing days, session
440 was included as a further fixed effect. The random effect structure comprised subject,
441 partner, and session ID (nested in subject) as random intercepts. We included session ID to
442 account for the possibility that the effect of session varied among individual chimpanzees.
443 As random slopes, we included session number in subject and partner, as well as condition
444 in subject and partner. For the preregistered models in Study 2, we included condition as
445 well as subject’s sex, age, and hierarchy position as fixed effects. Session was included as
446 a further fixed effect. The random effect structure comprised subject, partner, and session
447 ID (nested in subject) as random intercepts. As random slopes, we included session number
448 and condition in subject, as well as session number, condition and subject’s sex, age and
449 hierarchy position in partner. Session number, age, and hierarchy position were z-
450 transformed. Factors entered as random slopes (sex and condition) were dummy-coded and

451 centred. To avoid creating an excessively complex model, we did not include correlations
452 between random intercepts and random slopes or correlations among random slopes. Barr,
453 Levy, Scheepers, and Tily (2013) have shown that exclusion of these correlations does not
454 substantially affect Type I error rate.

455

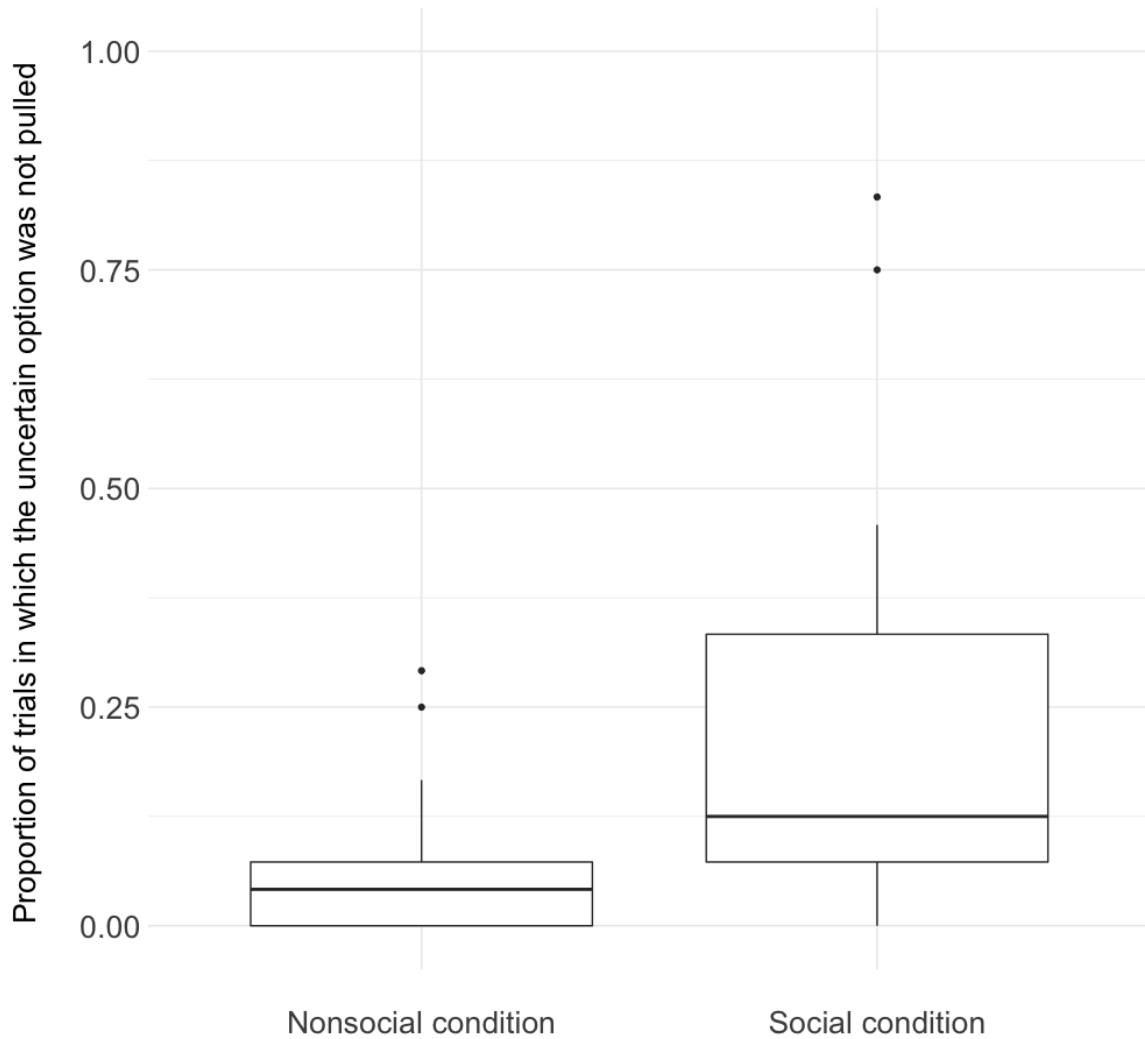
456 **RESULTS**

457 *Study 1: Social and Nonsocial Uncertainty*

458 For the analysis of Study 1 we investigated all trials in which only the uncertain
459 option was present.

460 According to P1, chimpanzees pull the uncertain option less often in the social than in the
461 nonsocial condition. To test this prediction, we used a generalized linear mixed model with
462 binomial error distribution and logit link function to analyse whether aversion to pull the
463 uncertain rope was influenced by condition (*Model 1.1*; see SM for details). The full model
464 differed significantly from the null model ($\chi^2_1 = 41.486$, $P = <0.001$, $N = 96$). More
465 specifically and consistent with P1, in the social condition, chimpanzees refused to pull the
466 uncertain rope in a total of 12% of uncertain trials but only in a total of 4% of the trials in
467 the nonsocial condition (Figure 3). We found no significant effect of session ($\chi^2_1 = 0.056$,
468 $P = 0.812$). Furthermore, we investigated whether order of presentation (social or nonsocial
469 condition first) affected the aversion to pull by including the first condition as a fixed effect
470 in the model. Order of presentation had no significant effect on the aversion to pull ($\chi^2_1 =$
471 0.076 , $P = 0.783$, $N = 96$).

472



473

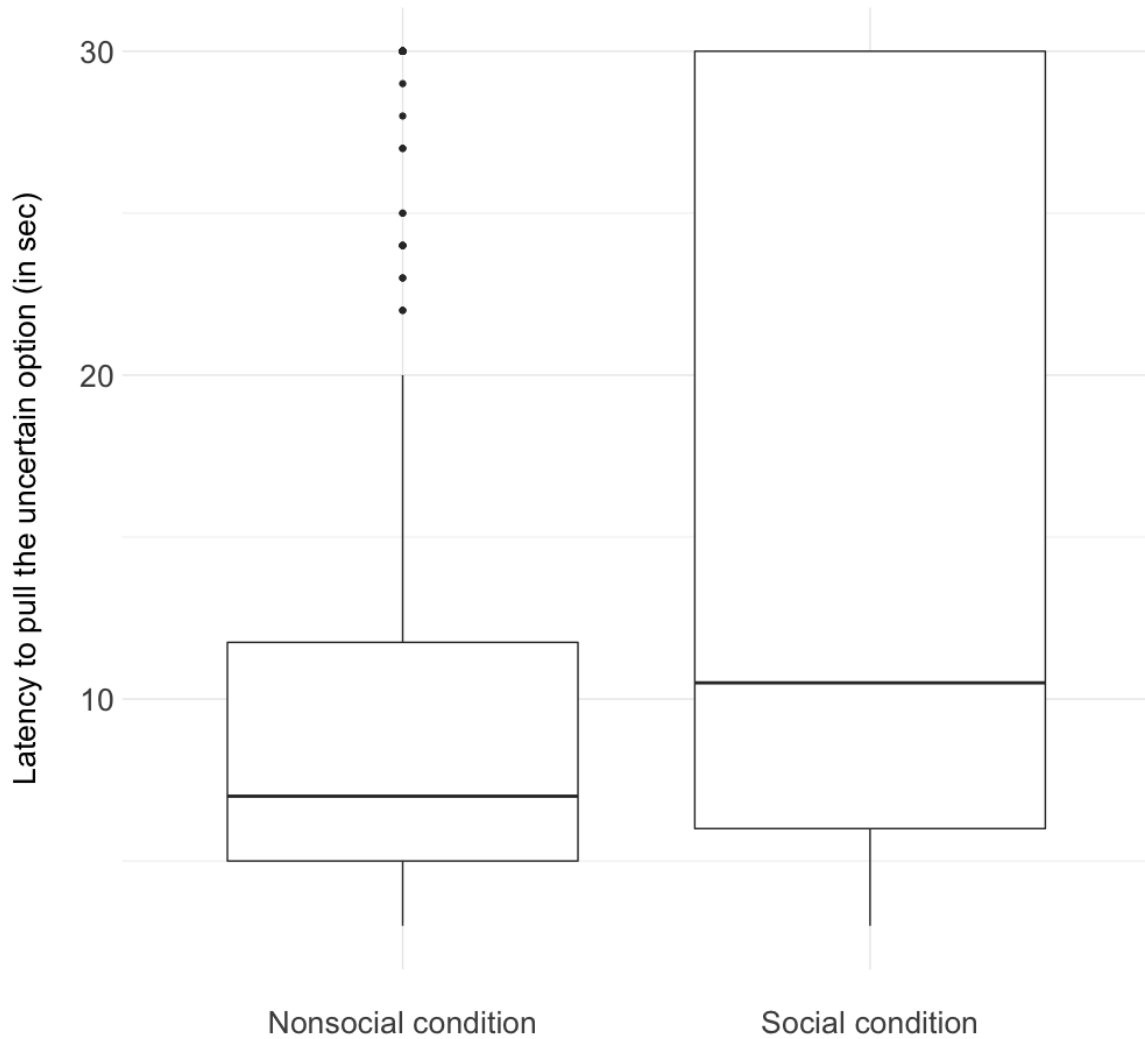
474

475 **Figure 3.** Aversion to pull the uncertain option in the nonsocial and the social condition (Study 1). The
 476 boxplots depict the proportion of trials in which the uncertain option was not pulled within 30 seconds. The
 477 thick vertical lines represent the median. The lower and upper hinges correspond to the first and third
 478 quartiles. The upper whisker extends from the hinge to the largest value no further than $1.5 \times$ IQR (inter-
 479 quartile range) from the hinge. The lower whisker extends from the hinge to the smallest value at most $1.5 \times$
 480 IQR of the hinge. Data beyond the end of the whiskers are outliers and plotted as individual points.

481

482 According to P2, chimpanzees' decision to pull the uncertain option takes longer in the
 483 social condition—more hesitation—than in the nonsocial condition. To test this prediction,

484 a linear mixed model (Baayen, 2008) analysed the effect of condition on the latency to pull
485 the uncertain rope (*Model 1.2*; see SM for details). The full model differed significantly
486 from the null model ($\chi^2_1 = 4.601$, $P = 0.032$, $N = 568$). More specifically and consistent
487 with P2, chimpanzees took more time before pulling the uncertain rope in the social
488 condition than in the nonsocial condition (Figure 4). We found no significant effect of
489 session ($\chi^2_1 = 0.565$, $P = 0.452$). Furthermore, we investigated whether order of
490 presentation (social or nonsocial condition first) affected the latency to pull by including
491 the first condition as a fixed effect in the model. Order of presentation had no significant
492 effect on the latency to pull ($\chi^2_1 = 0.069$, $P = 0.793$, $N = 568$).



493

494 **Figure 4.** Latency to pull the uncertain option (Study 1). The boxplots depict the latency (in sec) to pull the
 495 uncertain option in the nonsocial and the social condition. The thick vertical lines represent the median. The
 496 lower and upper hinges correspond to the first and third quartiles. The upper whisker extends from the hinge
 497 to the largest value no further than $1.5 * IQR$ (inter-quartile range) from the hinge. The lower whisker extends
 498 from the hinge to the smallest value at most $1.5 * IQR$ of the hinge. Data beyond the end of the whiskers are
 499 outliers and plotted as individual points.

500

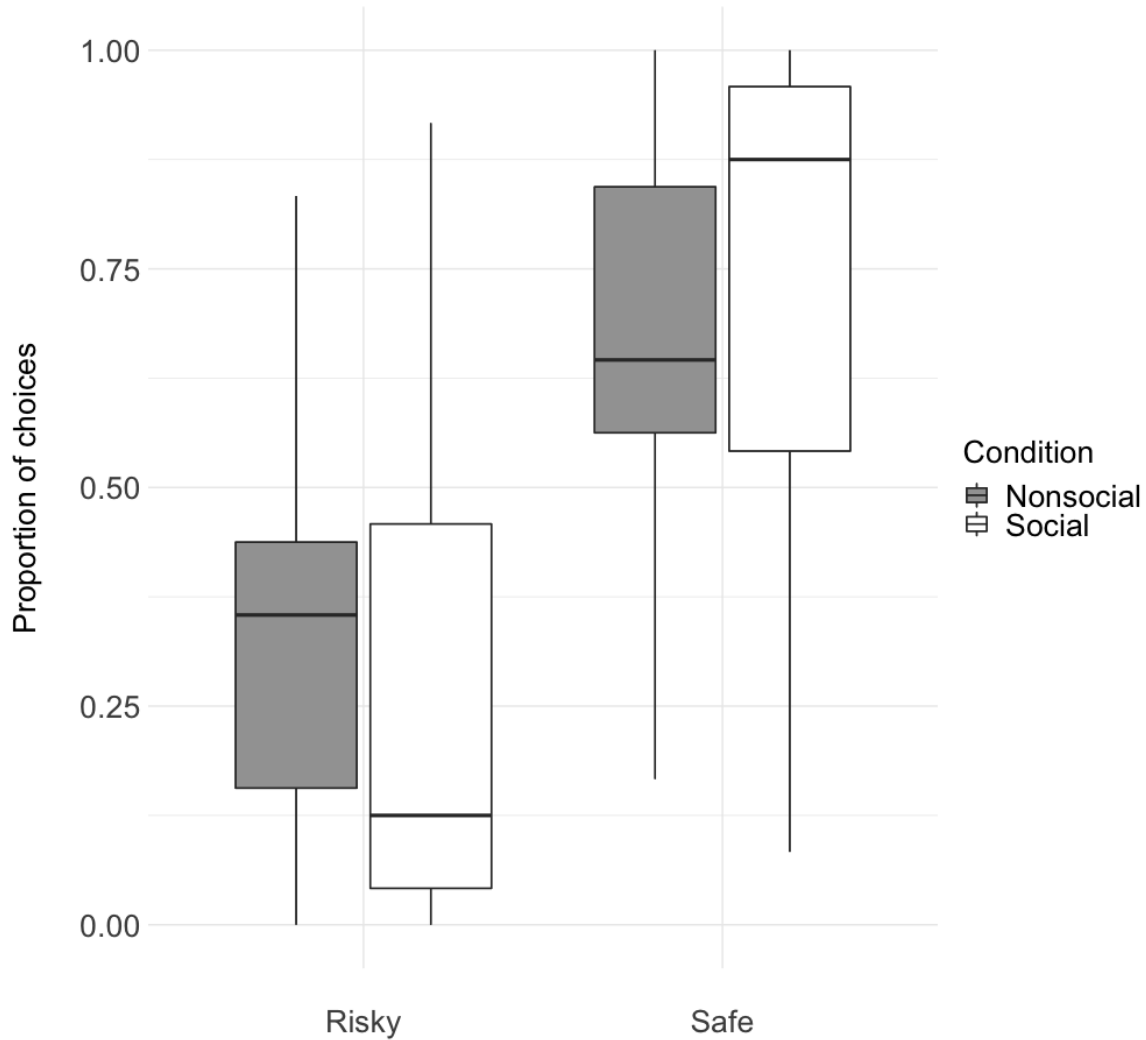
501

502 According to P3, chimpanzees show more negative emotional reactions to the uncertain
503 option in the social condition than in the nonsocial condition. To test this prediction, we
504 used a generalized linear mixed model with binomial error distribution and logit link
505 function to analyse whether negative emotional reactions in uncertain trials were
506 influenced by condition (*Model 1.3*; see SM for details). Inconsistent with P3, the full
507 model did not differ significantly from the null model ($\chi^2_1 = 1.443$, $P = 0.23$, $N = 95$). The
508 results suggest that chimpanzees' behaviour did not differ between conditions: In the social
509 condition, 10 subjects showed negative emotional responses in a total of 15% of the
510 uncertain trials. In the nonsocial condition, 11 subjects showed negative emotional
511 responses in a total of 11% of the trials.

512 ***Study 2: Social and Nonsocial Risk***

513 According to P4, chimpanzees are more averse to choosing the risky option in the social
514 condition than in the nonsocial condition. P5 (nondirectional): Additionally, we
515 investigated whether subjects' sex, age, and hierarchy position are possible predictors for
516 their risk-taking behaviour. Using a generalized linear mixed model with binomial error
517 distribution and logit link function, we investigated whether the choice of the risky option
518 was influenced by condition, subject's sex, age, and hierarchy position (*Model 2.1*; see SM
519 for details). Inconsistent with P4, the full model did not differ significantly from the null
520 model ($\chi^2_4 = 2.785$, $P = 0.594$, $N = 576$). In the social condition, chimpanzees chose the
521 risky option in a total of 27% of trials; in the nonsocial condition, they chose the risky
522 option in 33% of trials. Furthermore, we investigated whether order of presentation (social
523 or nonsocial condition first) affected the choice of the risky option by including the first
524 condition as a fixed effect in the model. The order of presentation had no significant effect

525 on the risky choice; the full model did not differ significantly from the null model ($\chi^2_5 =$
526 4.520, $P = 0.477$, $N = 576$). Across both conditions, a Wilcoxon signed-rank test revealed
527 that chimpanzees were significantly less likely to choose the risky option ($Mdn = 10$) than
528 the safe option ($Mdn = 38$, $n = 12$, $z = -2.36$, $p = 0.018$; see Figure 5).
529



530

531

532 **Figure 5.** Proportion of risky and safe choices (Study 2). The boxplots depict the proportion of risky and safe
533 choices in the social and nonsocial condition. The thick vertical lines represent the median. The lower and
534 upper hinges correspond to the first and third quartiles. The upper whisker extends from the hinge to the

535 largest value no further than $1.5 * IQR$ (inter-quartile range) from the hinge. The lower whisker extends from
536 the hinge to the smallest value at most $1.5 * IQR$ of the hinge.

537

538 We next used a generalized linear mixed model with binomial error distribution and
539 logit link function to investigate whether chimpanzees were more likely to choose the risky
540 option after rewarded risky trials (*Model 2.2*, see SM for details). We included the outcome
541 of the risky choice (rewarded or not rewarded) in the previous trial as a fixed effect. The
542 full model did not differ significantly from the null model ($\chi^2_1 = 3.255, P = 0.071, N = 141$).
543 The results, however, suggest a weak preference of chimpanzees to choose the risky option
544 more often after not being rewarded in risky trials: Chimpanzees chose the risky option in
545 76% of trials when they previously received nothing, relative to 64% of trials after the
546 previous risky choice was rewarded. Regardless of the previous outcome, in the trial
547 following a risky decision, chimpanzees stuck with the risky option in 70 % of the trials.

548 In an exploratory analysis, we investigated whether chimpanzees waited longer
549 before making a decision (i.e., pulling either rope) in the social condition than in the
550 nonsocial condition. We used a linear mixed model (Baayen, 2008) to analyse the effect of
551 condition on the latency to choose one option (*Model 2.3*; see SM for details) by including
552 condition as a fixed effect. Session was included as a further fixed effect. The full model
553 did not differ significantly from the null model ($\chi^2_1 = 0.612, P = 0.434, N = 557$), suggesting
554 that chimpanzees did not wait longer before making a decision in the social condition than
555 in the nonsocial condition. Moreover, we investigated whether the latency to pull the risky
556 option differed between conditions. This was not the case; chimpanzees pulled the risky
557 rope equally fast in the social (*Mdn* = 5; *IQR* = 4–6) and the nonsocial (*Mdn* = 5; *IQR* = 4–
558 7) condition. Furthermore, using a Wilcoxon signed-rank test we also found that in their

559 emotional reactions, chimpanzees did not differentiate between the social ($Mdn = 0.5$) and
560 nonsocial condition ($Mdn = 0$, $n = 12$, $z = -0.99$, $P = 0.32$). In the social condition, six
561 subjects showed negative emotional responses in a total of 5% of the trials. In the nonsocial
562 condition, five subjects showed negative emotional responses in a total of 3% of the trials.
563 Finally, we investigated whether the emotional reactions differed between Study 1 and
564 Study 2. A Wilcoxon signed-rank test revealed that across conditions the emotional
565 reactions were significantly stronger in Study 1 ($Mdn = 10$) than in Study 2 ($Mdn = 1$, $n =$
566 12 , $z = -2.95$, $P = 0.003$).

567

568 **DISCUSSION**

569 In two studies, we investigated whether chimpanzees distinguish between social and
570 nonsocial forms of uncertainty and risk. In Study 1, chimpanzees were exposed to social
571 and nonsocial uncertainty; in Study 2, they were exposed to social and nonsocial risk. In
572 Study 1, we found that our key variable of interest—uncertainty in social versus nonsocial
573 contexts—is relevant in chimpanzees' decision making. They were less likely to pull the
574 uncertain rope under social than under nonsocial uncertainty. Additionally, they hesitated
575 longer before trusting a conspecific compared to a machine. Predictions 1 and 2 were thus
576 supported. In Study 2, in contrast, chimpanzees' decision making in situations involving
577 risk did not differ along the social/nonsocial dimension. Prediction 4 was thus not
578 supported.

579 *Social and nonsocial uncertainty*

580 Our findings suggest that chimpanzees experience more cognitive conflict in uncertain
581 social contexts—which require them to trust a conspecific to return the food—than in

582 uncertain nonsocial contexts, where they must trust a machine to return the food. Thus,
583 chimpanzees appear to not only be concerned with outcomes per se but also with how they
584 come to be. They are less willing to engage when the agent of uncertainty is a conspecific
585 relative to a machine. In humans, similar preferences are explained in terms of the notion
586 of betrayal aversion (Bohnet et al., 2008). To examine whether this may be the driving
587 force for chimpanzees' discrimination between agents of uncertainty, we coded their
588 emotional responses before, during, and after decision making. In nonhuman animals, a
589 cognitive conflict is often accompanied by changes in arousal level, which, in turn, are
590 indicated by behavioural responses such as scratching (Call, 2012). However, we found no
591 evidence for a differential emotional response as a function of social versus nonsocial
592 context (Prediction 3). It is, however, possible that our behavioural coding did not detect
593 subtle shifts in the chimpanzees' affective response; therefore, future research should take
594 physiological indicators such as body posture or pupil dilation into account. Across
595 conditions, however, we found that emotional reactions were generally stronger in Study 1
596 compared to Study 2, which might be due to the fact that in Study 1 chimpanzees could not
597 preempt or terminate decisional conflict by choosing the safe reward.

598 In Study 1, chimpanzees were presented with one option at a time, rendering it possible
599 to examine chimpanzees' response to social and nonsocial uncertainty, without giving them
600 the choice to dodge the decision (by simply choosing the safe option). This design decision
601 was meant to mimic choices in the animals' natural habitat, in which they rarely encounter
602 foraging options simultaneously (an observation raised by Kacelnik, Vasconcelos,
603 Monteiro, & Aw, 2011; Simon, 1955). Kacelnik et al. further argued that the latency to act
604 mirrors a tendency to skip the encountered food in order to continue foraging. Results of

605 Study 1 suggest that in the absence of another option chimpanzees “skip” the food more
606 often in uncertain social situations than in uncertain nonsocial situations.

607 *Social and nonsocial risk*

608 Study 2 focused on risk rather than uncertainty. We found that animals’ choices,
609 latency, and emotional responses did not differ between the social and nonsocial condition.
610 As in most previous risky choice tasks, chimpanzees were simultaneously presented with
611 both options, which gives us the possibility to compare our result to previous findings. At
612 first sight, our result conflicts with Calcutt et al. (2019), who found that female
613 chimpanzees are less risk-taking in a social than in a nonsocial condition. Yet our results
614 and theirs actually converge. Calcutt et al. did not distinguish between uncertain and risky
615 trials and, instead, described both interactions as risky interactions: the initial ones when
616 chimpanzees were without knowledge of reciprocation probabilities, thus making a
617 decision under uncertainty, and the latter ones when chimpanzees had experienced the
618 respective relative frequencies, thus making decisions under risk. Importantly, however,
619 chimpanzees in the Calcutt et al. (2019) study weighted early interactions within the
620 experiment more heavily than later ones: The partner’s reciprocation rate in the first testing
621 block of the social condition significantly influenced the subject’s choice. This observation
622 is in line with our findings, suggesting that chimpanzees distinguish between the social and
623 nonsocial domain during early interactions when reciprocation rates are uncertain, but not
624 once reciprocation rates have been experienced, and uncertainty has morphed into risk. It
625 is important to point out that in everyday life, the decision of whether to engage in a social
626 situation is usually a decision under uncertainty, as humans and nonhuman animals rarely
627 know precisely with what probability others will cooperate. Future studies should examine

628 whether after having experienced the respective relative frequencies (i.e. when making
629 decisions under risk) and when only presented with one option at a time (like in Study 1),
630 chimpanzees would differentiate between social and nonsocial situations.

631 *Risk preference*

632 Irrespective of the factor social versus nonsocial, chimpanzees in Study 2 proved to be
633 risk averse. They preferred the safe option over the risky option, even though the expected
634 value of the latter was higher. This finding is in line with findings of risk aversion across
635 diverse nonhuman animals (e.g., Kacelnik & Bateson, 1996) and humans (see references
636 in Hintze, Olson, Adami, & Hertwig, 2015). However, it is not in line with past studies that
637 reported chimpanzees to be risk prone in nonsocial contexts (see Calcutt et al., 2019; Haun
638 et al., 2011; Heilbronner et al., 2008; but see Proctor et al., 2014). What could explain this
639 difference between the present and past results?

640 Possible explanations may pertain to the presentation and experience of probabilities
641 (see Hau, Pleskac, & Hertwig, 2010; Heilbronner & Hayden, 2016; Hertwig, 2015; Wulff,
642 Mergenthaler-Canseco, & Hertwig, 2018), as well as to specific elements of task design
643 (see Frey, Pedroni, Mata, Rieskamp, & Hertwig, 2017; Heilbronner & Hayden, 2013;
644 Rosati & Hare, 2016). Specifically, in Study 2, chimpanzees made decisions based on
645 experienced relative frequencies (probabilities), whereas in other studies (e.g. Haun et al.,
646 2011; Heilbronner et al., 2008; Rosati & Hare, 2010; Rosati & Hare, 2012) chimpanzees
647 inferred probabilities from the task design. For instance, in the study by Haun et al. (2011),
648 the number of cups represented the probability of success: The safe option consisted of one
649 cup, whereas the risky option comprised (depending on the condition) two ($P=.5$), three
650 ($P=.33$), or four ($P=.25$) cups. Learning the probabilistic structure of the choice context

651 through experience—rather than inferring it from the task design—seems a more
652 naturalistic way to study decisions under risk in chimpanzees (and humans). Probabilities
653 are rarely explicitly stated or presented to the decision maker, but are rather learned through
654 experience, resulting in what Knight (1921/1964) called statistical probabilities rather than
655 a priori probabilities.

656 A further difference between the current and previous studies (e.g. Heilbronner et al.,
657 2008; Rosati & Hare, 2010; Rosati & Hare, 2012) is that in the present study the
658 uncertain/risky decision was an all-or-none decision insofar as one possible outcome of the
659 nonsafe option was the animal coming away empty-handed. In past studies, in contrast, the
660 risky option always provided food; even bad luck still resulted in low-value food. This
661 meant that the choice was indeed less risky per se (in terms of outcome variance). It is not
662 implausible to argue that risk in the real world implies the threat of receiving nothing. It
663 will be important to see in future studies whether this crucial aspect of outcome variance
664 and the presence of the threat of coming away empty-handed make chimpanzees more risk
665 averse and thus more akin to humans and other nonhuman animals in their appetite for risk.

666 *Potential correlates of risk preference*

667 Research on risk preference in humans has identified a number of robust correlates.
668 Sex, age (e.g. Josef et al., 2016), and income have been found to be consistently associated
669 with risk preference (see Frey et al., 2020). Chimpanzees' sex, age, and hierarchy position
670 did not affect their risk preference in Study 2. This could be due to two factors: small
671 sample size and behavioural risk measures. Frey et al. (2020) found that behavioural
672 measures of risk, relative to self-reports, largely fail to pick up associations between
673 correlates and risk preference. Future studies may take on the challenging task of increasing

674 sample sizes and exploiting different risk measures (e.g., behavioural and observational) to
675 investigate correlates and heterogeneity of risk preference.

676 *The influence of previous outcomes on risky choice*

677 We noted earlier that our implementation of the risky option in Study 2 entailed the
678 possibility of coming away empty-handed. Both the experience of such a ‚loss‘ as well as
679 the experience of gain may systematically influence the choice whether to gamble again in
680 the next trial. When testing for this, we found that the outcome of the previous risky choice
681 had a weak influence on the decision in the following trial: Chimpanzees tended to gamble
682 more when they previously received nothing. Rosati & Hare (2013) found that bonobos,
683 but not chimpanzees, modulated their choices based on previous outcomes. In our study,
684 regardless of the outcome and in the trial following a risky decision, chimpanzees chose
685 the risky option more often than they chose the safe one. Our results suggest that
686 chimpanzees are generally risk averse, preferring the safe option over the risky one.
687 However, once chimpanzees chose the risky option, they tended to gamble again,
688 especially if they had not been rewarded in the previous risky trial. One possible
689 explanation for this behaviour is that chimpanzees interpreted unsuccessful trials as a loss
690 and thus aimed at restoring the previous state of affairs by gambling again (see Scholer et
691 al., 2010 for a discussion of risk-seeking behaviour under loss in humans). This explanation
692 implies that chimpanzees' choices are not simply guided by a process of reinforcement
693 learning (in which the value of each action is updated according to its outcome) but also
694 by some kind of belief updating process in which the present outcome informs expectations
695 about what is going to happen in the next round.

696

697 *Conclusion*

698 Our findings indicate that chimpanzees—like humans—distinguish between social and
699 nonsocial contexts when making decisions under uncertainty. Chimpanzees are more
700 reluctant to engage in a situation when the source of uncertainty is a conspecific than when
701 it is a machine. This aversion manifests both in choice behaviour and in response latency.
702 Having observed this dynamic, one key question for the future is: Why do chimpanzees
703 experience interactions with social partners as less predictable, and why are they less
704 trusting and more hesitant to make daring decisions in uncertain social contexts? Unlike in
705 the world of uncertainty, chimpanzees did not discriminate between social and nonsocial
706 contexts in the world of risk. Furthermore, we found them to be—like humans and various
707 nonhuman animals—risk averse, with a tendency to seek risk after the experience of
708 coming away empty-handed. Another key task for the future is to reveal the cognitive,
709 possibly heuristic mechanisms behind chimpanzees' choices: How do they search for
710 information in order to reduce uncertainty before making a choice?

711

Acknowledgments

712

We thank Richard Vigne, Samuel Mutisya, Stephen Ngulu and the board

713

members and staff of Sweetwaters Chimpanzee Sanctuary in Kenya for their crucial

714

support throughout this research. Special thanks go to Joseph Maiyo, David Mundia,

715

Steven Mukundi, and Charles Mussasia. We thank Ol Pejeta Conservancy, Kenya

716

Wildlife Service (KWS), and the National Council for Science and Technology (NCST)

717

for approving our research. Thanks go to Roger Mundy for statistical advice, Oded Ritov

718

for reliability coding, Sebastian Schütte for building the apparatus, Shona Duguid and

719

Hanna Schleihau for helpful discussions, and Susannah Goss and Deb Ain for editing the

720

manuscript.

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Appendix

Supplemental Information

950

951

952 *Participants*

953 All partners (except Romeo, who did not pass the apparatus understanding test)
954 completed all test sessions as subjects before taking on the role of partner. One chimpanzee
955 (Bahati) from the original sample did not follow the procedure on the first day of testing:
956 She did not pull the uncertain rope in Study 1 and thus could not learn the payoff structure
957 for the risky option of Study 2. We therefore adopted a new procedure for all following
958 chimpanzees: If subjects did not pull the rope within 30 seconds, the experimenter pulled
959 the rope after 30 seconds to ensure that all chimpanzees had the same experience of the
960 statistical probabilities (in preparation for Study 2). Bahati was excluded from all analyses.

961 *Prior experimental experience*

962 Chimpanzees had some exposure to cognitive testing, having participated in
963 cooperation tasks (Engelmann & Herrmann, 2016; Engelmann, Herrmann, & Tomasello,
964 2015), social facilitation (Engelmann, Haux, & Herrmann, 2019; Herrmann, Haux, Zeidler,
965 & Engelmann, 2019), and an executive function and physical cognition test battery
966 (unpublished). However, only the setup in the study investigating trust in cooperation was
967 similar to the current project.

968 *Observational phase*

969 To control for the social relationships between subjects and partners, we determined
970 a neutral partner for each subject.

971 *Collection of observational data.* Prior to the experimental studies, three research assistants
972 collected observational data (412 hours) between March 2017 and March 2018 using a

973 Samsung tablet equipped with CyberTracker software (Version 3.389). Observations were
974 recorded as follows: Scan samples were collected for 60 minutes. During this time, research
975 assistants conducted a scan every 10 minutes, noting the activities of each group member
976 in the same predefined order. These activities included *grooming* (assistant noted who the
977 focal animal groomed and/or was groomed by), *contact* (defined as any affiliative body
978 contact between two individuals), *arm's reach* (two individuals sitting at a distance that
979 would allow them to have contact if both extended their arms), and *co-feeding* (two
980 individuals eating simultaneously while within arm's reach). In addition, it was noted
981 whether a given individual was *present* or not.

982 *Analysis of observational data.* We first calculated the frequency with which each
983 individual was grooming, in contact, at arm's reach, or co-feeding with all other individuals
984 (by, e.g., dividing the number of grooming events between individual A and B by the
985 number of times A and B were simultaneously present). The frequencies of the four
986 activities were positively correlated within dyads and consequently cannot be considered
987 independent sources of information about relationship quality. Using the obtained
988 frequencies, we then calculated the composite index of sociality (CSI) for each dyad using
989 the following formula (based on Silk, Cheney, & Seyfarth, 2013):

$$\text{CSI}_{xy} = \frac{\sum_{i=1}^4 \frac{f_{ixy}}{\bar{f}_i}}{4}$$

990

991 In this equation, f_{ixy} is the frequency of behaviour i for dyad xy , and \bar{f}_i is the mean
992 frequency of behaviour i across all dyads. Since the CSI involves dividing the frequency
993 of a given behaviour within a dyad (f_{ixy}) by the average of that behaviour across all dyads

994 (\bar{f}_i), its outcome describes the extent to which a particular dyad deviates from the average
995 of all dyads. Dyads with a high score are more closely bonded than the average dyad;
996 conversely, dyads with a low score are less closely bonded than the average dyad.

997 *Determination of a neutral partner.* A neutral partner was defined as being neither one of
998 the three individuals with the highest CSI for the subject, nor one of the three individuals
999 with the lowest CSI for the subject. We strictly adhered to the results of the CSI
1000 computations, and did not, for example, selectively focus on same-sex dyads. Because we
1001 were interested in social bonds among unrelated partners, the one exception to this general
1002 rule was kinship. While both male–male (Muller & Mitani, 2005; Watts, 2000) and female–
1003 female (Langergraber, Mitani, & Vigilant, 2009) bonds are common in chimpanzees,
1004 Langergraber, Mitani, Watts, and Vigilant (2013), suggest that bonds between sexes also
1005 exist.

1006 ***Models***

1007 We assessed *P* values for the individual effects based on likelihood ratio tests
1008 comparing the full with respective reduced models (Barr, Levy, Scheepers, & Tily, 2013)
1009 using R function drop1 with argument 'test' set to "Chisq". Confidence intervals for the
1010 estimates were assessed by using the function confint.merMod. Variance Inflation Factors
1011 (VIF; Field, 2005) were derived using the vif function of the 'car' package (Fox &
1012 Weisberg, 2011), applied to a standard linear model excluding the random effects. We
1013 assessed model stability by comparing the estimates obtained from the model based on all
1014 data with those obtained from models with the levels of the random effects excluded one
1015 at a time.

1016 *Model 1.1, Study 1:* We first used a generalized linear mixed model with binomial error
1017 distribution and logit link function to analyse whether aversion to pull the uncertain rope
1018 was influenced by condition. Due to singular fit warnings, we simplified the random slope
1019 structure: The random slopes of session in subject and condition in partner were estimated
1020 to be essentially 0. Because of further singular fit warnings, we continued to simplify the
1021 random effect structure. The final model comprised condition and session as fixed effects
1022 and subject as a random effect. We checked whether the assumptions of normally
1023 distributed and homogenous residuals were fulfilled by visually inspecting a qqplot and the
1024 residuals plotted against fitted values. Both indicated no obvious deviations from these
1025 assumptions. Collinearity was no issue (maximum variance inflation factor: 1.0 for
1026 condition and session). The model revealed to be stable (for the model output, see Table
1027 A2).

1028 *Model 1.2, Study 1:* We used a linear mixed model (Baayen, 2008) to analyse the effect of
1029 condition on the latency to pull the uncertain rope. Due to singular fit warnings, we
1030 simplified the random slope structure: The random slopes of session and condition in
1031 partner were estimated to be essentially 0; we therefore did not include them in the final
1032 model. We log transformed the variable latency to pull the uncertain rope because the
1033 distribution of the response was right skewed. We checked whether the assumptions of
1034 normally distributed and homogenous residuals were fulfilled by visually inspecting a
1035 qqplot and the residuals plotted against fitted values. Both indicated no obvious deviations
1036 from these assumptions. Collinearity was no issue (maximum variance inflation factor: 1.0
1037 for condition and session). The model was revealed to be stable (for the model output, see
1038 Table A3).

1039 *Model 1.3, Study 1:* We used a generalized linear mixed model with binomial error
1040 distribution and logit link function to analyse whether negative emotional reactions in
1041 uncertain trials were influenced by condition. Due to singular fit warnings, we simplified
1042 the random effect structure: The random effect of partner and the random slope of session
1043 in subject were estimated to be essentially 0; we therefore did not include them in the final
1044 model (for the model output, see Table A4).

1045 *Model 2.1, Study 2:* We used a generalized linear mixed model with binomial error
1046 distribution and logit link function to investigate whether the choice of the risky option was
1047 influenced by condition and subject's sex, age, and hierarchy position. Due to singular fit
1048 warnings, we simplified the random effect structure: The random effect of partner was
1049 estimated to be essentially 0; we therefore did not include it in the final model (for the
1050 model output, see Table A5).

1051 *Model 2.2, Study 2:* To investigate whether chimpanzees chose the risky option more often
1052 after being rewarded in risky trials, we used a generalized linear mixed model with
1053 binomial error distribution and logit link function. As we did not find an effect of subject's
1054 sex, age, or hierarchy position in the previous model, we did not include them as fixed
1055 effects. Due to singular fit warnings, we simplified the random effect structure: The random
1056 effect of partner and the random slope of session and condition in subject were estimated
1057 to be essentially 0; we therefore did not include them in the final model (for the model
1058 output, see Table A6).

1059 *Model 2.3, Study 2:* We used a linear mixed model (Baayen, 2008) to analyse the effect of
1060 condition on the latency to choose one option. The random effect structure comprised
1061 subject, partner, and session ID (nested in subject) as random intercepts and session number

1062 and condition in subject and partner as random slopes. We log transformed the variable
1063 latency to pull either rope because the distribution of the response was right-skewed. Due
1064 to singular fit warnings, we simplified the random effect structure: The random effect of
1065 partner was estimated to be essentially 0; we therefore did not include it in the final model
1066 (for the model output, see Table A7).

1067 *Effect size*

1068 We calculated the effect size and confidence intervals for the choice of the risky
1069 option in the social and nonsocial condition of Study 2. The effect size was calculated in R
1070 (R Core Team, 2019) using the function `cohen.d` (Cohen's d) of the `effsize` package
1071 (Torchiano, 2020). This revealed a small effect size ($d = 0.22$, 95% CI = [-0.53, 0.98]).
1072 As our analysis revealed a nonsignificant result, the confidence interval of the effect size
1073 spans the null value of zero. Calcutt et al. (2019) reported a medium effect size ($d = 0.69$,
1074 95% CI = [-0.08, 2.01]). The two confidence intervals overlap in the range of no or a small
1075 effect size, and the confidence interval in our study is narrower. This suggests that the null
1076 hypothesis of no (or a small) effect is true (see Colegrave & Ruxton, 2003; Kelly, 2006).

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1082 **Table A1**

1083 *Sex and Age of All Subjects and Partners Participating in Studies 1 and 2.*

No.	Subjects			Partners		
	Name	Sex	Age	Name	Sex	Age
1	Roy	Male	11	Romeo	Male	14
2	William	Male	18	Romeo	Male	14
3	Niyonkuru	Male	28	Roy	Male	11
4	Tess	Female	26	Roy	Male	11
5	Uruhara	Male	29	Roy	Male	11
6	Chipie	Female	27	William	Male	18
7	Kisa	Male	25	Chipie	Female	27
8	Akela	Female	30	Chipie	Female	27
9	Amizero	Female	29	Chipie	Female	27
10	Joy	Female	13	Bahati	Female	25
11	Dufatanya	Female	27	Bahati	Female	25
12	Jane	Female	14	Bahati	Female	25

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1090 **Table A2**

1091 *Output of Model 1.1, Study 1*

	Estimate	SE	χ^2	p	95% CI	
(Intercept)	-3.385	0.541				
Condition	1.763	0.295	41.486	<.001	1.196	2.376
Session	0.032	0.131	0.056	0.812	-0.230	0.294

1092

1093 **Table A3**

1094 *Output of Model 1.2, Study 1*

	Estimate	SE	χ^2	p	95% CI	
(Intercept)	2.069	0.144				
Condition	0.336	0.142	4.601	0.032	0.034	0.638
Session	0.025	0.033	0.565	0.452	-0.046	0.096

1095

1096 **Table A4**

1097 *Output of Model 1.3, Study 1*

	Estimate	SE	χ^2	p	95% CI	
(Intercept)	-1.617	0.453				
Condition	0.434	0.334	1.443	0.230	-0.328	1.136
Session	-0.036	0.132	0.070	0.791	-0.313	0.237

1098

1099 **Table A5**

1100 *Output of Model 2.1, Study 2*

	Estimate	SE	χ^2	p	95% CI	
(Intercept)	-0.408	0.805				
Condition	-0.604	0.805	0.542	0.462	-2.416	1.156
Session	-0.040	0.269	0.021	0.886	-0.626	0.574
Sex	-1.924	1.412	1.676	0.195	-5.013	1.160
Age	-0.165	0.422	0.146	0.702	-1.084	0.767
Hierarchy position	-1.094	0.711	2.107	0.147	-2.673	0.446

1101

1102

1103 **Table A6**

1104 *Output of Model 2.2, Study 2*

	Estimate	SE	χ^2	p	95% CI	
(Intercept)	0.752	0.457				
Rewarded risky decision in the previous trial	-0.763	0.428	3.255	0.071	-1.656	0.065
Condition	0.771	0.479	2.573	0.109	-0.173	1.766
Session	-0.110	0.237	0.211	0.646	-0.608	0.379

1105

1106 **Table A7**

1107 *Output of Model 2.3, Study 2*

	Estimate	SE	χ^2	p	95% CI	
(Intercept)	1.665	0.057				
Condition	-0.062	0.078	0.612	0.434	-0.229	0.105
Session	0.006	0.020	0.089	0.766	-0.036	0.047

1108