

1 Non-human primates use combined rules when deciding under ambiguity

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26

27 **Abstract**

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30 Decision outcomes in unpredictable environments may not have exact known probabilities. Yet
31 the predictability level of outcomes matters in decisions, and animals, including humans,
32 generally avoid ambiguous options. Managing ambiguity may be more challenging and requires
33 stronger cognitive skills than decision-making under risk, where decisions involve known
34 probabilities. Here we compare decision-making in capuchins, macaques, orangutans, gorillas,
35 chimpanzees and bonobos in risky and ambiguous contexts. Subjects were shown lotteries (a
36 tray of potential rewards, some large, some small) and could gamble a medium-sized food item
37 to obtain one of the displayed rewards. The odds of winning and losing varied and were
38 accessible in the risky context (all rewards were visible) or partially available in the ambiguous
39 context (some rewards were covered). In the latter case, the level of information varied from
40 fully ambiguous (individuals could not guess what was under the covers) to predictable
41 (individuals could guess). None of the species avoided gambling in ambiguous lotteries and
42 gambling rates were high if at least 2 large rewards were visible. Capuchins and bonobos
43 ignored the covered items and gorillas and macaques took the presence of potential rewards
44 into account, but only chimpanzees and orangutans could consistently build correct
45 expectations about the size of the covered rewards. Chimpanzees and orangutans combined
46 decision rules according to the number of large visible rewards and the level of predictability,
47 a process resembling conditional probabilities assessment in humans. Despite a low sample
48 size, this is the first evidence in non-human primates that a combination of several rules can
49 underlie choices made in an unpredictable environment. Our finding that non-human primates
50 can deal with the uncertainty of an outcome when exchanging one food item for another is a
51 key element to the understanding of the evolutionary origins of economic behavior.

52 **Keywords:** gambling, risk, conditional probability, decision-making, monkeys, apes

53

54 **Introduction**

55 Although making decisions is a usual aspect of our life, making the right decision at the right
56 time can sometimes be crucial for our future wellbeing, career development or even survival
57 (1). Given the ever-changing characteristics of their environment, animals including humans
58 make most of their decisions in a context that economists would consider ambiguous as opposed
59 to risky (2,3,see also 4). The most critical difference between these two contexts is how much
60 an individual knows about the likelihood of the outcomes of each possible choice. Indeed, under
61 ambiguity, people have little or no information about these likelihoods. In contrast, people
62 making decisions under risk know the likelihood of each alternative (for example a one in six
63 chance to win) before deciding.

64 Humans sometimes exhibit marked attitudes toward risk (i.e. they can be either risk seekers for
65 small risks like gambling in a casino, or risk averse for high risks, leading most people to take
66 out insurance contracts). They also subjectively evaluate outcomes, and are prone to errors of
67 judgment (5,6). The hot hand effect, for example, consists of continuing to take risks after a
68 series of gains (7). Humans are also generally more affected by losses than by equivalent gains
69 (loss aversion, 8). Some of these characteristics are shared with other species when choosing
70 under risk, and especially our closest living relatives (loss aversion, 9,10, hot hand effect, 11).
71 This suggests that the determinants of our decisions could be inherited from naturally selected
72 features in our ancestors (12–17).

73 The investigation of decision-making under ambiguity is a recent field in non-human primates.
74 It has been studied less than decision-making under risk (14). Ultimately, comparing decision-
75 making under risk and under ambiguity in several primate species may enable us to decipher
76 the cognitive, adaptive and/or ecological mechanisms that shape our choices. Humans value
77 options differently under risk than they do in a context of ambiguity (3,4,18), and human
78 attitudes and choices in one context do not always help to predict accurately choices in the other
79 (19). For example, a risk seeker is not necessarily an ambiguity seeker (see 20 for a review).

80 There is a general consensus in the literature that humans show ambiguity aversion (6,20–22).
81 This is also true of non-human primates (23,24). When given a choice between an ambiguous
82 option or an option that is either risky or safe, bonobos (*Pan paniscus*), chimpanzees (*Pan*
83 *troglydytes*, 24) and rhesus macaques (*Macaca mulatta*, 23) avoided the ambiguous option.
84 Given that most aspects of their environment have an element of unpredictability, this
85 widespread aversion to ambiguity is quite intriguing (14). It is unclear whether individuals
86 reject ambiguity due to a lack of information or because dealing with ambiguity may be
87 cognitively more challenging than dealing with risk. Indeed, in an ambiguous context,
88 individuals may have to compute a range of probabilities to make the best possible decision
89 whereas under risk individuals have all information needed to evaluate the likelihood of options.
90 Earlier risk studies have revealed that several species of great apes, macaques and capuchins
91 take the predictability of outcomes into account to maximize their benefits (11,23,25–28). Other
92 studies have shown intuitive probabilistic inferences in capuchins (*Sapajus apella*, 29) and great
93 apes (30,31). Thus, non-human primates are equipped with the cognitive skills needed to
94 process odds of outcome. However, there are some indications that the decision-making process
95 may shift from odds evaluation to simpler decision rules when the cognitive load of a task
96 increases. In a recent study we presented great apes and monkeys with a risky food gambling
97 task in which information about the odds of winning was displayed in front of them before each
98 trial. To gamble in this game, subjects had to relinquish a food item that was already in their
99 possession to obtain the contents of one out of six cups displayed in front of them. The cups
100 contained different amounts of food, with rewards that were larger, smaller or the same size as
101 the food item the subject already possessed. In the first version of the task, the chances of
102 winning progressively decreased throughout the study, and individuals successfully used the
103 odds associated with each outcome before gambling (11). This gradual decrease in the chances
104 of winning probably facilitated the extraction of information about odds. Odds were modified
105 from one trial to the next in a second version of this task (32), thus requiring individuals to pay

106 close attention to the odds displayed to them at each trial. Here, many individuals applied a
107 Maximax heuristic, and were more likely to gamble when there was at least one chance of
108 winning (disregarding potential losses). Heuristics are simplified decision rules that help
109 individuals to deal with situations that require a high cognitive investment (33,34). Thus,
110 individuals apply heuristics when faced with an increased difficulty in extracting information
111 about the odds. Under ambiguity, where information is partial, individuals may be more likely
112 to make use of simple decision rules rather than attempting to evaluate the odds of winning or
113 losing, but this has not been investigated to date.

114 This study investigated the role played by information about odds in decisions made under risk
115 and ambiguity by capuchin monkeys, Tonkean macaques (*Macaca tonkeana*), orangutans
116 (*Pongo abelii*), gorillas (*Gorilla gorilla*), chimpanzees and bonobos. We used a modified
117 version of the risky gambling game mentioned above. In this task, subjects could bet a food
118 item in their possession in exchange for the contents of one of the six cups displayed in front of
119 them. Each cup contained either a larger or smaller amount of food than the amount possessed
120 by the subject. The decision was made under risk when the subjects could visually assess the
121 odds of winning and losing (for example, they had 5 chances out of 6 to receive more food if 5
122 cups contained a larger cracker and 1 cup contained a smaller cracker than the one they already
123 possessed). Ambiguity was implemented by covering some of the cups. By changing the
124 presence and location of the covers, we could vary the amount of information available so that
125 subjects made their decision under four conditions: *i.* risky lotteries, where subjects could see
126 all the potential outcomes; *ii.* predictably advantageous lotteries, where subjects could not see
127 but could infer (according to how the lotteries were set up, see Methods) that the covered cups
128 contained large rewards; *iii.* predictably disadvantageous lotteries, where subjects could not see
129 but could infer that the covered cups contained small rewards, and *iv.* ambiguous lotteries,
130 where subjects could not guess the exact probabilities associated to potential outcomes. The
131 safe choice was therefore to keep the food they already possessed, while the risky or ambiguous

132 choice was to gamble. This experimental set up allowed us to investigate which elements
133 subjects used to make their decision. We anticipated three decision-making scenarios. First,
134 subjects may reject ambiguous lotteries altogether by only gambling in lotteries without covers
135 (risky lotteries). Second, they may ignore ambiguity and gamble based on visible information
136 through simple heuristics such as counting the number of large visible rewards. Third, subjects
137 may consider the level of information about odds, thus responding differently to contexts in
138 which they can predict their odds of gains and those where they cannot. Unlike the two previous
139 alternatives, this third alternative is more complex because it requires subjects to build correct
140 expectations about the content of the covered cups in predictable lotteries. Great apes, macaques
141 and capuchin monkeys can make inferences based on partial visual information (35–37), and
142 may therefore have the cognitive skills to build correct expectations. However, we cannot
143 exclude that the great apes might be more skilled in doing so. We know more about the
144 inferential skills of great apes than those of other species (38). Evaluating the odds of outcome
145 in risky lotteries or the range of possible odds of outcome odds in the ambiguous one may be
146 less demanding for them than for monkeys. Each species may also have its own decisional
147 pathway, and choices could reflect a species' general sensitivity to risk or ambiguity. For
148 example, macaques (11) and capuchins have sometimes been described as rather risk prone
149 (39), and chimpanzees have been described as more risk prone than bonobos in some studies
150 (27,40). These species might be more likely to gamble in higher risk lotteries than others, and
151 they may be less averse to the ambiguity of the task than the other species.

152

153

154 **Material & Methods**

155 *Subjects*

156 Thirty subjects were involved in the study: 4 brown capuchin monkeys, 5 Tonkean macaques,
157 5 orangutans, 4 gorillas, 7 chimpanzees and 5 bonobos (Table S1). All subjects were socially

158 housed in enclosures with access to indoor and outdoor areas. Water was available *ad libitum*
159 and subjects were not food deprived. Procedures were non-invasive and subjects could choose
160 to stop participating at any time. All individuals had previous experience in a food gambling
161 task and were familiar with exchanging food items of different sizes with a human experimenter
162 (see supplementary material and Table S2 for training and pre-analyses procedures).

163 *Apparatus and experimental procedure*

164 The procedure was a food gambling task similar to that used by Pelé et al. (2014). Six cups
165 were presented aligned in front of the subject. Each cup contained one piece of cracker that
166 could be large (4*4*0.5 cm) or small (1*1*0.5cm) (Figure 1). We manipulated the contents of
167 the cups to offer lotteries with varying gain predictability (Table 1). Crackers were always
168 placed in the cups according to their size and were aligned in decreasing order of size from the
169 left to the right. Lotteries were presented under four conditions (Table 1): a) *risky*: no cups were
170 covered, thus all potential crackers were visible (Figure 1a), b) *predictably advantageous*: two
171 of the six cups were covered, but the ranking of crackers by size enabled subjects to infer that
172 two large crackers were hidden under the covers (see for example lottery 6, Table 1), c)
173 *predictably disadvantageous*: two of the six cups were covered, and the individual could infer
174 from their position that they contained small crackers (see for example lottery 22, Table 1), and
175 d) *ambiguous*: two of the six cups were covered and subjects could not predict the size of the
176 hidden crackers (Figure 1b). Note that all subjects had already experienced the ordering of
177 crackers by size in the lottery cups in a previous study on decision-making under risk (32).

178 In each trial the experimenter sat in front of the subject's compartment holding an initial food
179 item (always a medium-sized cracker measuring 2*2*0.5 cm) in one hand, and the lottery in
180 the other hand (i.e. the tray of six aligned plastic cups). The experimenter ensured that the
181 subject had seen the six-cup tray, and then gave him or her the initial food item. The
182 experimenter held out her empty hand and offered the subject the opportunity to gamble by
183 giving the initial food item back. If the subject chose to keep the initial allocation, the trial

184 ended. If the subject gambled, it received the contents of one of the six cups, randomly
185 determined prior to testing. While the subject consumed the cracker (either the initial food item
186 or the lottery cracker), the experimenter refilled the cups out of the subject's sight before
187 starting the next trial with the next lottery. In the cases where the lottery contained covered
188 cups, a subject who decided to keep the initial allocation would be shown the contents of the
189 covered cups and the trial would end. If the subject chose to return the initial allocation, the
190 experimenter removed the covers then gave the subject the contents of a randomly assigned cup
191 which could sometimes be one of the covered cups. A total of 28 lotteries (Table 1) were used,
192 each presented once in a random order within a series of 28 trials (i.e. one lottery after the
193 other), and each series was repeated 18 times (18 sessions). To prevent satiety, the great apes
194 participated in 14 trials per day and the monkeys in 7 trials per day.

195

196 *Data analysis*

197 We sought to identify which of the following variables best explained the responses of subjects:
198 the species, the number of visible large rewards (#LR_v, from 0 to 6), the level of information
199 (risky, predictably advantageous, predictably disadvantageous, or ambiguous), the point in the
200 study duration (either during the first 9 sessions from S1 to S9 or the last 9 sessions, from S10
201 to S18), and the size of the outcome received at the previous trial (large-, medium-, or small-
202 sized rewards). We added subjects, study site (as a proxy for housing conditions) and age
203 (juvenile or adult) as random factor (with the following nested structure : 1/Age/Subjects and
204 1/Study site/subjects). We first ran a GLMM model (package *lme4*, in R) with a model selection
205 procedure based on Akaike's second-order information criterion (function *dredge* in R, package
206 *MuMin*, 41, AIC_c, 42) in order to identify the variables contributing to the best model, all
207 species included. Given that the best model was statistically equivalent in terms of data fit to
208 the full model ($\Delta < 2$), we chose the model with the highest explanatory power, i.e. the full
209 model.

210 For each species, we then used the decision tree approach with these variables (except the
211 variable “species”) to analyse the data because we 1) expected interactions between variables
212 and non-linear effects and 2) wanted to capture the hierarchical decision pathway (order of
213 variables, potential threshold of these variables) for each species. The random factors study site
214 and age were not included in this analysis as each species had only one study site, and some
215 species had only adult individuals. Generalized Linear Mixed Models (GLMMs) allow for the
216 incorporation of within individual repetitions and the dependent variable (gambling) was
217 binomial. We therefore used model-based recursive partitioning (a type of decision tree) based
218 on GLMMs called generalised linear mixed effects models trees (GLMM trees). The algorithm
219 identifies subgroups, i.e. the terminal nodes, which differ according to the gambling rate. To
220 identify these subgroups, the observations in the dataset are partitioned with respect to defined
221 splitting variables, like in any tree algorithms. The main interest of tree-based algorithms is that
222 they can handle high-order interactions, which in our case correspond to the decision pathway.
223 Unlike other tree algorithms, GLMM trees take into account the clustered structure of datasets
224 by including a cluster random effect, which allows us to account for the pseudo replication of
225 the same individual in the dataset. Since we wanted to identify subgroups differing from each
226 other by their gambling rate, we specified the node-specific model that included only one
227 intercept (i.e., the gambling rate mean per subgroups). Specifically, the tree algorithm proceeds
228 via the following steps, all of which are adjusted for the random effects: at each node, the
229 algorithm assumes that there is at least one splitting variable, which, at a certain threshold (i.e.,
230 optimal split point) divides the observations in two subsets, ultimately leading to more stable
231 (i.e., with a lower variance) intercept coefficients (i.e., gambling rate values) than at the
232 beginning. This stability is objectified via the parameter instability test. The algorithm estimates
233 an optimal split point for each splitting variables and applies instability tests. If several
234 instability tests show significant results ($p < 0.05$ for several splitting variables), the node
235 observations are partitioned into two subsets with respect to the splitting variable associated

236 with the highest instability (lowest p value). This process is repeated recursively until no further
237 significant instabilities are found (i.e., all $p > 0.05$) or the subgroups become too small. All tests
238 are Bonferroni-adjusted to account for multiple testing across all covariates.

239 We used the function `glmertree` of the package `glmertree` (43). For each species, we specified a
240 model with only the intercept in order to identify subgroups differing on their gambling rate.
241 To account for individual differences, we set individual identity as a random intercept. Finally,
242 we specified the splitting variables “number of large visible rewards”, “level of information”,
243 “point in the study duration”, and “previous outcome” as potential partitioning variables.
244 Because the response variable is a binary variable, we specified “binomial” as the model family
245 whose link function is the function logit by default. Further details on the R code are given in
246 the supplementary material. Because of our initial specifications in the model (including only
247 the intercept), we only obtained the intercept coefficient (μ) corresponding to the logit
248 transformation of the gambling probability. These gambling probabilities were computed using
249 the inverse of the logit function (1) to extract the mean of gambling rate per model.

$$250 \quad \text{logit}^{-1}(\mu) = \frac{1}{1 + e^{-\mu}} \quad (1)$$

251 In the decision trees, we report the value of (μ) and the gambling probabilities as percentages
252 (Figure 2 to 7). We also calculated the intra-class correlation (ICC, see supplementary
253 procedure for the R code) for each species to evaluate how much variance could be explained
254 by inter-individual variations.

255 In addition, we ran a second analysis to evaluate if the previous choice and its outcome could
256 influence the next decision (stay with or shift from the previous decision to exchange or not).
257 To do so, we looked at all the lotteries where subjects received information that their choice
258 had been right or wrong. This analysis was based on a subset of data involving 9934 decisions.
259 The dataset was restricted to the following four cases: 1) trials where individuals exchanged
260 and were right to do so (when they subsequently won, whatever the lottery); 2) trials where they

261 refrained from exchanging and were right to do so. But note that this ‘rightness’ could only be
262 experienced by subjects in lotteries 25, 26, and 27, where they could see that they would have
263 lost if they had exchanged, i.e. by seeing only small rewards when the covers of the cups were
264 removed. In other lotteries, the subjects had no way to guess which cup they would have
265 received. We cannot therefore make a judgment about whether or not individuals felt that their
266 choice not to exchange had been wise; 3) trials where they exchanged and were wrong to do so
267 (when they subsequently lost, whatever the lottery); 4) trials where they did not exchange and
268 were wrong to do so. But note here also that this ‘wrongness’ could only be experienced by
269 subjects in lotteries 2, 3 and 4, where they could see that they would have won if they had
270 exchanged, i.e. seeing only large rewards when the covers of the cups were removed. In other
271 lotteries, the subject had no way to guess which cup they would have received. Thus, we could
272 not evaluate whether individuals would have regretted their decision to not exchange. For each
273 of these four cases, we then looked at whether they maintained the strategy in the following
274 trial (right-keep, right-shift, wrong-keep, wrong-shift: an example of right-keep would be to see
275 the individual refusing to exchange after having being right to not exchange in the previous
276 trial).

277

278 If individuals were influenced by the result of the previous decision, we predicted that being
279 right at a given trial should make subjects adopt the same strategy in the following trial
280 (whatever the strategy, i.e. exchanging or not). We also predicted that subjects should shift
281 strategy if they had been wrong in the previous trial (whatever the strategy). We conducted a
282 GLMM analysis with a logit link function and binomial distribution to evaluate if the
283 predictions were verified (1: prediction verified, 0: prediction unverified) according to the
284 species and the type of decision (right or wrong), with individuals as random factor. We ran a
285 model selection analysis to select the best model.

286

287 **3. Results**

288 *Identifying the main decisional variables and building the decision tree*

289 The results of the best model selection procedure indicate that the full model including the five
290 variables was the best model (see Table S3 in the supplementary material). The results of the
291 decision tree analysis are shown for each species in Figures 2 to 6 and summarized in Table 2.
292 As expected, the first splitting variable is the number of large visible rewards (#LRv) for all
293 species. The scenarios then differ according to each species. Some trees remain “simple” with
294 5 terminal nodes in capuchins, 6 in bonobos and 7 in gorillas, while others are more complex
295 with 9 nodes in macaques, 11 nodes in chimpanzees and 13 nodes in orangutans. Species results
296 are presented in increasing order of terminal nodes in the decision trees. For individual
297 gambling rates, see Table S4 in the supplementary results section and see Table 2 for the
298 proportion of total variance explained by inter-individual variance (ICC).

299 The simplest tree, i.e., the one with the fewest nodes, is that of capuchins (Figure 2).
300 They start gambling more than 50% of the time when at least one large reward is visible, as
301 indicated by the probability of gambling shown below each terminal node of the figure (here,
302 from node 4 in Figure 2). The first splitting variable is the number of large visible rewards
303 (LRv). They distinguish between lotteries with 0, 1, 2, and 3-6 LRv, gambling more as the
304 number of LRv increases. For lotteries with at least 3 LRv, the probability that capuchins will
305 gamble is higher by the end of the study (96.32%, node 9) compared to the beginning (89.87%,
306 node 8). Previous outcomes do not play any role and the level of information is never a splitting
307 variable, suggesting that capuchins do not consider the level of information provided by the
308 different lotteries (i.e. the fact that the covers hide rewards).

309 For bonobos, the number of LRv is also the first splitting variable (Figure 3). They start
310 gambling more than 50% of the time in lotteries with at least 2 LRv (from node 7). They
311 distinguish between 0, 1, 2, 3 and 4-6 LRv (gambling more as the number of LRv increases).
312 In lotteries with 2 LRv, they are less likely to gamble at a given trial if the previous outcome

313 was a medium-sized reward (i.e., if they had not exchanged; 67.67% of gambling, node 7) than
314 a reward of any other size (81.27% of gambling, node 8). Like for the capuchins, the level of
315 information is never a splitting variable, suggesting that they do not consider the level of
316 information provided by the different lotteries.

317 For gorillas, the first splitting variable is also the number of LRv (Figure 4). They
318 gamble more than 50% of the time for lotteries with at least 1 LRv (node 7) and they distinguish
319 between lotteries with 0, 1, 2, 3-5 and 6 LRv. For lotteries with 0 LRv, the level of information
320 is also a splitting variable. They are more likely to gamble in lotteries with covered cups
321 (19.14% of the time, node 3) than in risky lotteries (4.61%, node 4). This evidence strongly
322 suggests that the subjects knew that some of the covered cups can contain large rewards but do
323 not make any distinction between the different levels of information. For lotteries with 1 LRv,
324 the previous outcome can play a role on the decision as gorillas are more likely to gamble
325 (86.67%, node 8) if they received a large or a small reward (i.e., if they had exchanged) at the
326 previous trial than if they had received a medium-sized reward (66.70%, node 7) in other words,
327 if they had not exchanged.

328 For Tonkean macaques, the first splitting variable is also the number of LRv (Figure 5).
329 They generally start gambling more than 50% of the time for lotteries with at least 2 LRv (from
330 node 8) but the level of information, point in the study duration, and previous outcomes are also
331 splitting variables. With 0 LRv, they almost never gamble (1.43%, node 3) and gamble more
332 with 1 LRv (29.31%, node 4). With 2 LRv they are more likely to gamble if they received a
333 small reward at the previous trial (94.93%, node 10) than if they received any other size of
334 reward (equal to or less than 81.16%, node 8 and 9). With 2 LRv, if the previous reward was
335 large or medium-sized they took into account the level of information, playing more in
336 predictably advantageous lotteries (81.16%, node 8) than in the others (65.68%, node 9). For
337 lotteries with 3 LRv or more, they generally gamble more at the end of the study (92.01%, node
338 17) than at the beginning (node 14-16, but not 15), and at the beginning of the study, they can

339 be influenced by both previous outcomes and #LRv (nodes 14 to 16, see Figure 5 for more
340 details).

341 The first splitting variable for chimpanzees is also the number of LRv (Figure 6). They
342 gamble more than 50% of the time for lotteries with at least 1 LRv (from node 10 and 11). For
343 lotteries with 0 LRv, the level of information is also a splitting variable. Chimpanzees rarely
344 gamble, but they are more likely to gamble for ambiguous lotteries (16.11%, node 3) than
345 predictably disadvantageous and risky lotteries (below 7.02%, node 5 and 6). In the last two
346 types of lotteries, the point in the study duration is also a splitting variable, as the probability to
347 gamble is lower at the end of the study (1.54%, node 6) compared to the beginning (7.02%,
348 node 5). For lotteries with 1 LRv, the level of information is, again, a splitting variable.
349 Chimpanzees gamble more at predictably advantageous lotteries (75.38%, node 10) than at the
350 others (59.27%, node 11). For lotteries with 2 LRv, previous outcome and point in the study
351 duration play a role. They are less likely to gamble after receiving a medium-sized reward at
352 the beginning of the study (node 14) compared to the end (node 15). This outcome effect is also
353 detected for 3-6 LRv lotteries, but only occurs at the beginning of the study (node 19).

354 Orangutans distinguish between lotteries with 0, 1, 2, 3, 4-5, and 6 LRv (Figure 7). They
355 are more likely to gamble more than 50% of the time for lotteries with at least 1 LRv (node 11
356 and 13, but not 14). The level of information is a splitting variable in two cases. The first case
357 is lotteries with 0 LRv. In the first 9 sessions, the subjects never gamble for risky lotteries (node
358 7) and are more likely to gamble at ambiguous lotteries (node 5) compared to predictably
359 disadvantageous lotteries (node 6). After the first 9 sessions, they gamble from time to time but
360 at very low rates, whatever the level of information (node 8). The second case concerns lotteries
361 with 1 LRv. Here subjects are more likely to gamble more for predictably advantageous lotteries
362 compared to others, but they only do so in the second half of the study (node 13 versus 14).
363 They also gamble more for 2 LRv lotteries at the beginning of the study than they do at the end.

364

365 *Investigating the potential effects of previous decisions*

366 In general, subjects followed the prediction (keep the strategy when right and shift when
367 wrong) in 5142 trials (51.76%) and did not follow the prediction (shift when right, or keep when
368 wrong) in 4792 trials (48.24%). However, the best model selection indicates that the variables
369 species and type of decision (right or wrong), and the interaction between them, influenced the
370 likelihood to follow the prediction (see supplementary Table S5).

371 A pairwise comparison with a Bonferroni correction indicated that capuchins, macaques
372 and orangutans were more likely to not follow the “right keep/wrong shift” strategy than to
373 follow it (capuchins: estimates = -0.32 ± 0.11 , 95% CI = -0.61 to -0.03; macaques: estimates =
374 -0.36 ± 0.09 , 95% CI = -0.59 to -0.13; orangutans: estimates = -0.27 ± 0.08 , 95% CI = -0.5 to -
375 0.05). This effect was not detected in other species. The effect of the type of decision indicates
376 that correct predictions (right keep/wrong shift) were more likely than incorrect predictions
377 (right shift/wrong keep) after a right decision (mean correct predictions: 63%; GLMM:
378 estimates = 0.5 ± 0.04 , 95% CI = 0.42 to 0.59), and that incorrect predictions were more likely
379 than correct predictions after a wrong decision (mean incorrect prediction: 72.5%; GLMM:
380 estimates = -0.98 ± 0.05 , 95% CI = -1.09 to -0.87).

381 The pairwise comparisons of the interaction between the variables “type of decision”
382 and “species” indicate that for the right decisions, keeping the same strategy was more likely
383 than shifting in all species except in the Tonkean macaques (macaques: estimates = 0.13 ± 0.09 ,
384 95% CI = -0.12 to 0.39; capuchins: estimates = 0.42 ± 0.09 , 95% CI = 0.14 to 0.69; orangutans:
385 estimates = 0.75 ± 0.09 , 95% CI = 0.5 to 0.99, chimpanzees: estimates = 0.59 ± 0.07 , 95% CI =
386 0.39 to 0.8, gorillas: estimates = 0.72 ± 0.09 , 95% CI = 0.44 to 0.99; bonobos: estimates = $0.42 \pm$
387 0.09 , 95% CI = 0.14 to 0.69). In the wrong decisions, all the species were also more likely to
388 maintain their decision than to shift strategy (macaques: estimates = -0.85 ± 0.12 , 95% CI = -
389 1.19 to -0.5; capuchins: estimates = -1.05 ± 0.15 , 95% CI = -1.49 to -0.61; orangutans: estimates
390 = -1.29 ± 0.11 , 95% CI = -1.63 to -0.96, chimpanzees: estimates = -0.88 ± 0.09 , 95% CI = -1.15

391 to -0.61, gorillas: estimates = -1.14 ± 0.12 , 95% CI = -1.5 to -0.79; bonobos: estimates = -0.67
392 ± 0.12 , 95% CI = -1.04 to -0.31, see Supplementary Figure 1). This analysis also indicated that
393 chimpanzees, gorillas, and orangutans were more likely to keep the same strategy after a right
394 decision than Tonkean macaques (comparison chimpanzee-macaque: estimates: 0.46 ± 0.11 , z
395 = 4.04, $p < 0.01$; comparison gorilla-macaque: estimates: 0.59 ± 0.13 , $z = 4.50$, $p < 0.001$;
396 comparison macaque-orangutans: estimates: -0.61 ± 0.12 , $z = -4.97$, $p < 0.001$). Finally,
397 bonobos were more likely to shift strategy after a wrong decision than orangutans (estimates:
398 0.62 ± 0.17 , $z = 2.75$, $p = 0.02$). Thus, while making the right decision may have slightly biased
399 individuals' next decision, making the wrong decision did not affect the following choice.

400

401

402 **4. Discussion**

403 The main goal of this study was to comparatively evaluate the cognitive strategies involved
404 in the resolution of an ambiguous gambling decision in several species of non-human primates.
405 We summarized the results in Table 2. Capuchins and bonobos did not consider the level of
406 information, ignoring the fact that rewards could be hidden. Gorillas seemed to know that
407 covers could hide large rewards, but they did not discriminate between predictable and
408 ambiguous lotteries (see Figure 4, nodes 3 and 4). Tonkean macaques may have discriminated
409 between predictably advantageous and other lotteries, but it occurred in a limited number of
410 occasions (only for 2LRv lotteries, and only after receiving a large or a medium-sized reward,
411 see Figure 5, node 8). Only orangutans and chimpanzees formed correct expectations about the
412 contents of the cups in more than one instance in the decision tree. A potential ceiling effect
413 (high rates of gambling as soon as more than 1 or 2 large rewards were visible) may have
414 prevented the detection of marked attitudes towards ambiguity. Nonetheless, our results stand
415 out from previous studies reporting strong aversion to ambiguity in most tested primate species

416 (23,24). Far from being unsettled by the ambiguity of this particular context, each species in
417 this study resolved each trial with its own strategy.

418 One of our hypotheses was that heuristics could be used in this ambiguous context. Indeed,
419 these simple decision rules could alleviate the cognitive load of each decision. Note that
420 although humans can estimate probabilities, they often rely on heuristics to increase the speed
421 of the decision or to avoid the cognitive cost/challenge (44). In our study, capuchins and
422 bonobos clearly used a simple strategy based solely on the number of large visible rewards.
423 Capuchins gambled in 52% of the trials if at least one large reward was visible. This is
424 reminiscent of the Maximax heuristic reported in a previous study testing decision under risk
425 (32). Similarly, bonobos used a simple decision rule and mostly gambled in lotteries with at
426 least 2 large visible rewards. They may therefore have used the number of large visible rewards
427 as a proxy to evaluate the odds, which is a heuristic in itself. We know that these species (like
428 all the non-human primate species tested so far) can easily discriminate between different food
429 quantities (45–47). Focusing on the size and number of large crackers thus appears a good way
430 to make a rapid decision. A focus on reward magnitude has also been shown to impact decision
431 under risk in humans and non-human primates (48). In this recent study, Farashahi et al. (2019)
432 showed that in an uncertain environment, decisions were more likely to follow an additive
433 model of choice rather than a multiplicative one. When individuals have no exact information
434 about odds, they first compare what they already possess and what they may obtain, then
435 evaluate reward probabilities separately and make their choice based on a combination of these
436 two pieces of information. The heuristic detected in capuchins and bonobos is mostly based on
437 the number of large visible rewards and could correspond to a model of this type.

438 Other species seem to understand that some information was missing and that the covers hid
439 some rewards. Tonkean macaques might belong to this category, although the effect of the level
440 of information was only detected in lotteries with 2 LRV and only when the previous outcome
441 had been large or medium sized (figure 5, node 8), a result which we cannot explain. If Tonkean

442 macaques had indeed considered that covers always hid large rewards in predictably
443 advantageous lotteries, we would not have expected an effect of outcome. In addition, we would
444 have expected to detect an effect of covers in other lotteries (0 LRV and 1 LRV lotteries), which
445 was not observed. Thus, the evidence concerning the expectations of Tonkean macaques is
446 inconclusive. Gorillas may also belong to the group of species understanding that some
447 information was missing. They generally were very likely to gamble as soon as 1 LR was
448 visible. We could therefore only detect an effect of the level of information in lotteries with no
449 LRV, where they gambled as if they expected potential large rewards whatever the type of
450 lotteries (ambiguous or predictably disadvantageous, see Figure 4, nodes 3 versus node 4). This
451 response may be due to some attraction to ambiguity, but given that we did not detect it
452 elsewhere, we cannot affirm this. Given that their expectations were not necessarily correct
453 (they gambled similarly in node 3 in ambiguous lotteries, which could indeed yield a reward,
454 and in predictably disadvantageous ones, which could not), they seem to have failed to grasp
455 the “predictable” component of the task.

456 Chimpanzees and orangutans displayed a more complex understanding than the other species
457 that some information was missing and that covers hid some rewards. One of our predictions
458 was that individuals would be able to guess what was underneath the covers in the predictable
459 lotteries and would gamble more if they expected large rewards and less if they expected
460 smaller rewards, or if they were faced with risky lotteries. The response of chimpanzees and
461 orangutans confirmed this prediction for lotteries with 1 LRV. The visible odds of winning
462 cannot explain this result. Note that this effect was not detected in lotteries with 2 LRV or more,
463 as both species already gambled at high rates in these cases. These two species also
464 distinguished between the different levels of information in lotteries with no LRV, seemingly
465 forming the correct expectations that ambiguous lotteries were more likely to be advantageous
466 than the others. Great apes are generally capable of dealing with visible and invisible
467 information in tasks built around disjunctive syllogisms. They can make inferences and deduce

468 that if no reward is visible in box A and no information is available about box B, then they are
469 more likely to find food in box B than in box A (36). Moreover, they can also make inferences
470 about the location of food in invisible displacements (49–51) and two-item tasks (49,52). There
471 is also some evidence that great apes are capable of diagnostic and predictive inference (see 38
472 for a review). In economics, making inferences involves a computation of conditional
473 probabilities using Bayes' rule, a cognitively demanding task. However, it is not clear what
474 kind of reasoning chimpanzees and orangutans used in our task. A more detailed evaluation of
475 their decisional steps shows that individuals first used the number of LRv, which is a visual and
476 real cue, followed by their own expectations about what was hidden by the covers. Here is an
477 example of how chimpanzees may have psychologically apprehended lottery 15 compared to
478 the other 1 LRv lotteries: "If I see 1 LRv then I should not gamble, but I can guess that there
479 are two large rewards underneath the two covers. Therefore, I will gamble". In humans, such
480 an attitude would be modelled as follows: "If there is a 100% probability of having two large
481 rewards under the covers, conditional on there being one large visible reward on the right of the
482 cover, then one must rationally gamble in 100% of cases". To our knowledge, this combination
483 of factual and expected information has not been reported in gambling and decision-making
484 studies in primates, and is surprising insofar that expectation pushes the individual into taking
485 actions that are contrary to the facts (i.e. gambling despite the fact that there is no interesting
486 reward visible).

487 Interestingly, the decisions made by orangutans changed throughout the study with the
488 parallel occurrence of a simplification of the decision for 0 LRv lotteries and a complexification
489 of the process for 1 LRv. It seems that the orangutans decided to invest less energy in the 0 LRv
490 lotteries by the end of the study and focus more on the 1 LRv lotteries. This is a rather efficient
491 strategy as they were highly likely to lose in 0 LRv lotteries whatever the condition. Experience
492 with the set up and the different lotteries probably explains these adjustments in the decisional
493 process. Indeed, we gave each subject the possibility to see what was underneath the covered

494 cups after each trial. We did so to ensure that individuals received the correct information at
495 each trial and would not progressively build erroneous beliefs based solely on their own
496 outcomes. In a complementary analysis, we evaluated how seeing underneath the covers could
497 affect individuals of each species. Indeed, the notions of regret (for example not gambling then
498 realizing that large rewards had been hidden, 53–56) or confirmation (having gambled and
499 obtained a large reward, thus validating its choice, 57) can impact the next decision. Our results
500 show that confirmation about the rightness of a previous choice may have encouraged subjects
501 to select the same choice in the next trial (albeit in about 60% of the cases, which is admittedly
502 slightly more than a 50% random choice, see also 58, for a lack of win-stay/lose-shift strategy
503 in rhesus macaques). However, regrets about a wrong choice did not lead individuals to shift
504 their decisions in the next trial. We also showed that the size of the reward received in the
505 previous trial could influence the decision for all species except capuchins and orangutans. In
506 most of these cases but one (in macaques), individuals were less likely to gamble if they had
507 just received a medium-sized reward rather than a small or large one. In other words, they were
508 less likely to gamble if they had not gambled at the previous trials (retaining a medium-sized
509 reward) compared to when they had gambled (and either lost or won). Thus, it was not really
510 the previous outcome that influenced the decision, but rather the previous decision in itself.
511 This suggests that individuals could sometimes make a decision that they would apply in at
512 least two consecutive trials, whatever the lottery. This may indicate a decrease in their attention
513 level after a correct decision. Few existing risk studies have considered how subjects are likely
514 to change the way they evaluate each option with time and experience, or explored the
515 motivational factors involved (10). Further studies with more in-depth econometrics measures
516 are needed to investigate these questions in our set up.

517 The current results raise the difficult question of interspecies differences and whether the
518 latter could be explained by different cognitive toolboxes and/or different socioecology (59).
519 The ability of chimpanzees and orangutans to combine facts and abstractions in this study

520 contrasts with the simplicity of the responses of bonobos and capuchins, which used simpler
521 decision rules. We expected the strategies of great apes to be more complex than those of
522 monkeys, using more steps and more adjustments to various modalities of the task. However,
523 the responses of gorillas and macaques are intermediate and not so clear-cut. The response of
524 bonobos can also be considered surprising, i.e. a behaviour that is very much like that of
525 capuchins. One possibility is that responses here are not connected to their cognitive abilities
526 but rather to the more general difficulty bonobos have dealing with risk and ambiguity in
527 comparison to chimpanzees, which could be linked to the feeding ecology of each species
528 (24,40,59). However, both species exhibited similar ambiguity aversion when compared in an
529 ambiguous gambling game where they had no information about the odds (24). This logically
530 leads to the question of whether each species could be influenced by a specific attitude towards
531 risk and ambiguity. The fact that capuchins, chimpanzees, orangutans, and gorillas gambled
532 above 50 % of the time for the risky 1 LRv lottery may suggest risk-seeking behavior (Table
533 2). Several studies using standard risky choice tasks have reported marked attitudes towards
534 risk in capuchins (risk seekers, 39), macaques (risk seekers 60), bonobos (risk avoiders 40) and
535 chimpanzees (risk seekers, 40). However, these attitudes strongly depend on various parameters
536 including the type of task (in macaques 58), or experience with the set up (in macaques 61). In
537 a former study using a risky food gambling task very similar to the current one, we showed that
538 capuchins, macaques, chimpanzees, gorillas and bonobos were mostly risk averse (10). In the
539 current study, we did not have sufficient statistical power to run an econometric analysis on
540 attitudes towards risk, but the possibility that these attitudes could have influenced the responses
541 of individuals whatever their species cannot be entirely excluded.

542 Another key future improvement to this study would be to test a larger number of subjects
543 per species. Our sample size remains comparable to or larger than what is usually done in the
544 field of primate cognition. However, our data have shown that in some cases, individual
545 variations explained a large part of the variance, thus calling for a larger sample size. Our

546 limitation lies in the small number of subjects available to take part in such studies. Although
547 the diversity in the housing facilities of individuals could be considered another limitation, all
548 individuals lived in a captive group setting with indoor-outdoor access, enrichment and frequent
549 cognitive stimulations, which made their environments very similar. We nevertheless took this
550 factor into account by implementing the study site as a random factor in the main model. It is
551 also important to highlight that all the subjects here, except the chimpanzees, had already had
552 extensive experience of cognitive studies, having been involved in dozens of them in the
553 facilities in which they were housed. The skills detected in our study may therefore be
554 potentially harder to detect in less trained or wild individuals. Age can also impact decision-
555 making strategies under risk and ambiguity in young and adolescent humans compared to adults
556 (62–65), but this factor was taken into account as it was implemented as a random factor in the
557 main model. Additional work is needed on the responses of these species under ambiguity and
558 how this may be linked to both their socioecology and/or cognitive limitations.

559 Each species produced its own solution when faced with ambiguity. Some are based on facts
560 and ignore invisible cues, whilst others are based on decision rules combining observable facts
561 and expectations. More detailed analyses would be required to evaluate decisions at the
562 individual level. Here, we used a new methodological approach that can detect the diversity of
563 strategies at the species level while taking into account individual repetitions. All species
564 successfully applied one strategy that would minimize the potentially disruptive role of
565 ambiguity. Given that ambiguous situations are likely to be frequently met in the environment,
566 this response is unsurprising. Interestingly, we did not find any evidence of strong ambiguity
567 aversion (gambling solely for risky lotteries for example) as the individuals could gamble
568 regardless of the amount of information available. One possibility is that our set up was not
569 ambiguous enough to elicit such a strong ambiguity aversion. Indeed, the lack of information
570 could be overcome by various strategies such as guessing, ignoring or imagining the presence
571 of a reward hidden in the cups. Further studies with increased levels of ambiguity may be

572 needed to evaluate how these species cope in this context. Making a decision based on the
573 amount of information (high under risk, low under ambiguity) rather than a purely automatic
574 rejection of ambiguity appears to be less costly in terms of survival and was most probably
575 promoted through natural selection.

576 It is still unclear whether the strategies observed in this study reflect those used by
577 individuals in their everyday lives when dealing with ecological and social challenges in
578 captivity, and whether these strategies reflect the decision-making profile of their wild
579 counterparts. Nonetheless, showing that some great apes could use advanced reasoning
580 processes like conditional inferences to decide whether to gamble and exchange food is a
581 significant step in our understanding of the evolution of economics in humans.

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583

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729 **Figures**



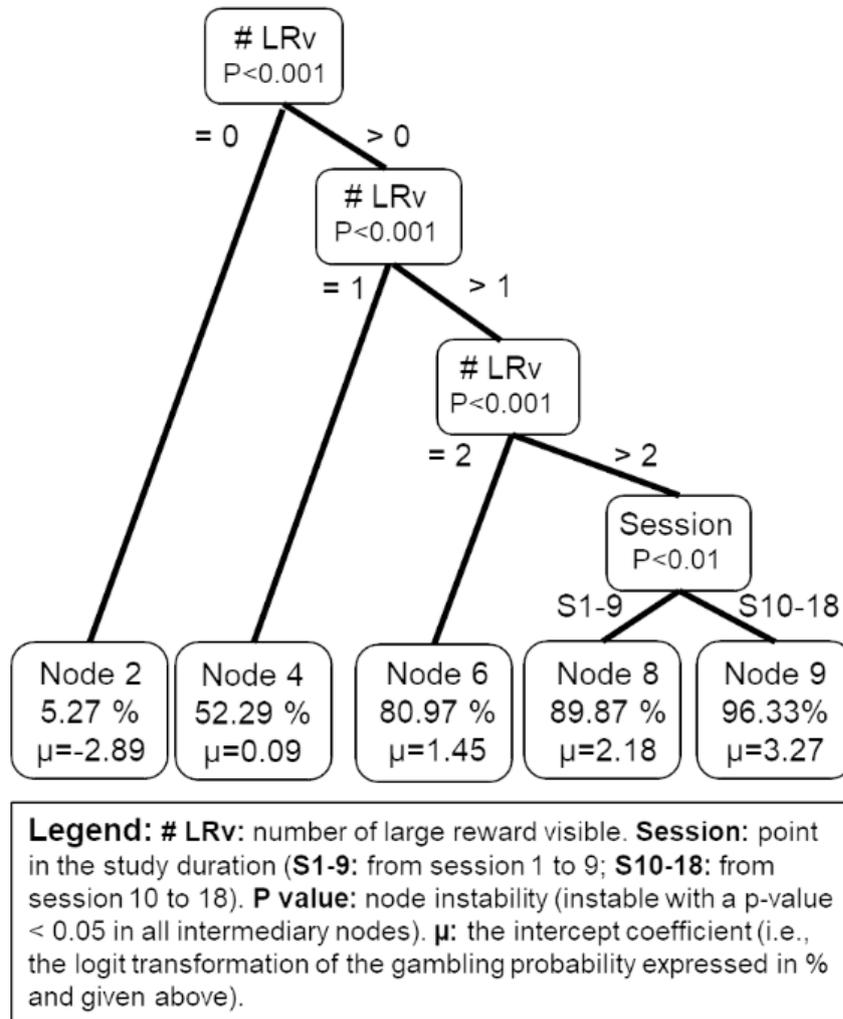
730

731 **Figure 1.** Example of two lotteries presented to the subjects. a) A tray of six plastic cups containing
732 pieces of crackers that are either larger or smaller than the food item they have already been given. In
733 this risky lottery (#16), 3 cups contain a large cracker (cups 1-3, left) and 3 cups contain a small cracker
734 (cups 4-6, right). There are no covers and individuals can see that there is a 50% chance of success. b)
735 In this ambiguous lottery (either lottery #10, #14 or #18), there are 2 covers in the middle that can each
736 hide small or large crackers. Individuals cannot precisely estimate their chances of winning. Large
737 crackers: 4 x 4 x 0.5 cm. Small crackers: 1 x 1 x 0.5 cm.

738

739

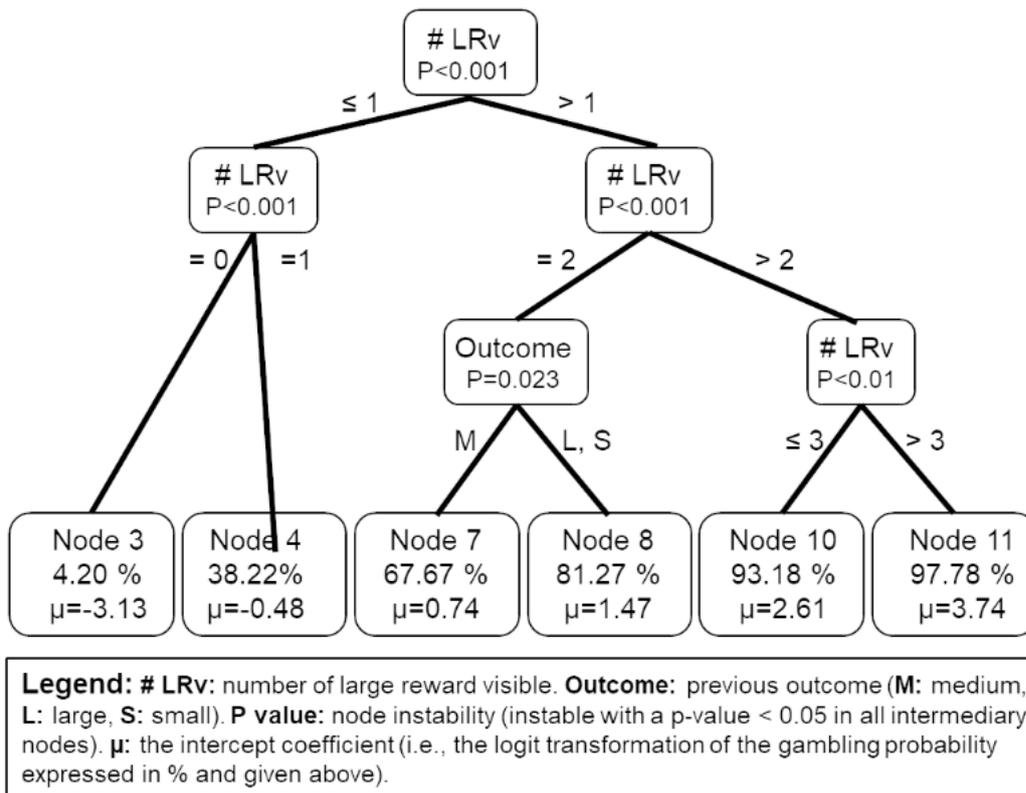
740



741

742 **Figure 2.** Decision tree for the capuchin monkeys showing the hierarchical organisation of the
 743 variables structuring the decision. Capuchins gamble more than 50% of the time when at least
 744 one large reward is visible (from node 4). For 3 LRv lotteries (node 8 and 9), they also gamble
 745 more at the end of the study compared to the beginning.

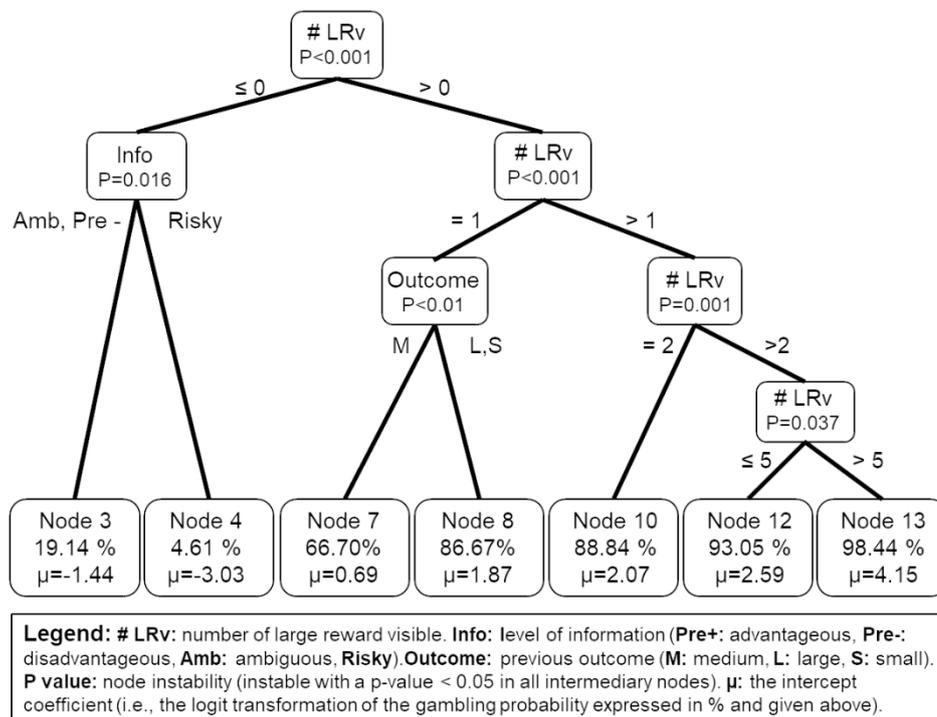
746



747

748 **Figure 3.** Decision tree for the bonobos. Bonobos gamble more than 50% of the time in lotteries
 749 with at least 2 LRv (from node 7). In lotteries with 2 LRv, they are less likely to gamble if the
 750 previous reward was medium-sized.

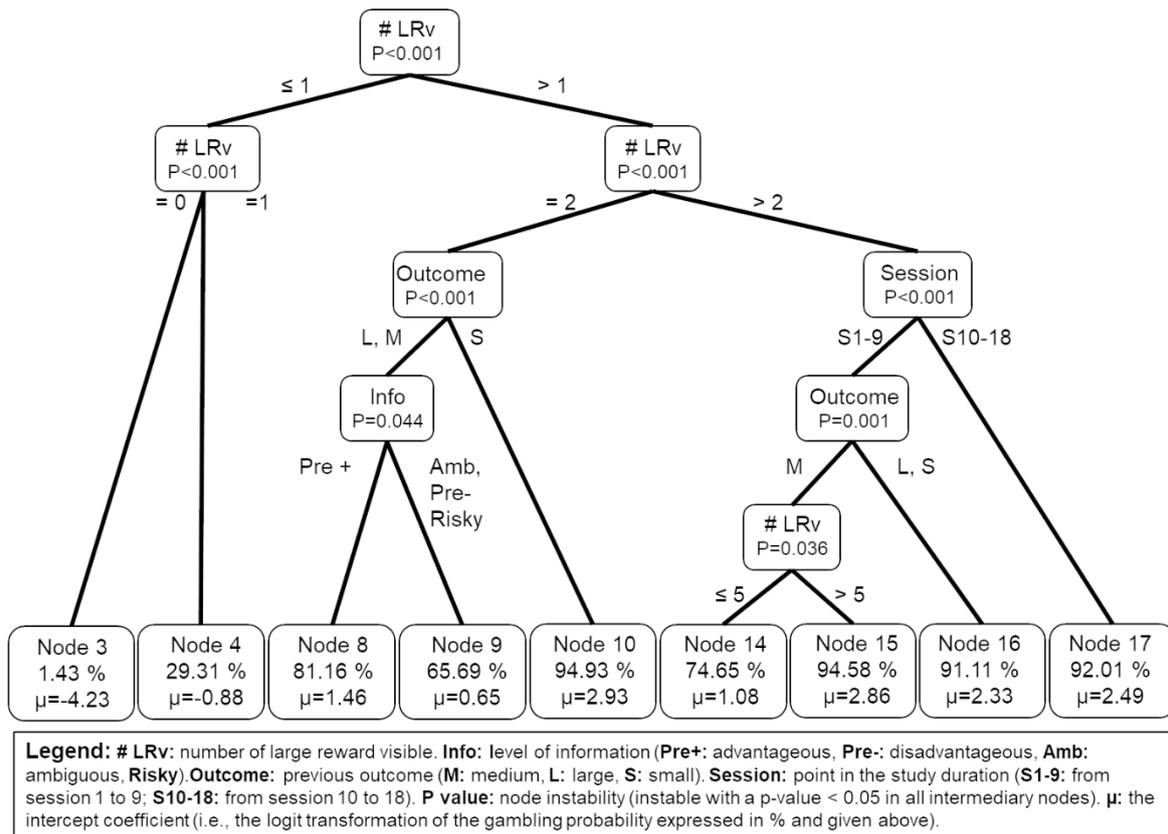
751



752

753 **Figure 4.** Decision tree for the gorillas. Gorillas gamble more than 50% of the time for lotteries
 754 with at least 1 LRv (from node 7). The level of information plays a role in 0 LRv lotteries: they
 755 are more likely to gamble in lotteries with covered cups (node 3) than in risky lotteries (node
 756 4). Previous outcome can play a role for lotteries with 1 LRv (node 7 and 8).

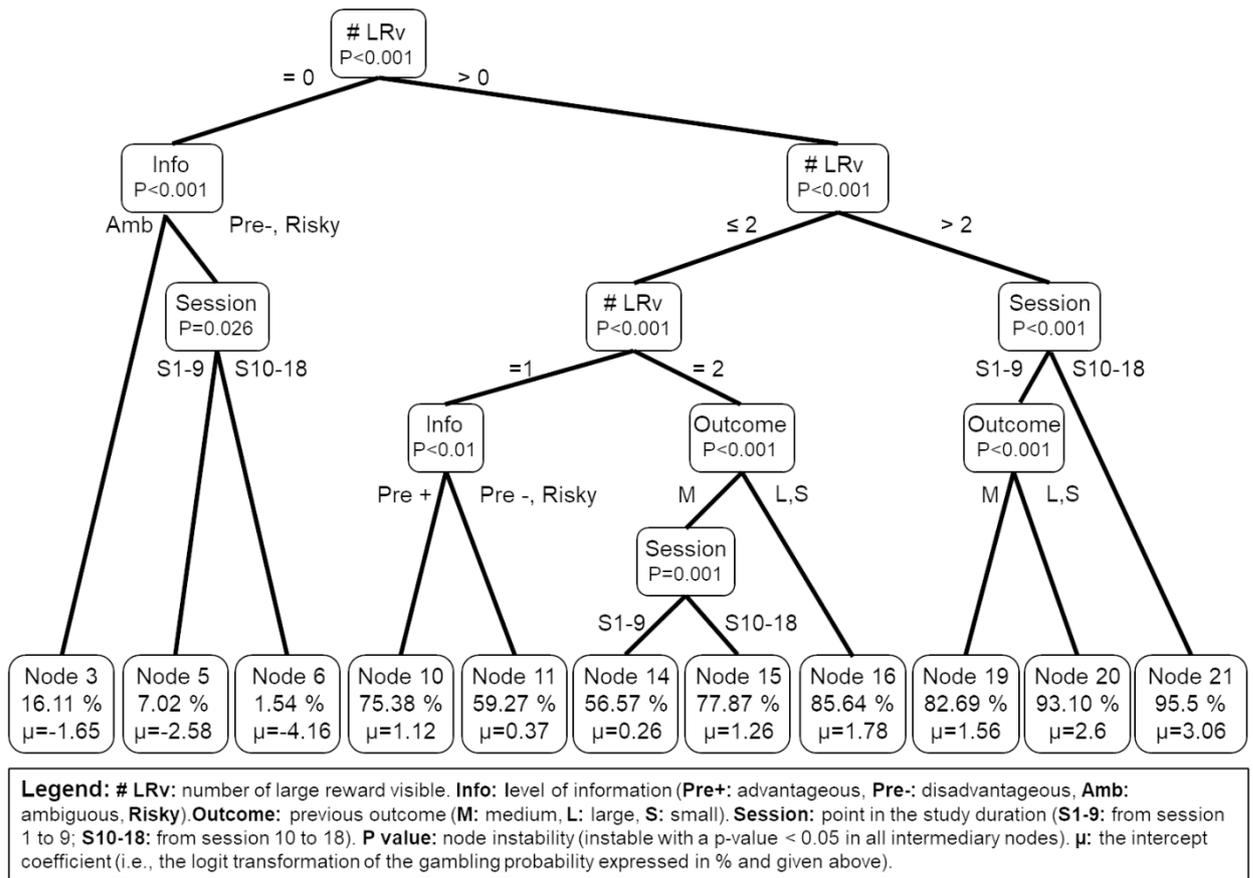
757



758

759 **Figure 5.** Decision tree for the Tonkean macaques. Tonkean macaques gamble more than 50%
 760 of the time for lotteries with at least 2 LRV (from node 8). Level of information, point in the
 761 study duration, and previous outcomes are also splitting variables in various parts of the
 762 decision tree. They can distinguish between predictably advantageous lotteries and the other
 763 ones, but only for 2 LRV lotteries and only if the previous outcome was a medium-sized or large
 764 reward.

765

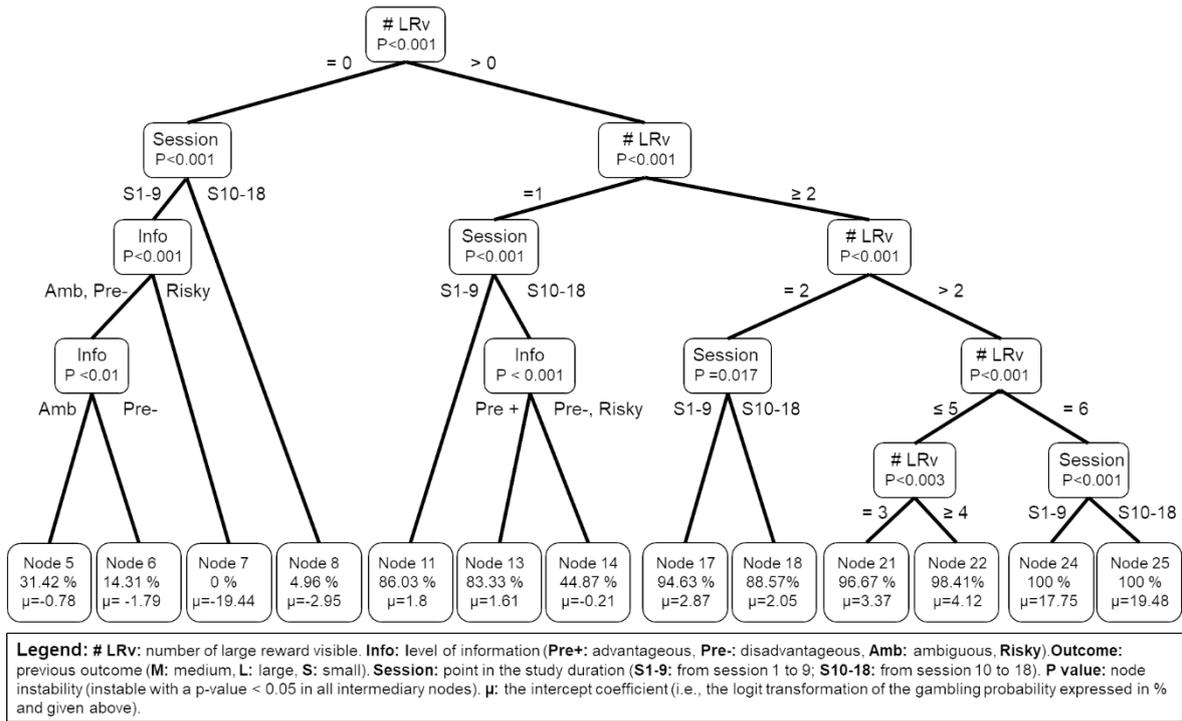


766

767 **Figure 6.** Decision tree for the chimpanzees. Chimpanzees gamble more than 50% of the time
 768 for lotteries with at least 1 LRv (from node 10 and 11). The level of information plays a role at
 769 0 LRv and 1 LRv lotteries and chimpanzees gamble more at lotteries that are indeed more likely
 770 to provide large rewards under the covers (node 3 and 10). The point in the study duration and
 771 the size of the outcome can also play a role in the decision-making process (see the results
 772 section).

773

774



775
 776 **Figure 7.** Decision tree for the orangutans. Orangutans gamble more than 50% of the time for
 777 lotteries with at least 1 LRv (from node 11, except for node 14). The level of information plays
 778 a role at 0 LRv (especially at the beginning of the study), and 1 LRv lotteries (especially at the
 779 end). Like chimpanzees, orangutans gamble more at lotteries that are more likely to provide
 780 large rewards under the covers (nodes 5 and 13). The point in the study duration can also play
 781 a role for 2LRv (see results’description).
 782

783

784 *Table 1.* The 28 lotteries. LRv: number of large rewards visible. Large square (■): large reward; small
 785 square (■): small reward. Blue rectangle: position of cup with cover.

Lottery number (#)	Lottery configuration	Visible probability of gain	Real probability of gain	Nbr of LRv	Level of information
1		1	1	6	Risky
2		1	1	4	Ambiguous
3		1	1	4	Predictably advantageous
4		1	1	4	Predictably advantageous
5		1	0.83	4	Ambiguous
9		1	0.67	4	Ambiguous
8		0.83	0.83	5	Risky
6		0.75	0.83	3	Predictably advantageous
7		0.75	0.83	3	Predictably advantageous
13		0.75	0.5	3	Predictably disadvantageous
12		0.67	0.67	4	Risky
16		0.5	0.5	3	Risky
11		0.5	0.67	2	Predictably advantageous
10		0.5	0.67	2	Ambiguous
14		0.5	0.5	2	Ambiguous
18		0.5	0.33	2	Ambiguous
17		0.5	0.33	2	Predictably disadvantageous
20		0.33	0.33	2	Risky
15		0.25	0.5	1	Predictably advantageous
21		0.25	0.17	1	Predictably disadvantageous
22		0.25	0.17	1	Predictably disadvantageous
24		0.17	0.17	1	Risky
19		0	0.33	0	Ambiguous
23		0	0.17	0	Ambiguous
27		0	0	0	Ambiguous
25		0	0	0	Predictably disadvantageous
26		0	0	0	Predictably disadvantageous
28		0	0	0	Risky

786 *Table 2: Summary of the main results of the study. * Based on the response at risky lottery 24,*
787 *significant difference between choices of the risky versus safe option. ** Based on the analysis*
788 *of the decision tree, when ambiguous lotteries are preferred to equivalent risky ones. *&**:*
789 *Note that future studies should run econometric evaluations to confirm these attitudes. ICC :*
790 *intra-class correlation: percentage of total variance explained by individual variance.*

791

	Significant variables in the decision trees	Gambling > 50%	Can make correct expectations	Made correct expectations in more than one type of lottery	Potential (*) attitude toward risk	Potential (**) attitude toward ambiguity	ICC (%)
Capuchins	#LRv	# LRv ≥ 1	No	No	Risk seeking		41
Bonobos	#LRv, outcome	# LRv ≥ 2	No	No			29
Gorillas	#LRv, outcome, level of information	# LRv ≥ 1	No	No	Risk seeking	Ambiguity seeking	0.3
Macaques	#LRv, outcome, level of information, point in the study duration	# LRv ≥ 2	Yes	No			55
Chimpanzees	#LRv, level of information, point in the study duration, outcome	# LRv ≥ 1	Yes	Yes	Risk seeking		19
Orangutans	#LRv, point in the study duration, level of information	# LRv ≥ 1	Yes	Yes	Risk seeking		58

792

793

794

795 **Supplementary material**

796 **Training procedure**

797 All subjects had experience of exchanging food items of different qualities and quantities with
798 a human experimenter from previous studies (Pelé et al. 2010b, 2014, Broihanne et al. 2018).
799 In this study, all individuals of the six species were trained as follows: subjects were given a
800 small piece of cookie (1 x 2 x 0.5 cm) and were encouraged to exchange it for a larger one (4 x
801 4 x 0.5 cm). This phase was run until subjects reached a criterion of 100% success in one
802 session. Subjects then had to exchange a small food item for a medium-sized one (2 x 2 x 0.5
803 cm) until they reached the same success criterion and finally exchange a medium-sized food
804 item for a larger one, also until they reached a 100% success rate. A final training phase was
805 run to familiarize the subjects with the experimental apparatus, namely a tray of six aligned
806 plastic cups. The experimenter sat in front of the subject and showed a piece of cookie
807 measuring 2 x 2 x 0.5 cm in one hand and the tray with the six aligned plastic cups in the other.
808 The experimenter gave the small piece of cookie to the subject, and then slowly turned his/her
809 hand upward to present it palm open to the subject, asking him/her to give the initial item back.
810 If the subject did so, the experimenter rewarded him/her by giving him/her the contents of one
811 of the six aligned cups, chosen at random. In the test sheet, the column containing the number
812 of the rewarding cup was covered by a piece of paper that was progressively moved
813 downwards (trial by trial) to ensure that the experimenter would not know in advance which
814 cup the subject would receive in the case of an exchange.

815 Each training session consisted of 12 trials. At first, all the cups contained large rewards (4
816 trials), then medium-sized rewards (4 trials), then only small rewards (4 trials). Several sessions
817 were run (one per day) until each individual exchanged the initial reward for larger rewards and
818 kept it when offered smaller rewards in 90% of trials in two consecutive sessions. There was
819 no criteria for trials where only medium-sized rewards were shown (individuals were free to
820 either gamble or keep the initial item). This training phase was designed to ensure that subjects
821 paid attention to the content of the cups. The subjects also understood that although they could
822 predict the size of the reward they would receive, they could not predict the cup from which it
823 would come. The subject then started the testing phase.

824 To check whether subjects paid attention to the content of the cups, we first analysed their
825 responses in two “control” lotteries, lottery #1 with a certain gain (only large crackers) and
826 lottery #28 with a certain loss (only small crackers). Individuals should mostly gamble in the
827 former, and are expected to keep their initial food item in the latter. We use a binomial test to
828 check if subjects did indeed gamble significantly above chance in #1, and below chance in #28.
829 Twenty-eight of the thirty subjects reached this criterion. One capuchin (Raven) and one
830 bonobo (Joey) did not meet these success criteria and were excluded from further analysis – see
831 Table S2).

832

833

834

Species	Sub	Sex	Age (years)	Location	Prior experience in exchange experiments
Brown capuchin	Raven	M	8	GFPA, Rieti, Italy	1, 3 , 5, 9
Brown capuchin	Samir	M	7	GFPA, Rieti, Italy	5, 9
Brown capuchin	Petula	F	9	GFPA, Rieti, Italy	1, 3 , 9
Brown capuchin	Rosy	F	8	GFPA, Rieti, Italy	8 , 9
Tonkean macaque	Rimbaud	M	8	GFPA, Rieti, Italy	1, 2, 5, 9
Tonkean macaque	Sherlock	M	7	GFPA, Rieti, Italy	1, 2, 5, 8 , 9
Tonkean macaque	Simbad	M	7	GFPA, Rieti, Italy	1, 5, 8 , 9
Tonkean macaque	Sybille	F	6	GFPA, Rieti, Italy	1, 5, 9
Tonkean macaque	Tania	F	6	GFPA, Rieti, Italy	9
Orangutan	Pini	F	23	WKRPC, Leipzig Zoo, Germany	3 , 4, 7, 9
Orangutan	Padana	F	14	WKRPC, Leipzig Zoo, Germany	3 , 4, 7, 9
Orangutan	Dokana	F	22	WKRPC, Leipzig Zoo, Germany	3 , 4, 6, 7, 9
Orangutan	Raja	F	8	WKRPC, Leipzig Zoo, Germany	9
Orangutan	Bimbo	M	31	WKRPC, Leipzig Zoo, Germany	4, 6, 7, 9
Gorilla	Kibari	F	7	WKRPC, Leipzig Zoo, Germany	9
Gorilla	Gorgo	M	30	WKRPC, Leipzig Zoo, Germany	9
Gorilla	Viringika	F	16	WKRPC, Leipzig Zoo, Germany	4, 9
Gorilla	Louna	F	5	WKRPC, Leipzig Zoo, Germany	9
Chimpanzee	Clara	M	31	CIRMF, Franceville, Gabon	9
Chimpanzee	Moanda	M	31	CIRMF, Franceville, Gabon	9
Chimpanzee	Chiquita	F	32	CIRMF, Franceville, Gabon	9
Chimpanzee	Makoku	F	32	CIRMF, Franceville, Gabon	9
Chimpanzee	Dominique	F	30	CIRMF, Franceville, Gabon	9
Chimpanzee	Vaillant	M	33	CIRMF, Franceville, Gabon	9
Chimpanzee	Nuria	F	26	CIRMF, Franceville, Gabon	9
Bonobo	Kuno	M	15	WKRPC, Leipzig Zoo, Germany	4, 7, 9
Bonobo	Joey	M	29	WKRPC, Leipzig Zoo, Germany	4, 7, 9
Bonobo	Ulindi	F	18	WKRPC, Leipzig Zoo, Germany	4, 7, 9
Bonobo	Luisa	F	6	WKRPC, Leipzig Zoo, Germany	9
Bonobo	Yasa	F	17	WKRPC, Leipzig Zoo, Germany	4, 7, 9

835 *Table S1.* Name, age sex, location and previous experience of subjects involved in studies with
836 exchange tasks carried out by our team. 1: Pelé et al. 2010a; 2: Pelé et al. 2010b ; **3 : Pelé et al.**
837 **2014** ; 4 : Pelé et al. 2009 ; 5 : Steelandt et al. 2011 ; Dufour et al. 2009 ; 7 : Bourjade et
838 al.2014 ; 8 : Bourjade et al. 2012 ; 9 : **Broihanne et al. 2019**. **In bold** : studies involving
839 decision under risk using the same “six-cup” design.

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847 **Supplementary information about the statistical procedure**

848 Script used in R and example for the building of the capuchins' tree

849 #Downloading packages

```
850 rm(list = ls())
851 library(glmertree)
852 library(tidyverse)
853 library(lme4)
854 library(MuMIn)
```

855

856 #Splitting the dataset into the 1 to 9 and 10 to 18 sessions

```
857 TAB.0<-read.csv2("data.csv",dec=".")
858 TAB <-TAB.0 %>% mutate(Sessions_cut = case_when(Sessions <=9 ~ "s1_9",Sessions <=18 ~
859 "s10_18"))
860 TAB$Sessions_cut<-as.factor(TAB$Sessions_cut)
```

861

862 #Running the main GLMM, all species included and with nested random effects and best model selection procedure

```
864 Model1<-glmer(Exchange~#LRv+Info+Sessions_cut+Species+Outcome+(1|study
865 site/Individual)+(1|Age/Individual),data=TAB,family=binomial)
866 options(na.action = "na.fail")
867 dredge(Model1)
```

868

869 #Selecting capuchins data

```
870 TAB_capuchin<-TAB[which(TAB$Species=="Capuchin"),]
```

871

872 #Running the GLMMtree analysis

```
873 glmmt_cap<glmertree(Exchange~1|Individu|Nbr_of_LR_visible+info+Sessions_cut,data=
874 TAB_capuchin, family="binomial")
```

875

876 #Calculating intra class correlation (ICC)

```
877 varcor<-VarCorr(glmmt_cap)
878 varcor
879 res_var<-attr(varcor,"sc")^2
880 int_var<-as.numeric(varcor$Individual)
881 ICC<-int_var/(res_var + int_var)
882 ICC
```

883

884 #Drawing the tree

```
885 plot(glmmt_cap)
```

886

887 #Extracting coefficients and probability of gambling at each terminal node (in %)

```
888 coef(glmmt_cap)
889 1/(1+exp(-coef(glmmt_cap)))
```

890

891

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894

	Lottery #1	Lottery #28	<i>Exchange:</i> > 66.6% in #1 and < 33.3 % in #28
Gambling rate (average value for all sessions) (measured in percentage of return)			
Capuchins			
Petula	100	5.56	Yes
Raven	61.11	5.56	No
Rosy	94.44	0	Yes
Samir	100	5.56	Yes
Macaques			
Rimbaud	100	0	Yes
Sherlock	100	0	Yes
Simbad	88.89	0	Yes
Sybille	94.44	0	Yes
Tanya	77.78	5.56	Yes
Orangutans			
Bimbo	100	0	Yes
Dokana	100	0	Yes
Padana	100	0	Yes
Pini	100	0	Yes
Raja	100	0	yes
Gorillas			
Gorgo	94.44	11.11	Yes
Kibara	100	0	Yes
Louna	94.44	5.56	Yes
Viringika	100	0	Yes
Chimpanzees			
Chiquita	100	0	Yes
Clara	94.44	0	Yes
Dominique	88.89	0	Yes
Makoku	100	16.67	Yes
Moanda	100	5.56	Yes
Nuria	88.89	11.11	Yes
Vaillant	100	0	Yes
Bonobos			
Joey	44.44	5.56	No
Kuno	94.44	0	Yes
Luiza	100	0	Yes
Ulindi	100	0	Yes
Yasa	94.44	0	Yes

898 *Table S2.* Rate of exchange for each subject in lotteries #1 and #28. Raven and Joey were not
899 included in the analysis.

Models	(Int)	# LRv	Info (Level of information)	Previous outcome	Species	Point in the study duration	df	LogLik	AICc	Delta	Weight
24 (best)	-1.76	1.3	+	+	+		15	-4739.6	9511.2	0	0.37
8	-1.56	1.3	+	+			10	-4744.7	9511.5	0.31	0.32
32 (full)	-1.78	1.3	+	+	+	+	16	-4739.4	9512.8	1.59	0.17

901 *Table S3:* results of the best model selection for the identification of the variables in the best
 902 explanatory models. The best model comprises all the variables except the point in the study
 903 duration. However, the best model was statistically equivalent in terms of data fit to the full
 904 model ($\Delta < 2$), thus we chose to retain all the variables, as the full model had the highest
 905 explanatory power. Because we implemented the variable “previous outcome” in this analysis,
 906 we had to remove all trials where individuals had not received any prior rewards: i.e., the first
 907 trial of the day (trials 1, 8, 15 and 22 for capuchins and macaques, trials 1 and 15 for great apes,
 908 see in the supplementary dataset “Romain data GLMM1”).

909

	Lotteries #																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Capuchin																												
Petula	100	100	94.4	94.4	100	100	100	94.4	100	88.9	100	94.4	88.9	83.3	88.9	100	83.3	77.8	11.1	94.4	83.3	88.9	11.1	77.8	11.1	11.1	16.7	5.6
Rosy	94.4	94.4	88.9	88.9	88.9	88.9	77.8	83.3	77.8	50.0	66.7	72.2	83.3	66.7	33.3	66.7	66.7	61.1	0	55.6	16.7	16.7	5.6	33.3	0	0	0	0
Samir	100	88.9	100	94.4	100	88.9	94.4	94.4	88.9	77.8	88.9	100	88.9	88.9	66.7	83.3	83.3	88.9	5.6	83.3	33.3	44.4	0	38.9	0	16.7	5.6	5.6
Bonobo																												
Kuno	94.4	83.3	100	100	100	77.8	88.9	94.4	94.4	38.9	83.3	88.9	88.9	44.4	27.8	83.3	33.3	38.9	0	55.6	22.2	22.2	0	22.2	5.6	0	5.6	0
Luiza	100	100	100	94.4	100	94.4	100	100	100	88.9	94.4	100	100	83.3	77.8	94.4	94.4	88.9	16.7	88.9	44.4	33.3	5.6	44.4	0	5.6	0	0
Ulindi	100	100	100	100	100	100	100	100	100	100	94.4	100	100	88.9	61.1	100	83.3	94.4	0	88.9	50	50	11.1	33.3	5.6	0	5.6	0
Yasa	94.4	94.4	88.9	88.9	100	88.9	94.4	94.4	100	72.2	72.2	100	72.2	77.8	50	88.9	83.3	61.1	5.6	77.8	50	38.9	11.1	44.4	22.2	5.6	5.6	0
Macaque																												
Rimbaud	100	100	100	100	100	88.9	94.4	94.4	100	88.9	88.9	100	100	61.1	55.6	94.4	83.3	66.7	0	61.1	27.8	16.7	0	27.8	16.7	0	0	0
Sherlock	100	100	100	100	100	100	100	100	100	100	100	100	100	88.9	55.6	100	94.4	94.4	0	88.9	38.9	66.7	0	44.4	0	5.6	0	0
Simbad	88.9	61.1	50	72.2	77.8	61.1	61.1	61.1	77.8	50	61.1	50	66.7	38.9	5.6	50	27.8	33.3	0	22.2	5.6	5.6	0	11.1	0	0	5.6	0
Sybille	94.4	100	94.4	94.4	100	94.4	88.9	100	100	94.4	100	94.4	100	83.3	66.7	94.4	100	94.4	0	72.2	50	55.6	0	55.6	0	0	0	0
Tanya	77.8	55.6	61.1	72.2	61.1	61.1	66.7	72.2	66.7	66.7	50	50	50	38.9	38.9	33.3	55.6	61.1	0	55.6	61.1	27.8	11.1	27.8	0	11.1	11.1	5.6
Gorilla																												
Gorgo	94.4	94.4	94.4	83.3	77.8	94.4	94.4	88.9	77.8	88.9	83.3	100	94.4	83.3	77.8	94.4	83.3	88.9	44.4	94.4	83.3	88.9	22.2	66.7	22.2	16.7	44.4	11.1
Kibara	100	83.3	94.4	100	88.9	88.9	83.3	94.4	83.3	83.3	88.9	94.4	77.8	72.2	77.8	100	83.3	83.3	50	94.4	72.2	72.2	22.2	66.7	27.8	38.9	33.3	0
Louna	94.4	100	88.9	100	100	100	94.4	94.4	100	88.9	88.9	94.4	100	94.4	88.9	94.4	88.9	88.9	16.7	83.3	83.3	83.3	22.2	77.8	11.1	11.1	11.1	5.6
Viringika	100	100	88.9	100	94.4	94.4	94.4	100	94.4	100	94.4	100	94.4	100	94.4	100	94.4	94.4	5.6	100	83.3	100	5.6	83.3	0	5.6	11.1	0.0
Chimpanzee																												
Chiquita	100	100	100	100	83.3	100	94.4	100	94.4	88.9	94.4	100	100	100	83.3	100	94.4	94.4	16.7	100	72.2	50	11.1	61.1	0	5.6	5.6	0
Clara	94.4	88.9	77.8	83.3	72.2	83.3	88.9	88.9	100	83.3	77.8	72.2	88.9	77.8	83.3	94.4	66.7	72.2	33.3	61.1	50	61.1	33.3	61.1	0	16.7	33.3	0
Dominique	88.9	88.9	88.9	88.9	83.3	83.3	88.9	88.9	88.9	50	77.8	72.2	77.8	55.6	50	66.7	55.6	66.7	11.1	55.6	22.2	33.3	16.7	33.3	0	5.6	5.6	0
Makoku	100	100	94.4	88.9	88.9	83.3	94.4	94.4	88.9	50	77.8	94.4	83.3	72.2	72.2	88.9	66.7	66.7	5.6	72.2	33.3	38.9	22.2	44.4	11.1	5.6	16.7	16.7
Moanda	100	94.4	94.4	100	94.4	88.9	94.4	94.4	83.3	72.2	88.9	100	94.4	77.8	72.2	83.3	72.2	72.2	22.2	94.4	55.6	66.7	5.6	72.2	0	0	5.6	5.6
Nuria	88.9	94.4	94.4	100	94.4	94.4	94.4	88.9	88.9	100	77.8	88.9	94.4	83.3	66.7	100	94.4	72.2	33.3	88.9	66.7	72.2	16.7	83.3	11.1	16.7	33.3	11.1
Vaillant	100	88.9	94.4	100	100	100	94.4	100	100	94.4	94.4	88.9	72.2	77.8	100	83.3	88.9	11.1	88.9	88.9	77.8	11.1	88.9	0	0	11.1	0	
Orangutan																												
Bimbo	100	83.3	94.4	100	83.3	61.1	88.9	94.4	83.3	33.3	83.3	94.4	72.2	38.9	33.3	88.9	66.7	44.4	0.0	77.8	11.1	5.6	0.0	38.9	0	0	0	0
Dokana	100	100	100	100	100	94.4	100	94.4	94.4	94.4	94.4	100	94.4	94.4	100	100	100	100	11.1	88.9	88.9	77.8	22.2	72.2	0	0	22.2	0
Padana	100	100	100	100	100	94.4	100	100	94.4	100	100	100	100	100	94.4	100	100	94.4	44.4	100	77.8	100	27.8	66.7	16.7	22.2	38.9	0
Pini	100	100	100	100	100	94.4	100	100	100	100	94.4	100	100	88.9	72.2	100	77.8	94.4	5.6	83.3	61.1	61.1	33.3	44.4	5.6	5.6	22.2	0
Raja	100	100	94.4	94.4	88.9	88.9	100	100	94.4	83.3	83.3	94.4	100	94.4	94.4	94.4	94.4	94.4	33.3	100	77.8	83.3	44.4	94.4	55.6	44.4	50	0

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911 *Table S4:* Individual percentage of gambling at each lottery (this analysis includes all trials,
 912 see in the supplementary dataset “Romain data brut”).

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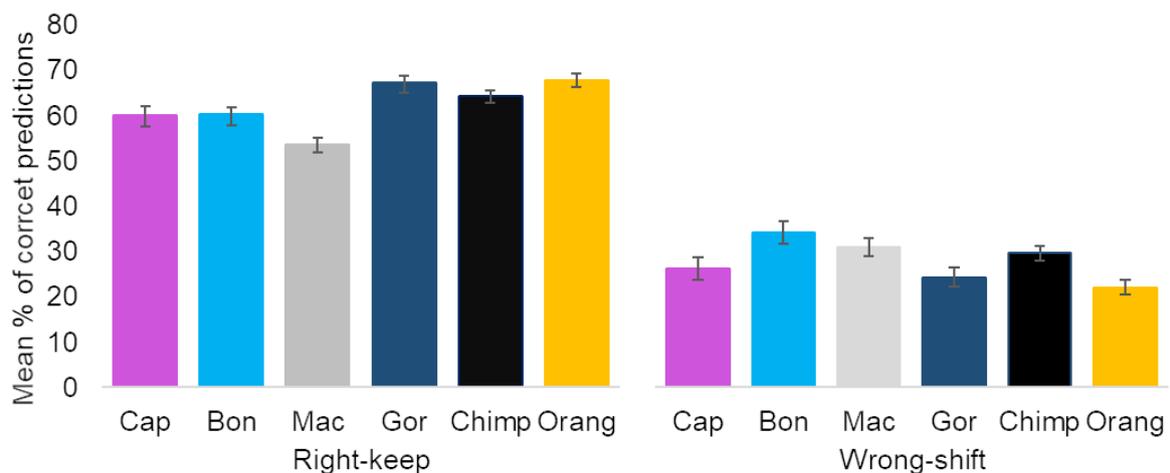
914 *Analysis of a potential right-keep, wrong-shift strategy*

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Model	(Int)	Type of decision (right or wrong)	Species	Type of decision * Species	df	LogLik	AICc	Delta	Weight
8	0.4185	+	+	+	13	-6278.89	12583.8	0	1
4	0.5278	+	+		8	-6310.09	12636.2	52.38	0
2	0.5166	+			3	-6315.79	12637.6	53.77	0
3	0.1177		+		7	-6866.39	13746.8	1162.97	0
1	0.06172				2	-6872.88	13749.8	1165.94	0

917
918 *Table S5:* results of the best model selection for the identification of a potential right-keep/wrong- shift strategy. The best model (model number 8) is the full model and includes all
919 variables and interactions between them. This analysis is conducted on a subset of data see
920 Methods, and the supplementary dataset “GLMM 2 win keep wrong shift”.

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923 *Figure S1:* Mean percentage (+/- standard error) of correct predictions according to the type of
924 potential strategy (right-keep or wrong-shift) and the species.



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