

1 Running head: Maximax heuristics in primates

2 **Title: Monkeys (*Sapajus apella* and *Macaca tonkeana*) and great apes (*Gorilla gorilla*,**
3 ***Pongo pygmaeus*, *Pan paniscus* and *Pan troglodytes*) play for the highest bid**

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1

2 **Abstract**

3 Many studies investigate the decisions made by animals by focussing on their individual
4 attitudes towards risk, i.e., risk seeking, risk neutrality or risk aversion. However, little attention
5 has been paid to how far individuals understand the different odds of outcomes. In a previous
6 gambling task involving up to 18 different lotteries (Pelé et al., 2014), non-human primates
7 used probabilities of gains and losses to make their decision. Although the use of complex
8 mathematical calculation for decision-making seemed unlikely, we applied a gradual decrease
9 in the chances to win throughout the experiment. This probably facilitated the extraction of
10 information about odds. Here, we investigated whether individuals would still make efficient
11 decisions if this facilitating factor was removed. To do so, we randomized the order of
12 presentation of the 18 lotteries. Individuals from four ape and two monkey species were tested.
13 Only capuchin monkeys differed in their gambling behaviour, playing even when there was
14 nothing to win. Randomising the lottery presentation order leads all species to predominantly
15 use a *maximax* heuristic in which individuals gamble as soon as there is at least one chance to
16 win more than they already possess, whatever the risk. Most species also gambled more as the
17 frequency of larger rewards increased. These results suggest the occurrence of optimistic
18 behaviour. The maximax heuristic is sometimes observed in human managerial and financial
19 decision-making, where risk is ignored for potential gains, however low they may be. Our
20 results suggest a shared and strong propensity in primates to rely on heuristics whenever
21 complexity in evaluation of outcome odds arises.

22

23 Keywords: risk preferences, heuristics, decision making, gambling, primates

24

1 **1. Introduction**

2 Decision making under risk in animals has been studied by researchers in both economics
3 (Battalio et al., 1985; Kagel et al., 1990; MacDonald et al., 1991; Chen et al., 2006; Pelé et al.,
4 2014) and biology (Heilbronner et al., 2008; Hurly & Oseen, 1999; Kacelnik and Bateson, 1996,
5 1997; Smallwood and Cartar, 1996). Deciding under risk means that the decision maker has an
6 exact knowledge of the probabilities associated with each outcome. This differs from decisions
7 under uncertainty, defined as having no precise knowledge (Knight, 1921; Luce & Raiffa,
8 1957). The term “under risk”, thus, is not related to a dangerous situation, but indicates that
9 potential outcomes are related to given probabilities rather than certain outcomes.

10 In animals, studies often investigate if attitudes toward risk (risk aversion, risk seeking or risk
11 neutrality) remain the same according to contexts, type of tasks and species (Hayden & Platt,
12 2007 ; Hayden et al., 2008; Heilbronner & Hayden, 2013; Kacelnik & Bateson, 1996; Long et
13 al. 2009; O’Neill & Schultz, 2010; So & Stuphorn, 2010, 2012; Watson et al., 2009). However,
14 an individual’s ability to understand what is at stake is a key cognitive element of decision-
15 making under risk. Individuals can base their choice on a probabilistic element (for example,
16 calculating their chances to obtain a 1 when throwing a dice), or like in many real life
17 circumstances, they may instead call upon heuristics (for example, always taking a risk when
18 there is at least one chance they will win, or on the contrary, not taking a risk if there is at least
19 one chance they will lose). These heuristics are used to avoid the complex task of assessing
20 likelihoods through the use of simpler, judgmental operations (Tversky and Kahneman, 1974).
21 These general decision-making strategies used by individuals are based on limited information,
22 i.e. they involve mental short cuts that reduce the cognitive burden associated with decision
23 making (Shah & Oppenheimer, 2008) when the cognitive process of evaluating probabilities
24 appears cognitively too demanding, time consuming or costly.

1 In humans, learning probabilities can originate from instruction (decisions from given), or
2 through frequencies from repeated draws out of distributions (decisions from experience).
3 Animal subjects are expected to learn about relative outcome frequencies from experience, but
4 previous studies on risk do not give clear evidence of whether or how this occurs (Bateson &
5 Kacelnik, 1997; Brito-e-Abreu & Kacelnik, 1999; De Petrillo et al., 2015; Hayden et al., 2008;
6 Heilbronner & Hayden, 2013, Proctor et al., 2014). For example, Yamada et al. (2013) showed
7 that, although macaques exhibited a strategy in the early stages of testing that was interpreted
8 as risk seeking, they shifted to neutral or slightly risk-averse attitudes after exposure to the tests.
9 Animals therefore generally evaluate the knowledge they have acquired through experience *a*
10 *posteriori*. Some neural activation studies (Monosov & Hikosaka, 2013; O'Neill & Schultz,
11 2010; So & Stuphorn, 2012; Yamada, Tymula, Louie, & Glimcher, 2013) do however confirm
12 that macaques can be trained to visually assess relative frequencies, i.e. outcome odds (and not
13 probabilities, which are a mathematical construct), and compute expected values (the value of
14 the reward multiplied by the probability of obtaining it) before making their decisions.

15 In humans, decisions under risk are based on the maximization of expected values in accordance
16 with Expected Utility Theory (Von Neumann & Morgenstern, 1944). As already stated for
17 human decision-making in Brandstätter et al. (2006), however, animals may not “*behave in the*
18 *same terms that Bernoulli used*”, i.e. “*as if they multiplied some function of probability and*
19 *value, and then maximized*”. But they may call upon alternative decision-making processes
20 from the broad category of heuristics models (for example, Brandstätter et al., 2006). Human
21 cognitive processes and inferences can be predicted by those models (Bröder, 2000; Bröder &
22 Schiffer, 2003; Dhimi, 2003; Newell, Weston, & Shanks, 2003; Payne et al., 1993; Payne,
23 Bettman, & Luce, 1996; Rieskamp & Hoffrage, 1999; Schkade & Johnson, 1989). Real choices
24 between gambles often involve a class of heuristics called lexicographic rules (Gigerenzer,
25 2004; Loewenstein, Weber, Hsee, & Welch, 2001; Sunstein, 2003), which rank decision

1 attributes according to the way they are examined by decision-makers. For example, in choices
2 between two-outcome options that solely involve gains, the priority heuristic is a lexicographic
3 rule that leads individuals to first examine the gamble in terms of the highest (either minimum
4 or maximum) possible gain and then consider the probability of the minimum gain (Brandstätter
5 et al., 2006). According to the maximin rule, for example, the decision-maker should choose
6 the outcome that guarantees the lowest possible losses. In the process, s/he loses out on the
7 opportunity to make big profits. This approach is appropriate for a pessimist who seeks to
8 achieve the best results if the worst happens. The maximax rule is suitable for an optimist. The
9 decision-maker that uses the maximax criterion is assuming that whatever action is taken, the
10 best will happen. Maximin and maximax are outcome heuristics that draw solely on information
11 about outcomes and ignore probabilities. Although non-human species may use similar rules to
12 reduce task complexity under risk and make fast decisions, we do not know if they use the same
13 heuristics as humans, and to what extent. The use of heuristics for convenience and speed may
14 have previously had a survival value (Stich, 1990). Testing non-human primates can help
15 understand the evolutionary origin of some heuristics, such as the minimax and maximax
16 heuristic described in humans.

17

18 In a recent study, we comparatively tested orangutans (*Pongo pygmaeus*), long-tailed macaques
19 (*Macaca fascicularis*), and capuchin monkeys (*Sapajus apella*) in a new design experiment that
20 involved multiple lotteries with different expected values (Pelé et al., 2014). At each trial in this
21 food gambling game, individuals were first given an initial food reward (the constant safe
22 option) then shown a lottery, i.e. a tray of 6 cups which contained a reward that was smaller,
23 larger or the same size as the initial food reward. Subjects were offered the possibility to gamble
24 their initial food and, if they chose to do so, they received one of the 6 cups, chosen at random.
25 The contents of the cups were modified from one lottery to another to provide 18 different

1 lotteries for which the odds of winning or losing were visually assessable (for example 5 cups
2 holding a smaller reward and 1 cup holding a larger one, making it a 1/6 chance to win).
3 Importantly, subjects were tested several times in a row for a given lottery before moving on to
4 tests in further new lotteries. The goal was to evaluate how far an individual's attitudes towards
5 risk and losses affected their decision making under risk. The three species tested decreased
6 their gambling rates when the expected value of lotteries decreased, as described in Expected
7 Utility Theory (Von Neumann & Morgenstern, 1944). Given that primates are not
8 "mathematically educated" or trained to compute relative outcome frequencies, this response
9 was noteworthy. However, the experiment was designed to facilitate their evaluation of
10 outcome odds and the changes in values from one lottery to the next. Indeed, the expected value
11 order of lotteries decreased gradually through the experiment (from the highest to the lowest
12 expected value lottery). This likely helped individuals to evaluate lottery profitability, leading
13 them to quickly decide on a course of action for each new set of "same lottery" trials (18 trials
14 in a row for a given lottery before moving on to the next lottery with a lower expected value).
15 This limited the cognitive focus needed to compute the odds of winning or losing, and facilitated
16 the memorising of the decisions and outcomes for a given lottery, possibly enhancing inter-trial
17 dependency (i.e., the fact that the result of one trial, for example winning, may impact the
18 decision to gamble at the next trial).

19 This initial ordering of lotteries in decreasing order of expected value helped individuals to
20 extract knowledge about outcome odds. In the present study, we investigated whether
21 individuals would still make efficient decisions if this facilitating factor was removed, or
22 whether s/he would opt for the use of heuristics. We also aimed to reduce the potential weight
23 of inter-trial dependency. To achieve these objectives, we used a similar experimental design
24 in which the same lotteries were randomly presented. Given the large number of different
25 lotteries, randomizing their presentation order should lead to a cognitive overload (i.e. too much

1 new information to process from one trial to another (Deck & Jahedi, 2015) and make the
2 outcomes of their previous choices at each lottery harder to memorise. Note that this task is the
3 equivalent of a non-experiential risky task, where individuals have information about the odds
4 shown to them prior to each trial. They do not therefore need to remember the different lotteries,
5 although they may still be influenced by previous experience at a given lottery. Subjects may
6 still gamble according to the expected value of outcomes, but it is likely that subjects also need
7 to use heuristics, possibly comparing the largest food items between the initial item and those
8 presented in the six-cup lotteries. As in humans, outcomes may outweigh probabilities and
9 in that case, we should check which outcome individuals consider first between minimum and
10 maximum gain. The maximin and maximax decision rules were therefore tested. According to
11 the maximin rule, the decision-maker was not expected to gamble when there was at least one
12 small reward in the lottery cups (representing at least one chance in six of losing). According
13 to the maximax rule, individuals were expected to gamble when there was at least one large
14 reward in the lottery (at least one chance in six of winning).

15

16 This study was conducted on six species of primates (compared to three in the previous study),
17 making it possible to investigate whether choices under risk are made similarly by all species,
18 or if some species show a higher reliance on heuristics, as would be expected from species that
19 differ in terms of cognitive skills (Tomasello & Call, 1998). We predict that non-human
20 primates will use heuristics, and that each species may use its computing capability to find its
21 own rule of thumb to facilitate the decision-making process. Given their skills in numerosity
22 tasks, we expect great apes to be less reliant on heuristics than monkeys are, as the cognitive
23 challenge of evaluating the outcome odd should be less demanding for them than for monkeys.
24 We may also observe a connection between the type of heuristic used and the attitudes towards
25 risk that are known to affect decision making in some species. For example, macaques (Pelé et

1 al., 2014) and capuchins have sometimes been described as rather risk prone (De Petrillo et al.
2 2015, but not in Pelé et al., 2014) and chimpanzees have been described as more risk prone than
3 bonobos in some studies (Heilbronner et al. 2008). Both capuchins and chimpanzees may thus
4 rely more on maximax (optimistic) than maximin (pessimistic) rules. However, it is important
5 to note that attitudes towards risk can differ strongly from one task to another, can be evaluated
6 in different ways (Pelé et al. 2014) and are often a matter of interpretation. Humans who apply
7 maximax may also be risk-seekers under some circumstances, but this does not mean that this
8 is true in all aspects of their decisions (see Lévy-Garboua et al., 2012).

9

10 **2. Methods**

11 *Subjects*

12 Forty-two subjects took part in the experiment: 6 brown capuchin monkeys (*Sapajus apella*), 5
13 Tonkean macaques (*Macaca tonkeana*), 6 orangutans (*Pongo pygmaeus*), 7 gorillas (*Gorilla*
14 *gorilla*), 12 chimpanzees (*Pan troglodytes*), and 6 bonobos (*Pan paniscus*) (Table S1 in
15 supplementary material). All subjects were socially housed in enclosures with access to indoor
16 and outdoor areas. Water was available *ad libitum*, and subjects were not deprived of food.
17 Procedures were non-invasive, and subjects could choose to stop participating at any time. All
18 individuals were trained to exchange food items of different sizes with a human experimenter
19 prior to this study. To summarize, individuals were trained to exchange a token for a food, then
20 to exchange a low-quality food for a high-quality food, then a low size reward for a larger size
21 one. Individuals had to meet a performance criterion (90% success in a twelve-trial session) to
22 pass from one step to another, insuring that only those who indeed highly preferred larger food
23 over smaller one would be involved in the testing procedure (see supplementary methods).

24

25 *Apparatus and experimental procedure*

1 For each trial, the experimenter sat in front of the subject's compartment holding an initial
2 reward (a medium-sized piece of cracker measuring 2 x 2 x 0.5 cm) in one hand, and the lottery
3 in the other (a tray holding six aligned plastic cups, each containing one of the following: a
4 small cracker measuring 1 x 1 x 0.5 cm, a medium cracker measuring 2 x 2 x 0.5 cm or a large
5 cracker measuring 4 x 4 x 0.5 cm, see Figure 1).

6 *Insert Figure 1 about here*

7 The experimenter checked that the subject had viewed the contents of the cups, then gave the
8 initial reward to the subject whilst showing the six-cup tray. Next, the experimenter held out
9 her empty hand, offering the subject the chance to give the initial reward back and to gamble.
10 If the subject chose to keep the initial reward, the trial ended. If the subject gambled, s/he
11 received the contents of one of the six cups (they had no means to ascertain which cup they
12 would receive, and the rewarding cup had been previously assigned on a random basis). While
13 the subject consumes the reward (either the initial reward or the lottery reward), the
14 experimenter refills the cups out of sight of the subject before beginning the next trial.

15 The contents of each cup are changed in every trial. Eighteen different lotteries ($\#_N$) are
16 presented in a random order to prevent any learning effect (see supplementary video). The
17 expected value of each lottery corresponds to the volume of the potential rewards multiplied by
18 the chance of obtaining them (lotteries and their associated expected values are detailed in Table
19 1). Subjects took part in 18 sessions (except for one chimpanzee, Bou, who took part in 13
20 sessions). The great apes (orangutans, gorillas, chimpanzees and bonobos) took part in one
21 session of testing per day (18 trials), and the monkeys (capuchins, macaques) participated in
22 half of the testing sessions (9 trials) per day to prevent satiety.

23

24 *Insert Table 1 about here*

25

1 *Statistics*

2 Logit models (with the clustered robust standard errors of subjects) and correlation were used
3 for data analysis using Stata. In this logit model, the dependent variable “exchange” has a value
4 of 0 or 1, and independent variables “sessions” and “lotteries” have values from 1 to 18 and
5 “ocumtype” is the sum of all preceding outcome types, where outcome type is 0 if the medium
6 reward was obtained, 1 if a large reward was obtained, and -1 if a small reward was obtained
7 for the same session in the preceding trial (lottery). The alpha level is set to 0.05.

8

9 **3. Results**

10 3.1 General results

11 To explore the effect of lotteries on gambling, the lotteries were ranked according to their
12 expected value (EV). For most species, higher EV values were correlated with higher levels of
13 gambling (Figure 2, Spearman rank correlation coefficient, capuchins: $r_s = 0.26$, $p < 0.001$;
14 macaques: $r_s = 0.42$, $p < 0.001$; gorillas: $r_s = 0.31$, $p < 0.001$; orangutans: $r_s = 0.45$, $p < 0.001$;
15 chimpanzees: $r_s = 0.27$, $p < 0.001$; bonobos: $r_s = 0.32$, $p < 0.001$). The coefficients remain
16 moderate, probably because most species except bonobos and capuchins gambled considerably
17 in more than 65% of tests when the expected value of the lottery was higher than the value of
18 the initial reward ($EV_i = 2$). They gambled in less than 50% of tests when the expected value
19 of the lottery was below the value of the initial reward. Bonobos gambled in less than 65% of
20 the tests when $EV = 3$ or less. Capuchins only gambled in less than 65% of tests for the lowest
21 EV (lottery 18, $EV = 0.5$). In this lottery, they still gambled in more than 25% of tests despite
22 having no chance of winning.

23 A particularly interesting case is lottery #17 ($EV_{\#17}=1.75$), where the average gambling rate of
24 all species is closer to that observed in lottery #15 ($EV_{\#15}=2$, 1 large-, 1 medium- and 4 small-
25 sized crackers) than that of lottery #16 (6 medium-sized crackers). This response does not

1 completely follow the expected value rule, as individuals would not be expected to gamble in
2 lotteries with expected value lower than 2. We will explain why the results of lottery #17
3 deserve to be studied in greater detail later in this paper (see 3.2).

4

5 *Insert Figure 2 about here*

6

7 We investigate the relationship between gambling rates, species, and position in the sequence
8 both in terms of sessions and in terms of lotteries. The types of outcomes (large, medium or
9 small) obtained in the preceding trials of the same session were used as an additional variable
10 of the model (Table 2).

11

12 *Insert Table 2 about here*

13

14 We find that the lottery significantly and negatively affects the decision to gamble. This result
15 is in line with the Spearman correlation coefficients computed in the first part of the results.
16 The sum of preceding outcome types at a given lottery has a positive impact on exchange rates
17 in macaques, capuchins, gorillas and chimpanzees. This indicates that the more these subjects
18 won, the more they gambled. However, the session has no significant impact in each species
19 (apart from a 6% significance level in bonobos). This result means that on average, subjects
20 always gamble in the same way in a given lottery, whatever their level of experience with that
21 lottery. As the impact of experience may only be gradual, we also examined the exchange rates
22 of the first and last sessions. We arbitrarily plotted the exchange rates in the first trials (sessions
23 1 to 3) against those of the last trials (sessions 16 to 18) for each species (Figure 3). Visual
24 inspection of the resulting graph shows that, on average, bonobos did indeed exchange less at
25 the beginning than at the end of the experiment for lotteries #1 to lotteries #13 or #14, indicating

1 a possible, albeit weak, use of prior experience for these lotteries. Interestingly, for all species
2 except capuchins, almost no difference was seen between the first and last trials for lotteries
3 #15 to #18, i.e. the lotteries with an expected value that was equal to or less than the initial
4 reward. We can thus conclude that although previous outcome and (to a certain extent)
5 experience may influence their decisions, most species can discriminate between lotteries from
6 the first session onwards. What is unclear is whether they do so by evaluating the EV of the
7 lotteries, or by using an alternative decision process based on heuristics.

8

9 *Insert Figure 3 about here*

10

11 *3.2. Alternatives to EV (Heuristic Decision Making)*

12 The readiness to gamble in lottery #17 despite an EV that is lower than that of the initial reward
13 may not reflect decisions that are solely based on EV. We tested two main alternatives, namely
14 maximin and maximax heuristics. In maximin heuristics, individuals are expected to select the
15 alternative that maximizes the minimum achievable payoff, i.e. they only gamble when there
16 are large rewards (lottery #1), do not gamble when there is at least one small reward (lotteries
17 #3, #5, #7, #8, #9, #10, #12, #13, #14, #15, #17, #18), and show indifference in all other cases
18 (lotteries #2, #4, #6, #11 and #16). In maximax heuristics, individuals are expected to select the
19 alternative that maximizes the maximum available payoff, i.e. gambling when there is at least
20 one large cracker to win in the lottery. They should therefore gamble in every lottery except
21 #16 (indifferent gambling attitude), and #18 (no gambling).

22 In Table 3a, we present the optimal decision in each lottery for each decision rule, i.e. expected
23 value, maximin and maximax. G refers to “gambling”, NG to “no gambling” and ~ to
24 “indifference”. Table 3b indicates observed exchange rates for each subject. In Table 3b, a

1 decision rule score for each subject as a sum of counts in all lotteries is computed as follows:
2 we assume that the observations of a subject are independent Bernoulli trials with a 50%
3 probability of gambling, then, a score of 1 is recorded for each lottery if the exchange rate is in
4 accordance with the decision rule, and zero is recorded for all other cases. In other words, for
5 an average gambling rate of $x\%$, we count 1 for $x \geq 66.7\%$ (i.e. 12 out of 18) if gambling (G) is
6 expected, 1 for $x \leq 33.3\%$ (i.e. 6 out of 18) if no gambling (NG) is expected, or 1 for
7 $33.3\% < x < 66.7\%$ if indifference (\sim) is expected. The maximum score is 18. The best decision
8 rule for each subject is indicated in grey. The average value is indicated for each species and a
9 score is also computed for the average subject in each species.

10

11

Insert Table 3a and 3b about here

12

13 At the species level, choices seem to be best aligned with the maximax heuristic predictions.
14 Results differ across species on an individual level: choices were made in accordance with the
15 maximax rule by 5 out of 6 capuchins, 4 out of 6 macaques, 4 out of 6 Orangutans, 6 out of 7
16 gorillas, 9 out of 12 chimpanzees and only 2 out of 6 bonobos. The maximin heuristic was only
17 seen in 2 bonobos, 2 chimpanzees and 1 gorilla. EV was observed in 2 bonobos, 2 chimpanzees,
18 2 orangutans, 2 macaques and 1 capuchin (note that for the same individual some identical
19 values are observed for maximax and EV scores). For lottery #17, most subjects chose the
20 maximax choice, with the only exception observed in bonobos, where only 1 out of 6 subjects
21 chose the maximax rule, while all the others follow EV prediction for this lottery.

22 These findings show that in all species, subjects initially give priority to outcomes in their
23 decision process and not to probabilities. They gamble when there is a possibility of obtaining
24 at least one reward that is larger than their initial reward.

25

1 **4. Discussion**

2 Although the concept of probability is a complex one (Bernoulli, 1954; Heilbronner & Hayden,
3 2013), adult apes (Haun, Nawroth, & Call, 2011; Rakoczy et al., 2014), capuchins (Tecwyn et
4 al., 2017) and human children aged 5-6 years (Schlottmann, 2001) appear to have some grasp
5 of probabilities in various settings. In the present study, the correlation between the decision to
6 gamble and the expected value of the lottery could initially be seen as evidence that all the ape
7 species studied seemed to mainly pay attention to the different probability distributions before
8 gambling and would thus process probabilities in a similar way to children of 5-6 years.
9 However, heuristics models provide an alternative hypothesis to EV evaluation, and provide a
10 better fit for the gambling rate in all 6 species. This is particularly striking for lottery #17. The
11 maximax heuristic, in which subjects choose between the initial reward and a lottery presenting
12 at least one of the largest available food items, is the best explanation of how subjects make
13 choices under risk. Decision makers using this heuristic are called optimists or risk seekers.
14 However, the maximax heuristic may often lead to risk ignorance, which is often observed in
15 managerial decisions (March & Shapira, 1987). Moreover, in the financial domain, investors'
16 decisions are better predicted by overconfidence than by risk, as measured by variance
17 (Broihanne et al., 2014; Nasic & Weber, 2010). Judgment anomalies such as loss aversion or
18 the over- and under-evaluation of probabilities have been reported in risk studies in several
19 primate species (Chen et al., 2006; Pelé et al., 2012). However, the use of a heuristic is not
20 considered an anomaly because it involves a different cognitive/evaluation process altogether:
21 it is essentially an attempt to reduce the complexity of a choice by using a simple decision rule.
22 To our knowledge, this is the first study to detect this heuristic in other non-human primate
23 species. Decision making based on the same heuristics as those used by human decision makers
24 can thus be found in other species and may have older evolutionary origins than previously
25 thought.

1 Ranking the maximum outcome first implies that non-human primates are risk seeking for
2 gains, at least when they have seen large potential rewards. As they do not focus on the
3 minimum outcome, we can consider that their intention is not to avoid the worst outcome.
4 Interestingly, empirical evidence in humans (with perhaps the exception of gamblers) seems to
5 favor the minimum outcome over the maximum outcome because people generally try to avoid
6 the worst outcome, which is consistent with risk aversion in the domain of gains (Edwards,
7 1954). However, the connections between the use of heuristics and attitudes towards risk are
8 not well known in humans. Conclusions could only be drawn about individual attitudes to risk
9 if the subjects use probabilities in their decision process; this is not always the case under
10 maximin and maximax, where risk ignorance is also a possibility. In humans, this motivation
11 to avoid winning nothing (or win the minimum amount) is an element of regret theory (Loomes
12 & Sugden, 1982) and disappointment theory (Bell, 1985), and plays a role in motivation to
13 avoid failure (Heckhausen, 1991). In a previous study of subjects participating in a lottery that
14 was presented in a decreasing order, we found that the gambling rate was globally much lower
15 for lottery #17, which was composed of 1 large- and 5 small-sized cracker rewards. The
16 difference between this earlier study and the current one can be attributed to the use of the
17 maximax heuristic. Making it harder to extract information (by randomizing the order of
18 presentation of lotteries) had a strong impact on how subjects perceived maximal versus
19 minimal outcomes. Further work has to be carried out in order to demonstrate that animals do
20 not avoid the disappointment of obtaining the worst possible outcome of the chosen gamble,
21 nor do they regret a choice that gave them an outcome of lower value than the unchosen
22 alternative.

23 When using heuristics, humans generally rank outcomes first, and probabilities (frequencies)
24 second in their decision-making process. This primacy of outcomes over probability has been
25 shown in many experiments (Brandstätter & Gussmack, 2013). Individuals in our study also

1 ranked outcome first, as they were more likely to gamble if there was at least one chance to win
2 a large cracker. However, the amount/choice of gambles increased with the EV (i.e. the
3 number/frequency of large crackers), showing that their decision was also partly influenced by
4 the frequency of large rewards. Given the random order of the lotteries over trials, this would
5 mean that subjects re-evaluated the frequencies for each choice at every trial. We may therefore
6 question whether animals re-evaluated frequencies based on “decisions from description”, i.e.
7 by visual inspection of the actual lottery, or based on “decision from experience” (Hertwig,
8 Barron, Weber, & Erev, 2004), i.e. by computing the frequency of all past gains from the same
9 lottery. All species, with the possible exception of bonobos, tended to gamble in a similar way
10 for a given lottery, irrespective of the number of times it was presented to them. Visual
11 information (i.e. the large number of crackers displayed) therefore mattered more than
12 experience with a given lottery.

13 One exception to this rule is perhaps the capuchin monkeys, which continued gambling at
14 disadvantageous lotteries including lottery 18, where only small crackers were available. The
15 other species did not gamble when there was nothing to win, suggesting that exchange was an
16 action that comes at a cost (even when EVs were identical, like in lottery #16). Action cost
17 avoidance was not observed in capuchins. If capuchins did not take into account the information
18 available through the cups, it could be argued that they gambled under uncertainty. Although
19 this is a possibility, it is not consistent with the general observation that primates are generally
20 uncertainty averse (see Paglieri et al., 2014 for a review). Instead, capuchins are described as a
21 persistent species, both in the wild, where they have been observed attempting to crack nuts
22 open several times before succeeding (Cummins-Sebree & Fragaszy, 2005; Ottoni & Mannu,
23 2001) and in captive conditions, where personality studies describe them as conscientious
24 animals, i.e. focussed and goal oriented (Morton et al., 2013). In our study, capuchins may
25 have considered gambling to be rewarding in itself, and did not refrain from gambling when

1 disadvantageous lotteries were presented. This could indicate a failure to inhibit their exchanges
2 in these lotteries.

3 In fact, for all species tested, we might question whether a basic failure to inhibit exchange as
4 soon as one large reward is visible could better explain our results at lottery #17 than the
5 maximax rule. First, it is highly likely that most heuristics are based on a failure to inhibit
6 actions, especially if finding out outcome odds requires complex calculation and/or delays the
7 whole decision process. However, very little is known about the cognitive mechanisms
8 underlying heuristics (Dummel, 2016). Second, the notion that individuals gamble when they
9 see a large reward (whatever the inhibition mechanisms underneath) is indeed what we test with
10 the maximax heuristic. The first “rule” for being likely to gamble is: “Is there at least one reward
11 larger than the one I have in hand?” However, if individuals were only driven by the sight of
12 one larger cracker and were therefore unable to inhibit gambling in that case, then they would
13 gamble 100% of the time for all lotteries with at least one large reward. We did not observe this
14 in our study, where individuals adapted to the frequency of large reward seen in the cups. Third,
15 the exchange behaviour is neither conditioned nor automatic (we ensured that this was not the
16 case during the last training step, see Supplementary Material). On the contrary, individuals
17 have to refrain from eating the middle size reward that they hold in their hand if they want to
18 gamble it. They may therefore exert self-control, both to refrain from eating the initial reward
19 and from exchanging it. This does not seem an easy explanation/mechanism. It appears unlikely
20 that the exchange behaviour would be impulsive, with the potential exception of the capuchins
21 (this remains to be tested further). One suggestion would be to control for this inhibition factor,
22 for example by using an automatic set-up, and tokens instead of food to remove the temptation
23 of eating a middle size cracker, and the possible need to barter as soon as a large reward is
24 shown. However, we have no technical solution that would enable us to make all species gamble
25 with a machine, as we want individuals to keep or return something. Using tokens instead of

1 food would impact the results in more ways than just removing the inhibiting components.
2 Indeed, it would also affect the motivation to gamble and the interest for the game (the reward
3 becomes an indirect incentive and its delayed reception could also affect decisions). It might
4 also be cognitively more demanding, as individuals would have to be trained to learn the
5 equivalence between each token and each potential rewards, which they may not all be able to
6 do. Note that, in humans, attitudes towards risk can differ if subjects are presented with
7 monetary reward (considered as direct incentive) instead of symbols/tokens (indirect incentives
8 that will be exchanged later for objects or money, Houser & McCabe, 2013, Rousu et al., 2015).
9 Differences in responses between the current set up and a token-based set-up would therefore
10 be due to more than the mere control of the inhibition factor. Further research may be conducted
11 to explore these issues in more detail.

12

13 We checked whether previous rewards affected choices, as the individual gain/loss history may
14 deviate from expected outcomes in each trial. A significant impact of outcomes was found in
15 macaques, capuchins, gorillas and chimpanzees, who gambled more at a session if previous
16 outcomes for the same session had been positive. Choices could also therefore be weighted by
17 previous outcomes in these species, which did not differentiate between the trials within any
18 same session. Orangutans were not affected by this outcome effect. This may be due to a clearer
19 and more rapid understanding of what the task involves than other species. Further studies
20 should be carried out to evaluate if orangutans consider each trial independently. Still, between-
21 species differences remain marginal in our study as the maximax heuristic was used in most
22 individuals per species. Macaques and capuchins did not differ strongly from great apes in that
23 respect. In a previous study (Heilbronner et al. 2008), bonobos preferred safe options while
24 chimpanzees preferred risky options. Here, chimpanzees may appear more prone to using
25 maximax heuristics compared to bonobos, but bonobos were not more prone to using maximin

1 rather than any other strategy (meaning that there is no direct connection to/evidence of a
2 potential in-built species aversion to risk). Interestingly the bonobos are the only species who
3 gambled less at lottery 17, as would be expected if they followed an EV strategy. They may
4 have had a better grasp of the probabilities despite the randomization of the lottery compared
5 to other species, and it may have been less costly for them to do so.

6

7 Altogether, our results suggest that most primates share a strong propensity to rely on heuristics
8 whenever complexity (or cognitive cost) in evaluation of outcome odds arises. One could
9 wonder whether using heuristics could be a hallmark of individuals with lower cognitive
10 abilities (human or not). In humans, heuristics are used mainly when uncertainty is high and
11 knowledge about the environment is incomplete (Gigenrenzer et al, 1999). Their success is
12 explained by the low cognitive effort they require, and their suitability in conditions such as
13 time pressure. However, this does not mean that heuristics are solely used by individuals with
14 low cognitive abilities (for example, see Dhimi, 2003 for judicial decisions); this remains to be
15 studied. In the same vein, the relationship between cognitive ability and risk preference has
16 been reviewed by Dohmen et al. (2018). Although the two seem to be associated, no clear
17 correlation is found between the measures of the latent characteristics of these concepts. In fact,
18 cognitive ability tends to be positively correlated with the avoidance of harmful risky situations
19 but tends to be negatively correlated with risk aversion in advantageous situations. It is therefore
20 hard to reach a conclusion because the findings are highly dependent on the type of task. Still,
21 given that heuristics can be observed in non-human primates and are still much used by humans
22 today, they are probably an inherited feature of our past decision-making system.

23

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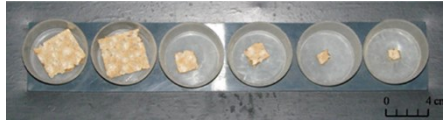
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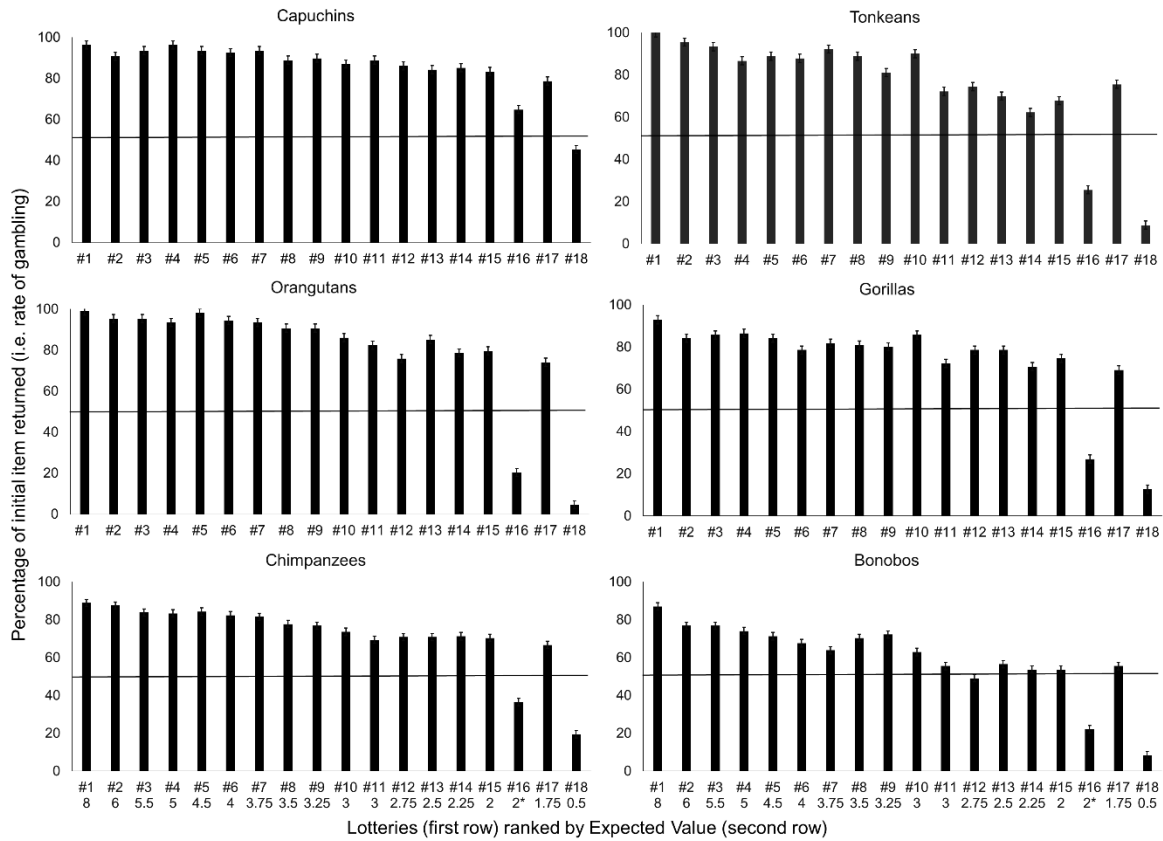
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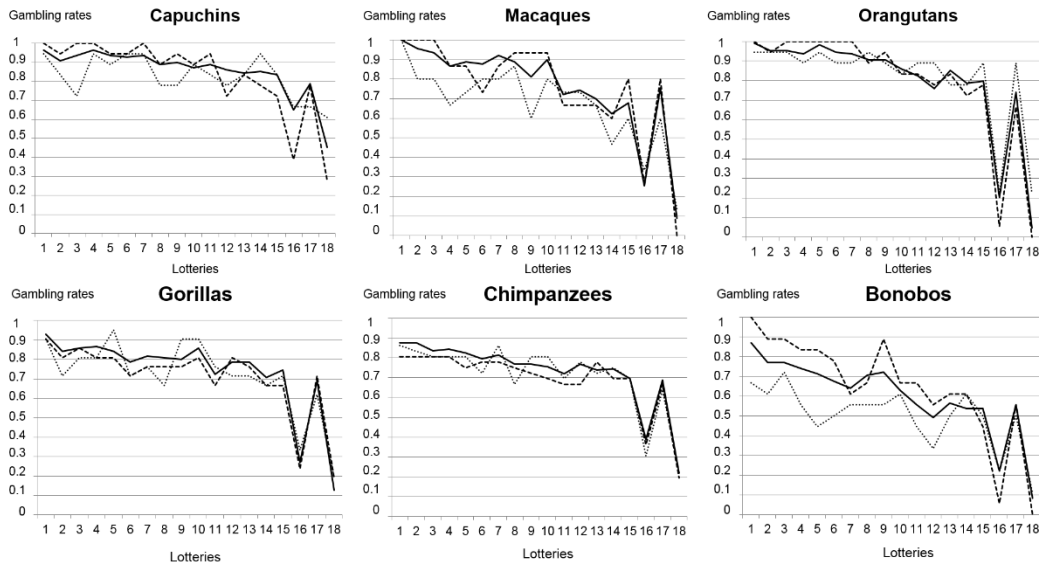
Figure 1. A tray of six plastic cups containing different sized pieces of crackers. Two cups contain one piece of large cracker (left positions), two cups contain one piece of medium cracker (middle positions), and two cups contain one piece of small cracker (right positions). Here, the lottery presented is #8. Large size: 4 x 4 x 0.5 cm. Medium size: 2 x 2 x 0.5 cm. Small size: 1 x 1 x 0.5 cm.



9

Figure 2. Mean percentage of initial reward gambled for each species and for each combination, ranked according to their Expected Value (detailed in Table 1). Whiskers are confidence intervals at the level of 95%. The horizontal line highlights the 50% gambling rate.

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1

2 **Figure 3.** Gambling rates and trial order in each species. For each, a graph presents gambling
 3 rates averaged over all trials (solid line), over the first three sessions (dots for session 1 to
 4 session 3) and over the last three sessions (dashes for session 16 to session 18).

5

1

Lottery number	Content of cups	Probability of gain	Expected value (EV)
1		1	8
2		0.67	6
3		0.67	5.5
4		0.5	5
5		0.5	4.5
6		0.33	4
7		0.33	3.75
8		0.33	3.5
9		0.33	3.25
10		0.33	3
11		0.17	3
12		0.17	2.75
13		0.17	2.5
14		0.17	2.25
15		0.17	2
16		0	2
17		0.17	1.75
18		0	0.5

2

3 **Table 1.** Details of lotteries (ordered according to their expected value here, but presented

4 randomly in the experiment). Expected value = *volume of the expected rewards x chances of*

5 *obtaining them*. The volume of a large reward is 8 (4 x 4 x 0.5 cm), medium is 2 (2 x 2 x 0.5

6 cm) and small is 0.5 (1 x 1 x 0.5 cm). For instance, lottery #₅ presents 3 large, 1 medium, 2

7 small, $EV_{\#5} = (3 \times 8/6 + 1 \times 2/6 + 2 \times 0.5/6) = 4.5$. Value of initial reward $EV_i = 2$.

8

9

1

	Capuchins	Macaques	Orangutans	Gorillas	Chimpanzees	Bonobos
Intercept	3.79***	3.57***	4.81***	2.64***	2.16***	1.25***
Ocumtype	0.03**	0.14***	-0.004	0.09***	0.11***	0.04
Session	-0.02	0.02	-0.004	-0.01	0.01	0.05
Lottery	-0.16***	-0.24***	-0.29***	-0.16***	-0.13***	-0.14***
Loglik.	-731.16	-726.70	-745.18	-1182.99	-2055.68	-1185.44
N	1944	1620	1944	2268	3798	1944

2

3 **Table 2.** Gambling rates determinants

4 In this Table, we present results of a logit model of “exchange” (variable that takes values 0 or
5 1) over “session” and “lottery” (both variables take values from 1 to 18) and “ocumtype”, i.e.
6 the sum of all preceding outcome types in the same session. Note that outcome type is 0 if the
7 medium reward was obtained, 1 if a large reward was obtained and -1 if a small reward was
8 obtained in the preceding lottery of the same session. Loglik stands for log-likelihood and the
9 estimated model is the one that maximizes this amount, i.e. that does the best fit. ***, **
10 indicate significance at the 0.1% and 1% (individuals clustered standard errors are computed).

11

1 **Table 3a and 3b** Exchange rates and decision rules for each subject. In Table 3a, decision rules
2 (Expected Value, Maximin, Maximax) are given for each lottery: G refers to gambling, NG to
3 not gambling and ~ to indifference. In Table 3b, for each subject, we present the average
4 exchange rates in each lottery. If the 18 (13 for the chimpanzee Bou) observations of a subject
5 are gamble decisions (G) then the exchange rate is 100%. We assume that observations of a
6 subject are independent from one another and are considered as independent Bernoulli trials
7 with a 50% probability of gambling and a 50% probability of not gambling, under the null
8 hypothesis (choice is made by chance). An appropriate test for statistical significance of choices
9 is then given by rejecting the null hypothesis of chance if the exchange rate is at least $Z/18$,
10 where Z is determined by a desired 95% significance level. Given 18 choices for each subject,
11 $Z=12$ ($Z=9$ for the 13 choices made by Bou), i.e. about 66.7% of choices (69.2% for Bou). We
12 then count 1 if the exchange rate is in accordance with the decision rule and zero otherwise. In
13 other words, for an average gambling rate of $x\%$, we count 1 for $x \geq 66.7\%$ if gambling (G) is
14 expected, 1 for $x \leq 33.3\%$ if no-gambling (NG) is expected, or 1 for $33.3\% < x < 66.7\%$ if
15 indifference (~) is expected. For example, for an average gambling rate of 61% in lottery #15,
16 we count 1 under EV (as $61\% \in]33.3\%; 66.7\%[$), 0 under Maximin (as $61\% \geq 33.3\%$) or under
17 Maximax (as $61\% \leq 66.7\%$). The sum corresponds to a score for each subject and decision rule
18 and is reported in the last three columns of Table 3b. The maximum score is 18. For each subject
19 the best decision rule is shown in grey. The same amounts are computed for the average subject
20 in each species.

		<i>Lotteries</i>																	
		<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>	<i>10</i>	<i>11</i>	<i>12</i>	<i>13</i>	<i>14</i>	<i>15</i>	<i>16</i>	<i>17</i>	<i>18</i>
Table 3a Decision rules	EV	G	G	G	G	G	G	G	G	G	G	G	G	G	G	~	~	NG	NG
	Maximin	G	~	NG	~	NG	~	NG	NG	NG	NG	~	NG	NG	NG	NG	~	NG	NG
	Maximax	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	~	G	NG

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Table 3b		Lotteries																		Ma xim in	Ma xim ax	EV
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18			
Spec.	Subj.	Exchange rate																				
Cap.	<i>Rav</i>	100	100	100	100	100	88,9	100	94,4	94,4	88,9	100	100	83,3	88,9	83,3	88,9	94,4	66,7	1	16	14
Cap.	<i>Sam</i>	100	94,4	94,4	94,4	94,4	100	94,4	83,3	88,9	88,9	88,9	94,4	77,8	77,8	83,3	55,6	72,2	38,9	2	17	15
Cap.	<i>Pao</i>	100	100	100	100	100	100	100	88,9	94,4	88,9	100	88,9	94,4	100	100	55,6	94,4	33,3	2	17	15
Cap.	<i>Pet</i>	83,3	72,2	77,8	94,4	72,2	77,8	77,8	77,8	72,2	77,8	66,7	66,7	83,3	72,2	55,6	38,9	66,7	50,0	3	13	14
Cap.	<i>Ros</i>	94,4	88,9	94,4	94,4	94,4	88,9	94,4	94,4	94,4	88,9	83,3	77,8	83,3	83,3	83,3	61,1	72,2	16,7	3	18	16
Cap.	<i>Vel</i>	100	88,9	94,4	94,4	100	100	94,4	94,4	94,4	88,9	94,4	88,9	83,3	88,9	94,4	88,9	72,2	66,7	1	16	14
<i>Average Cap.</i>		96,3	90,7	93,5	96,3	93,5	92,6	93,5	88,9	89,8	87,0	88,9	86,1	84,3	85,2	83,3	64,8	78,7	45,4	2	17	15
Mac.	<i>Rai</i>	100	100	100	88,9	100	94,4	94,4	94,4	77,8	100	77,8	83,3	66,7	72,2	83,3	11,1	83,3	11,1	2	16	14
Mac.	<i>She</i>	100	100	94,4	94,4	100	100	100	88,9	83,3	94,4	72,2	77,8	88,9	66,7	72,2	16,7	77,8	5,6	2	16	14
Mac.	<i>Sim</i>	100	88,9	88,9	72,2	66,7	61,1	88,9	77,8	66,7	55,6	44,4	38,9	38,9	38,9	38,9	27,8	50,0	11,1	4	7	8
Mac.	<i>Syb</i>	100	94,4	94,4	100	94,4	94,4	88,9	94,4	94,4	100	94,4	100	83,3	77,8	83,3	44,4	94,4	16,7	3	18	16
Mac.	<i>Tan</i>	100	94,4	88,9	77,8	83,3	88,9	88,9	88,9	83,3	100	72,2	72,2	72,2	55,6	61,1	27,8	72,2	0,0	2	15	15
<i>Average Mac.</i>		100,0	95,6	93,3	86,7	88,9	87,8	92,2	88,9	81,1	90,0	72,2	74,4	70,0	62,2	67,8	25,6	75,6	8,9	2	16	14
Ora.	<i>Pin</i>	100	100	100	100	100	100	100	100	88,9	100	100	94,4	100	88,9	88,9	27,8	83,3	11,1	2	17	15
Ora.	<i>Pad</i>	100	100	100	100	100	100	100	100	94,4	88,9	83,3	100	100	88,9	88,9	33,3	94,4	0,0	3	18	16
Ora.	<i>Dok</i>	100	100	94,4	94,4	100	88,9	94,4	100	94,4	94,4	100	88,9	100	100	100	5,6	88,9	5,6	2	17	15
Ora.	<i>Kil</i>	100	100	100	100	100	100	88,9	94,4	100	83,3	100	77,8	100	100	100	38,9	83,3	11,1	3	18	16
Ora.	<i>Raj</i>	94,4	83,3	88,9	100	94,4	94,4	88,9	88,9	83,3	88,9	61,1	66,7	72,2	66,7	55,6	5,6	50,0	0,0	3	12	13
Ora.	<i>Bim</i>	100	88,9	88,9	66,7	94,4	83,3	88,9	61,1	83,3	61,1	50,0	27,8	38,9	27,8	44,4	11,1	44,4	0,0	6	8	9
<i>Average Ora.</i>		99,1	95,4	95,4	93,5	98,1	94,4	93,5	90,7	90,7	86,1	82,4	75,9	85,2	78,7	79,6	20,4	74,1	4,6	2	17	15
Gor.	<i>Kib</i>	100	94,4	100	100	94,4	100	100	100	100	100	83,3	88,9	94,4	94,4	94,4	27,8	88,9	0,0	2	17	15
Gor.	<i>Gor</i>	83,3	77,8	88,9	77,8	83,3	72,2	83,3	83,3	88,9	83,3	77,8	83,3	88,9	77,8	83,3	61,1	83,3	61,1	2	17	15
Gor.	<i>Vir</i>	88,9	83,3	83,3	88,9	72,2	77,8	83,3	83,3	72,2	88,9	83,3	83,3	94,4	77,8	77,8	11,1	77,8	0,0	2	17	15
Gor.	<i>Lou</i>	100	83,3	83,3	100	88,9	83,3	66,7	94,4	77,8	83,3	88,9	94,4	88,9	100	83,3	55,6	61,1	11,1	3	16	15
Gor.	<i>Col</i>	77,8	50,0	44,4	55,6	50,0	27,8	50,0	27,8	38,9	55,6	38,9	38,9	44,4	27,8	33,3	11,1	33,3	0,0	7	2	3
Gor.	<i>Tani</i>	100	100	100	94,4	100	94,4	94,4	88,9	94,4	94,4	66,7	83,3	66,7	83,3	77,8	0,0	94,4	11,1	3	15	13
Gor.	<i>Djo</i>	100	100	100	88,9	100	94,4	94,4	88,9	88,9	94,4	66,7	77,8	72,2	33,3	72,2	22,2	44,4	5,6	3	14	13
<i>Average Gor.</i>		92,9	84,1	85,7	86,5	84,1	78,6	81,7	81,0	80,2	85,7	72,2	78,6	78,6	70,6	74,6	27,0	69,0	12,7	2	17	15

Chi.	Fre	77,8	83,3	72,2	55,6	83,3	72,2	66,7	72,2	72,2	66,7	66,7	77,8	72,2	72,2	72,2	66,7	72,2	55,6	4	13	11
Chi.	Pau	88,9	100	88,9	94,4	88,9	94,4	83,3	83,3	72,2	83,3	77,8	77,8	77,8	100	83,3	77,8	66,7	55,6	1	15	14
Chi.	Ren	94,4	100	100	94,4	94,4	100	100	94,4	100	94,4	94,4	94,4	100	88,9	88,9	94,4	88,9	66,7	1	16	14
Chi.	Cla	83,3	88,9	72,2	83,3	88,9	72,2	61,1	55,6	50,0	66,7	55,6	88,9	55,6	55,6	61,1	27,8	72,2	0,0	3	9	9
Chi.	Moa	100	94,4	100	100	100	100	94,4	100	100	83,3	94,4	94,4	94,4	100	100	38,9	83,3	5,6	3	18	16
Chi.	Chiq	72,2	72,2	61,1	55,6	38,9	38,9	38,9	50,0	44,4	44,4	27,8	33,3	16,7	27,8	11,1	11,1	27,8	0,0	8	3	4
Chi.	Mako	88,9	83,3	88,9	94,4	83,3	88,9	94,4	83,3	88,9	77,8	83,3	72,2	83,3	94,4	83,3	38,9	72,2	27,8	3	18	16
Chi.	Baku	94,4	94,4	94,4	100	100	100	94,4	100	83,3	94,4	100	94,4	94,4	88,9	94,4	22,2	94,4	5,6	2	17	15
Chi.	Domi	72,2	61,1	50,0	55,6	44,4	44,4	77,8	50,0	44,4	38,9	22,2	44,4	44,4	33,3	50,0	5,6	44,4	5,6	5	3	4
Chi.	Vail	94,4	94,4	94,4	100	94,4	94,4	100	88,9	100	94,4	94,4	100	94,4	88,9	72,2	0,0	66,7	0,0	2	16	15
Chi.	Nur	100	100	100	100	94,4	88,9	100	83,3	94,4	100	94,4	88,9	100	94,4	88,9	72,2	100	33,3	1	16	14
Chi.	Bou	84,6	76,9	76,9	76,9	76,9	53,8	61,5	53,8	69,2	53,8	46,2	46,2	46,2	38,5	15,4	0,0	23,1	0,0	6	7	8
Average Chi.		87,6	87,4	83,3	84,2	82,3	79,0	81,1	76,2	76,6	74,9	71,4	76,1	73,3	73,6	68,4	38,0	67,7	21,3	3	18	16
Bon.	Kun	88,9	72,2	94,4	72,2	72,2	55,6	55,6	77,8	83,3	72,2	38,9	44,4	55,6	44,4	50,0	16,7	44,4	0,0	4	9	10
Bon.	Joe	77,8	83,3	66,7	77,8	66,7	66,7	88,9	77,8	72,2	61,1	77,8	66,7	61,1	83,3	72,2	38,9	66,7	11,1	4	11	10
Bon.	Uli	94,4	94,4	83,3	94,4	77,8	94,4	88,9	94,4	88,9	77,8	88,9	83,3	94,4	88,9	88,9	33,3	83,3	27,8	3	18	16
Bon.	Lui	77,8	55,6	61,1	72,2	77,8	55,6	55,6	44,4	44,4	50,0	22,2	22,2	27,8	11,1	22,2	5,6	38,9	0,0	8	4	4
Bon.	Yaz	83,3	66,7	72,2	50,0	50,0	55,6	38,9	44,4	61,1	38,9	27,8	11,1	27,8	33,3	27,8	5,6	38,9	0,0	8	3	3
Bon.	Jaz	100	88,9	83,3	77,8	83,3	77,8	55,6	83,3	83,3	77,8	77,8	66,7	72,2	61,1	61,1	33,3	61,1	11,1	3	13	14
Average Bon.		87,0	76,9	76,9	74,1	71,3	67,6	63,9	70,4	72,2	63,0	55,6	49,1	56,5	53,7	53,7	22,2	55,6	8,3	3	9	10