

Corvids avoid odd evaluation by following simple rules in a risky exchange task

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Abstract

In their natural environment, animals often make decisions crucial for survival, such as choosing the best patch or food, or the best partner to cooperate. The choice can be compared to a gamble with an outcome that is predictable but not certain, such as rolling a dice. In economics, such a situation is called a risky context. Several models show that although individuals can generally evaluate the odds of each potential outcome, they can be subject to errors of judgment or choose according to decision-making heuristics (simple decision rules). In non-human primates, similar errors of judgment have been reported and we have recently shown that they also use a decisional heuristics when confronted with a risky choice in an exchange task. This suggests a common evolutionary origin to the mechanisms underlying decision-making under risk in primates. However, whether the same mechanisms are also present in more distantly related taxa needs to be further investigated. Other social species, like corvids, are renowned for their advanced cognitive skills and may show similar responses. Here, we analyse data on corvids (carrion crows, hooded crows, common ravens and rooks) tested in a risky exchange task comparable to the one used in non-human primates. We investigated whether corvids could exchange according to the odds of success or, alternatively, whether they used a heuristic similar to the one used by non-human primates. Instead, most corvids chose a course of action (either a low or high exchange rate) that remained constant throughout the study. In general, corvids' mean exchange rates were lower compared to non-human primates, indicating that they were either risk-adverse or that they do not possess the cognitive capabilities to evaluate odds. Further studies are required to evaluate the flexibility in exchange abilities of these birds in exchange abilities of these birds.

KEYWORDS

carrion crows, common ravens, decision-making, heuristics, hooded crows, rooks

1 | INTRODUCTION

Understanding how individuals deal with risk is one of the key issues in research on animal decision-making processes. In economics, researchers distinguish between risky contexts where individuals have complete information about the probability of the outcomes

of their choice (Knight, 1921; Luce & Raiffa, 1957) and ambiguous contexts where this information is missing or incomplete. Several studies show that, although individuals generally seek to maximise incomes when making decisions in risky contexts, they can make judgment errors (Blanchard, Wolfe, Vlaev, Winston, & Hayden, 2014; Chen, Lakshminarayanan, & Santos, 2006; Paglieri et al., 2014; Pelé, Broihanne, Thierry, Call, & Dufour, 2014; Tversky &

Kahneman, 1974; Watzek & Brosnan, 2018) and sometimes exhibit contrasting attitudes towards risk. It has been shown, for example, that humans are inclined to be risk-averse when making decisions about gains and risk-prone when making decisions about losses (Tversky & Kahneman, 1981, 1986). The same phenomenon has been shown in starlings (Marsh & Kacelnik, 2002) and capuchins (Lakshminarayanan, Chen, & Santos, 2011). The similarities in the expression of judgment errors and attitudes towards risk within and across species have been the focus of many studies on decision-making in humans and non-human animals (Bateson, 2002; Caraco, 1981, 1980, 1983; Caraco, Martindale, & Whittam, 1980; Hayden, Heilbronner, Nair, & Platt, 2008; Heilbronner & Hayden, 2013; Kacelnik & Bateson, 1996; Long, Kuhn, & Platt, 2009; McNamara, 1996; O'Neill & Schultz, 2010; So & Stuphorn, 2010, 2012; Watson, Ghodasra, & Platt, 2009). Indeed, similarities in economic preferences across taxa could mean a common evolutionary origin in the mechanisms involved in decision-making (Marsh & Kacelnik, 2002).

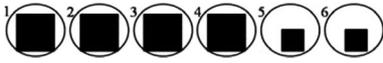
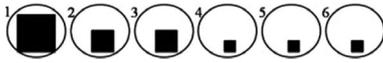
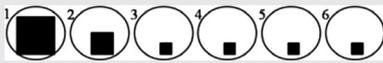
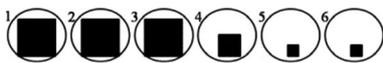
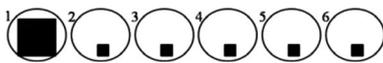
More surprisingly, little attention has been paid to the cognitive processes that underlie decisions. To maximise their outcome, individuals should first rank the different options and choose the one with the highest probability of occurrence (Tversky & Kahneman, 1974, but see Brandstätter & Gussmack, 2013 for different model of choices under risk). In humans, people usually learn about objective odds of outcomes in two ways: either from instruction or from experience. In the first case, they are either told the odds of outcomes or the layout of the task carries information about those. For example, people already know that they have a one chance in six of winning when throwing a dice. Note that also in macaques, it is possible to train subjects to pay attention to outcome odds which are displayed visually (Monosov & Hikosaka, 2013; O'Neill & Schultz, 2010; So & Stuphorn, 2012; Yamada, Tymula, Louie, & Glimcher, 2013). In the second case, individuals learn about the odds through subjective frequencies. Most studies on animal decision-making under risk are implemented in this way (Bateson & Kacelnik, 1997, 1998; Brito-e-Abreu & Kacelnik, 1999; De Petrillo, Ventricelli, Ponsi, & Addessi, 2015; Hayden et al., 2008; Heilbronner & Hayden, 2013) and individuals learn about outcome frequencies through repeated exposure to lotteries. However, it is not always clear whether and how individuals effectively learn information about odds in these studies (Broihanne & Dufour, 2018; Pelé et al., 2014). Alternatively, animals may not be cognitively equipped to evaluate the odds or to properly use odds to make decisions and in this case, they may call upon heuristics.

Heuristics are decision rules used to reduce the complexity of a task and make fast decisions. Different heuristic-based models based are available that explain decision-making in humans (Bröder, 2000; Bröder & Schiffer, 2003; Dhami, 2003; Newell, Weston, & Shanks, 2003; Payne, Bettman, & Johnson, 1993; Payne, Bettman, & Luce, 1996; Rieskamp & Hoffrage, 1999; Schkade & Johnson, 1989). For example, the Maximax heuristic predicts that individuals will only gamble if at least one chance to win is at stake. In these circumstances, individuals are considered optimistic since

they ignore any potential loss. By contrast, under the Maximin heuristic, individuals will not gamble if at least one losing opportunity is at stake (Brandstätter, Gigerenzer, & Hertwig, 2006). Here, individuals are considered pessimistic because they ignore any potential gain. Given the similarities between different taxa in decision-making (Blanchard et al., 2014; Chen et al., 2006; Watzek & Brosnan, 2018), heuristics should also occur in non-human species. In previous studies, it has been shown that non-human primates can use visual information about the odds of winning and losing in a risky exchange task, resembling a gamble. In a first study, non-human primates had to decide whether to exchange a medium-sized piece of food against a lottery, that is a set of six cups each containing a food that could be the same size, smaller or larger compared to the initial food item (Pelé et al., 2014). In this study, the odds of winning differed from one lottery to another, and the lotteries were presented in such a way that the chances of losing gradually decreased. The objective was to simplify the evaluation of the outcome odds of each lottery. In a second study, we increased the cognitive load required to evaluate the odds at each lottery by randomising the order in which the lotteries were presented. We showed that most subjects started relying on heuristics when deciding whether to exchange or not (Broihanne et al., 2018). Interestingly they used the Maximax heuristic, which is less predominantly used in humans compared to the Maximin heuristic.

The question of whether other species could rely on these heuristics has not been investigated. Among non-primate species, corvids excel in cognitive tasks in both the physical and social domain (Emery & Clayton, 2004; Emery, Seed, Bayern, & Clayton, 2007; Güntürkün & Bugnyar, 2016). Carrion crows (*Corvus corone corone*) and common ravens (*Corvus corax*) can weight prospective costs and benefits in an exchange task. Indeed, they have been shown to delay gratification from a few seconds to a couple of minutes in order to maximise the quality of outcomes received in an exchange task (Dufour, Wascher, Braun, Miller, & Bugnyar, 2011; but this task was more difficult when using quantitatively differing outcomes, Wascher, Dufour, & Bugnyar, 2012; Hillemann, Bugnyar, Kotrschal, & Wascher, 2014). Other studies have shown that ravens keep track of some characteristics (reliability) of a partner (Müller, Massen, Bugnyar, & Osvath, 2017) and that they stop cooperating with specific individuals if they have not benefitted from a previous cooperative action (Massen, Ritter, & Bugnyar, 2015). Here, we tested several species of corvids in an exchange task similar to the aforementioned study by Broihanne et al. (2018). Each individual had the opportunity to exchange an initial piece of food with a human experimenter for a better, identical or less preferred piece of food. As in Broihanne et al. (2018) six reward options were displayed in cups aligned in front of the subject, who could see the content of the cups and thus predict the odds of winning (e.g., five high and one low-quality rewards gives five out of six chances of winning a better item than they hold and one out of six chances of losing their initial piece for an item of lower quality). The chances of losing or winning were manipulated

TABLE 1 Lottery number (#) and content of cups for each lottery of rewards

Lotteries of rewards					
#	Content of cups	Nbr of H/L	#	Content of cups	Nbr of H/L
1		4/0	7		1/3
2		4/2	8		1/4
3		3/2	9		1/5
4		2/2	10		0/6
5		2/4	11		0/0
6		1/0	12		6/0

Note: Small black squares (■) represent the lowest quality food reward; medium black squares (■), the medium-quality food reward, large black squares (■), the high-quality food reward. Nbr of H/L represents the number of high- over low-quality food item in the lottery. This number can be used to make predictions and calculate a score for each decision rules (see Table 5). For example, if individuals follow a scenario where they exchange only when the number of high-quality rewards is superior to the number of low-quality rewards, they should exchange at lottery 1, 2, 3, 6 and 12, show indifference at lottery 4 and 11, and not exchange at all other lotteries.

through 12 different lotteries (Table 1). The rewards that the subject would receive in case of exchange of the initial food with the human experimenter were randomised among the six cups. Thus, subjects could also obtain less than the item they were exchanging, that is bear a loss. We tested individuals of four different species: five carrion crows, two hooded crows (*Corvus corone cornix*), four rooks (*Corvus frugilegus*) and two common ravens. For each species, we examined whether odds, previous outcomes or a combination of the two influenced the choices of corvids. To detect the potential use of a heuristics, the exchange rate of each bird was evaluated using three scenarios. In the first scenario, the decision (to exchange or not) is based on the number of high-quality items compared to the low-quality items in the lottery. In the second and third scenarios, individuals rely on standard heuristics described in humans, that is Maximax heuristic or Maximin heuristic, respectively. Non-human primates used heuristics in this version of the task, but we cannot assume that corvids will behave similarly. If corvids possess sufficient cognitive abilities to evaluate the odds at each new trial in this set-up, they should be able to adjust their exchange rate to the odds of winning of the various lotteries tested. All four species generally perform well in cognitive tasks and ravens, in particular, have shown promising skills in exchange tasks (Müller et al., 2017), but the rook is the most social species and may be cognitively more performant in this task (Bird & Emery, 2009). If so, it should adapt its gambling more precisely to each lottery than the other species of corvids. Alternatively, and like non-human primates, corvids may apply a simpler decision rule (i.e., heuristics), which would suggest a convergent evolution in decision-making under risk in these two taxa.

2 | METHODS

2.1 | Subjects

In the present study, we tested five captive carrion crows (four females and one male), two hooded crows (one female and one male), four male rooks and two male ravens. Background information about subjects is given in Table 2. All birds except the rooks were habituated to humans and were used to be tested in physical and visual isolation from others. Crows and ravens were held in large outdoor aviaries (15–45 m²) at the Konrad Lorenz Forschungsstelle (KLF) in Austria. At the time of the study, the crows were kept in adjacent subgroups, consisting of two male-female pairs and a trio of two males and one female. The hooded crows and the ravens were kept in pairs. The experiment was performed from July to September 2011 in two daily sessions 0,800–1,000 and 1,400–1,600. All birds voluntarily participated in the experiments. All procedures were in accordance with the laws of Austria and the Federal State of Upper Austria. The rooks belonged to a social group of 12 captive rooks held in a 108 m² aviary in Strasbourg, France. Most birds of this group were adults and not used to be separated from the others. However, subjects tolerated short separations from the group. They could fly away at any time thus the number of trials in a given testing session varies and the sessions were often shorter in rooks than in other species. Testing was conducted between May and October 2013. Prior to this study, three of the birds took part in one study involving exchange (similar to Wascher et al., this issue, and unpublished data). They were thus familiar with the exchange procedure.

TABLE 2 List of crows participating in the present study

Individual	Species	Year of birth	Sex	Upbringing	at KLF since	Exchange experience
Peter	Crow	2007	F	Handraised, singly by private person	2007	a,b
Gabi	Crow	2007	F	Handraised, singly by private person	2007	a,b
Baerchen	Crow	2008	M	Handraised, singly by private person	2008	a,b
Toeffel	Crow	2008	F	Handraised, in social group at KLF	2008	a
Resa	Crow	2009	F	Handraised, singly at the Vogelwarte Radolfzell	2010	b
Gertrude	Hooded Crow	2011	F	Handraised, singly by private person	2011	b
Nino	Hooded Crow	2011	M	Handraised, singly by private person	2011	
Kafka	Rook		M	Handraised, in social group at CNRS, Strasbourg	2005	b
Brain	Rook		M	Handraised, in social group at CNRS, Strasbourg	2005	b
Merlin	Rook		M	Handraised, in social group at CNRS, Strasbourg	2005	b
Osiris	Rook		M	Handraised, in social group at CNRS, Strasbourg	2005	b
Hugin	Raven	Unknown	M	Handraised, in social group at KLF	Unknown	a
Rumo	Raven	2008	M	Handraised, in social group at KLF	2008	a

Note: All birds were wild-caught, handraised by private people at different locations in Austria and Germany and given to the Konrad Lorenz Forschungsstelle (KLF) between 2007 and 2009. M = male; F = female.

^aIndividuals participating in the qualitative exchange task by Dufour et al. (2011), quantitative exchange task by Wascher et al. (2012) and inequity aversion task by Wascher and Bugnyar (2013).

^bIndividuals participating in the reciprocity exchange task, see Wascher et al. (this issue) for crows and ravens data (rooks, unpublished data).

2.2 | Experimental procedure

At both sites, from 2007 to 2013, depending on age and arrival of the corvids, birds were first trained to exchange a non-edible token for a food item with a human experimenter (for more details of the training procedure see Dufour et al., 2011). Some birds participated in up to four experiments applying this exchange paradigm prior to this study (Table 2), and all birds had their food preferences tested in the course of these experiments. The preference tests were conducted as follows: two pieces of food were presented simultaneously to the bird on the open palm of the experimenter's hand (any combination of two food items among bread, grape, cheese and sausage for birds in Austria and rice-cracker, peanut, cheese and dog food for birds in France). In order to avoid influencing the choice of individuals, the experimenter was looking at the ground during the entire procedure. Birds could choose one food over another by inserting their bill through the mesh in the direction of the preferred food item. Once the bird made its choice, the item was given immediately, and the alternative food was removed. The birds had 10 s between each trial to eat or cache the food obtained. Each possible combination of food was tested 12 times, randomly distributed over 12 sessions of six trials each. Only three types of items were used in the present study. For birds in Austria, these were cheese (high-quality item, 1 × 1 × 1 cm), which was preferred to grapes (medium-quality item, 1/8), and bread (the lowest quality item, 1 × 1 × 1 cm). In the rooks, all birds preferred dry dog food (high-quality item, 1/6) to cheese

(medium-quality item, 1 × 1 × 1 cm) and cheese to rice-cracker (low-quality item, 1 × 1 × 1 cm).

The birds were tested individually, separated from the experimenter (C. A. F. W. or V. D.) by a wire mesh. During testing, at each trial, subjects were first shown the initial item (food reward of medium quality) in one hand and a tray of six aligned cups containing food rewards visible from the subject in the other (the lottery). The experimenter ensured that the subject was attentive to the content of each cup (i.e., watching the cups) and gave him/her the item of medium quality. The lottery tray with the rewards remained visible to the subject throughout the trial. After a short delay (about 2 s), the experimenter held out her empty hand, palm open, offering the subject the opportunity to return the initial item. If the subject chose to keep the initial food item, the experimenter ended the trial, allowing the subject to consume the initial item. If the subject exchanged the initial item, she/he received the content of one of the cups randomly chosen before the experiment through a computerised randomisation programme (*Randomizer.org*). This means that the gamble was random and its outcome did not necessarily match the odds displayed by the lottery. Thus, regardless of the lottery, subjects could not predict which cup they would receive. This ensured that each trial remained independent from each other and that the birds did not systematically associate a given lottery with a type of reward. We ran a final training phase to habituate the subjects to the fact that they would receive a random cup. The training was as follows. In the training phase 1,

step 1 the subject had to exchange a low-quality food reward for a medium-quality reward. They received sessions with six trials each and the criterion was met when subjects successfully exchanged in 80% of the trials in two consecutive sessions (requiring an average of 2.77 sessions per bird, Table 3). In training phase 1, step 2, they then had to exchange a medium for a high-quality food reward. The same design and criterion were applied as in step 1 (requiring an average of 5.3 sessions per bird, Table 3). In the second training phase, the six cup-tray and random assigning of rewards were introduced to expose birds to the unpredictability of the rewards to be received out of the six options. In this training phase, the birds received six sessions of six trials each. In each session, they received two trials with lotteries displaying low-quality rewards only, two trials with medium-quality rewards only and two trials with high-quality rewards only. Thus, in each trial, the birds could predict which reward they would receive since all cups contained the same item, but they could not predict which cup they would receive.

Birds were tested with a set of 12 different lotteries where the odds of losing (receiving a low-quality food) or winning (receiving a high-quality food) were manipulated by presenting different reward combinations in the cups (Table 1). This provided subjects with a means of visually assessing the odds of losing or winning in relation to the initial item (medium-quality food) they had received. Lotteries were chosen to be similar to those used in the study by Broihanne et al. (2018), but with fewer options. Indeed, most primates accept sessions of 18 trials per day, but corvids lose their motivation quickly and refused to participate in a large number of trials per session. Therefore, we reduced the sessions to 12 trials per session, so we used 12 lotteries. The lotteries included three control lotteries where the outcome was certain, that is lottery #10, #11 and #12 where the six cups contained the same reward, and, respectively only low-, only medium- and only high-quality rewards. We also tested four lotteries where the number of high-quality rewards was higher than the number of low-quality rewards (Lottery #1, #2, #3 and #6), four lotteries where the number of low-quality rewards was higher than the number of high-quality rewards (Lottery #5, #7, #8 and #9) and one lottery where the number of high- and low-quality rewards was identical (#4). These lotteries were chosen to reflect various combinations of high- versus low-quality rewards (Table 1) and thus increase the chances of identifying potential decision rules (see Statistical Analysis section below). We conducted 18 sessions with 12 trials each in all birds except in one rook (Osiris, who received 16 sessions). In each session of 12 trials, each lottery was presented once, and its order of appearance was randomised at each session to provide a level of difficulty in odds evaluation similar to that of Broihanne et al. (2018; e.g., lottery #10 could be the 2nd lottery presented in session 1 and the 5th lottery in session 3). In the rooks, the sessions were frequently interrupted by the subject's departure (after an average of five trials). Testing was resumed if the bird came back, which could be within 5 min, a few hours or the next day.

2.3 | Statistical analysis

In a first step, we used generalised linear mixed models (GLMMs) with binomial error distribution and a logit function. The response variables were the individual's behavioural response in each trial: exchange (yes/no). Lottery, species and previous outcomes were used as fixed factors. For each response (exchange or no exchange) to a given trial n , the previous outcome was the outcome obtained since the beginning of the session calculated by adding 1, 0 or -1 each time a subject won, received (or kept) the same reward or lost (respectively). For example, an individual who lost in trials 1 and 2 would have a cumulative outcome of -2 when starting trial 3. We also included a species \times lottery interaction and a species \times previous outcomes interaction in the full model. Indeed, species may differ in the way lotteries or previous outcomes influenced their decision. To account for repeated measures for each individual, individual identity was included as a random factor. We selected the final model using a model selection procedure based on the dredge function, in R. The procedure selects the best model based on Akaike's second-order information criteria (AICc). This criterion compares the adequacy of several models and identifies the model that best explains the variance of the dependent variable as the one with the lowest AICc value (Burnham & Anderson, 2004; Tabachnick & Fidell, 2007, see Table 4, for the results of the model selection). Post-hoc analyses on the main effects were conducted using LSmean package with a Bonferroni correction (Lenth, 2016) and we used LStrends for post-hoc tests of correlation on interactions. All analyses were performed in R (R version 3.5.2; R Core Team, 2018).

In a second step, we explored the data to investigate the use of heuristics by individuals. For each individual, we calculated a score under three possible scenarios: (a) Subjects may have counted the number of high-quality rewards and exchanged only when high-quality rewards were more frequent than low-quality rewards (lotteries #1, #2, #3, #6 and #12, see Table 2). They may have shown indifference when this number was equal (no predictions for lotteries #4 and #11) and should not have exchanged for all other lotteries (#5, #7, #8, #9 and #10). This first scenario is not a standard heuristic per se, but allows to check whether some individuals were able to have used information on the frequency of each potential reward when deciding to exchange or not. (b) Birds may have followed the Maximin heuristic, exchanging when only large rewards were available (#12), not exchanging if at least one item of low quality was visible (lotteries #2, #3, #4, #5, #7, #8, #9 and #10), and showing indifference in all other cases (#1, #6 and #11). (c) The third scenario considers that birds may have followed the Maximax heuristic, in which individuals should exchange when there is at least one high-quality reward in the lottery (lotteries #1 to #9), show indifference when no maximisation is possible (#11) and not exchange when the loss is certain (#10). These predictions are summarised in Table 5. Note that the Maximin and Maximax scenario differed due to different predictions in nine lotteries, the Maximin and number of high- versus low-quality rewards scenario

TABLE 3 Results from the training phases 1 (steps 1 and 2) and 2 at individual and species levels

Subjects	Training phase 1		Training phase 2					
	Step 1 (low for mid)	Step 2 (mid for high)	Cups containing only			% of exchanges at session		
	nbr of sessions for criterion	nbr of sessions for criterion	High rewards	Medium rewards	Low rewards	1 & 2	3 & 4	5 & 6
Peter	2	5	16.67	16.67	16.67	8.33	33.33	8.33
Gabi	2	2	50	41.67	75	25	75	66.67
Barchen	2	10	33.33	33.33	16.67	0	0	83.33
Toeffel	4	2	58.33	41.67	41.67	83.33	16.67	41.67
Resa	2	2	41.67	50.00	66.67	33.33	50	75
Nino	4	8	66.67	41.67	33.33	75	66.67	0
Gertrude	6	4	41.67	8.33	0	25	8.33	16.67
Rumo	4	2	50	0	0	0	16.67	33.33
Hugin	2	2	91.67	25	33.33	66.67	33.33	50
Kafka	2	11	75	16.67	50	8.33	75	50
Merlin	2	9	100	25	8.33	33.33	25	41.67
Brain	2	8	33.33	0	8.33	8.33	0	33.33
Osiris	2	4	58.33	25	0	33.33	16.67	33.33
<i>Mean</i>	2.77	5.31	55.13	25	26.92			
Carrion crows	2.4	4.2	40	36.67	43.33			
Hooded crows	5	6	54.17	25	16.67			
Ravens	3	2	70.83	12.5	16.67			
Rooks	2	8	66.67	16.67	16.67			

Models	df	LogLik	AICc	Δ AICc	Weight
Lottery, species, outcome \times species	20	-1,719.81	3,479.9	0	0.99
Lottery, outcome	14	-1,733.77	3,495.7	15.77	0
Lottery	13	-1,735.11	3,496.3	16.42	0
Full model	53	-1,694.3	3,496.4	16.62	0
Null model	2	-1,773.52	3,551	71.13	0

TABLE 4 Model selection table from the dredge function

Note: The best model is the model with the lowest AICc.

due to different predictions in five lotteries, and the Maximax and number of high- versus low-quality rewards scenario due to different predictions in six lotteries (Table 5).

2.4 | Ethical statement

For the work conducted with the rooks, the study was in accordance with the French laws regarding animal studies for scientific purposes and was approved by the regional ethical committee on animal experimentation under the license no. A67-382. Keeping of all the other birds was accredited by the Austrian and local government (licence AT00009917). This study adheres the ASAB Guidelines for the Use of Animals in Research.

3 | RESULTS

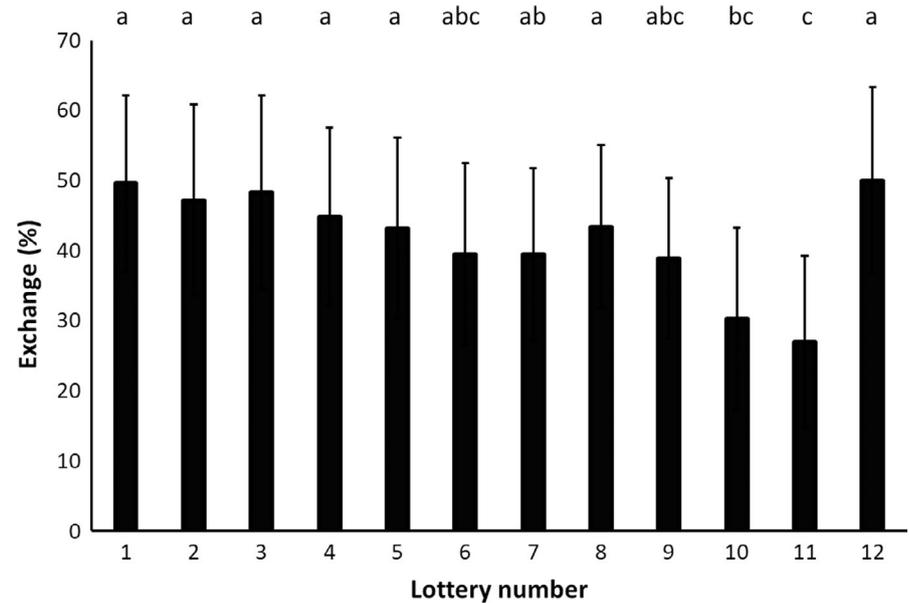
All corvids did choose to exchange in an average of 44.96% of all trials (ranging from 3.2% to 74.53%, Figure 1 and Table 6). The best model selection procedure indicates that the best model includes the effects lottery, species and the interaction species \times previous outcomes (Table 4). For the effect of lottery ($df = 11$, $F = 6.5$, $p < .0001$), the post-hoc pairwise comparison (Bonferroni adjusted $p_{\text{value}} = .05$, accounting for 66 comparisons) indicates that lottery #10 (medium-quality items only) significantly differed from most other lotteries (from lotteries #4, #5 and #8 with $p < .05$, from lottery #1 with $p < .01$, and from lotteries #2, #3 and #12 with $p < .001$; Figure 1). Lottery #11 (low-quality items only) also differed significantly from most other lotteries (from lottery #7 with

TABLE 5 Predictions on exchanging decisions according to decision rules for each subject

	Prediction (E: exchanging, NE: not exchanging, ~: indifference) at each lottery											
	1	2	3	4	5	6	7	8	9	10	11	12
Nbr of H > L	E	E	E	~	NE	E	NE	NE	NE	NE	~	E
Maximin	~	NE	NE	NE	NE	~	NE	NE	NE	NE	~	E
Maximax	E	E	E	E	E	E	E	E	E	NE	~	E

Note: Decision rules (number of high-quality items vs. low-quality items, Maximin, Maximax) are given for each lottery: E refers to exchanging, NE to not exchanging and ~ to indifference. For example, if subjects follow a Maximin heuristics, they should not exchange if at least one low-quality item is visible in the cups (most lotteries except #1, #6, #11 and #12).

FIGURE 1 Mean percentage (\pm SE) of exchange according to the lottery and results from the post-hoc pairwise comparison test. Lotteries having no letters in common significantly differ from each other



$p < .05$ and from lotteries #1, #2, #3, #4, #5, #8 and #12 with $p < .001$). Birds exchanged significantly less in these two lotteries (without high-quality rewards) than in most other lotteries. The exchange rates of the other lotteries did not generally differ significantly from each other (see Figure 1 for more details on the pairwise comparison).

Species ($df = 3, F = 1.67, p = .26$) and previous outcomes effects ($df = 1, F = 2.34, p = .09$) did not produce significant effects but the interaction species \times previous outcome did ($df = 3, F = 7.7, p < .001$). The post-hoc test indicates a difference in each species in how the previous outcomes (the outcomes accumulated since the beginning of the session) correlate with the decision to exchange at a given trial of this session. In the crows, the correlation was significant and negative (estimate = -0.22 ; 95% IC: -0.32 to -0.13): the more positive outcomes they had received the less likely subjects were to exchange. A significant correlation was also found in the hooded crows, but it was positive (estimate = 0.16 ; 95% IC: 0.01 to 0.32): the more positive outcomes they had received the more likely subjects were to exchange. In rooks and ravens, no such correlation was detected (rooks: estimate = 0.05 ; 95% IC: -0.11 to 0.22 ; ravens: estimate = 0.03 ; 95% IC: -0.09 to 0.154).

Exchanging at a given lottery may also depend on the number of times individuals have already experienced this lottery. To evaluate this long-term impact of experience, we investigated the exchange rates of each individual's first and last 36 trials, that is the first and last three trials of each lottery (Figure 2). In the first 36 trials, the exchange rate varied from one lottery to another with low exchange rates between 20% and 40% for lotteries #1, #4, #6, #9, #10 and #11 and higher rates between 40% and 60% for all other lotteries. In the last 36 trials, the percentage of exchanges was similar for all lotteries with exchange rates between 40% and 60% except for lotteries #10 and #11. Contrary to what might have been expected, experience of a particular lottery did not appear to influence individual's decision for this lottery. In fact, the initial discrimination between the lotteries disappeared after repeated exposure. Therefore, the subjects did not seem to learn about the odds of these lotteries.

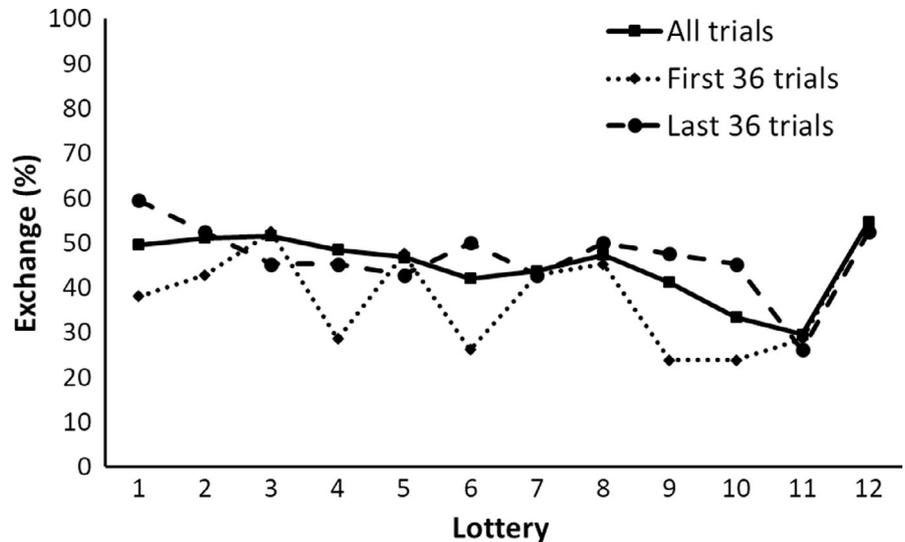
Instead, individuals may have used a simpler decision rule, a heuristic. For each individual, we tested three possible scenarios by establishing a score for each scenario. This score is the sum of 1/0 obtained by individuals if their response to a given lottery (exchanging, not exchanging or indifference) correspond to the prediction of the scenario (described in Table 5). For example, an individual would

TABLE 6 Individual results on each lottery and decision rule (exchange only if high-quality rewards are more frequent than low-quality rewards (nbr H > L), Maximin (maxi min) or Maximax heuristics (maxi max))

Lottery number	Score												Nbr H > L	Maxi min	Maxi max	Range %
	1	2	3	4	5	6	7	8	9	10	11	12				
Carion crows																
Barchen	0	5.55	5.55	0	5.55	0	0	5.55	0	5.55	0	11.11	5	8	1	11.11
Gabi	50	55.55	50	44.44	38.89	38.89	44.44	44.44	33.33	22.22	16.67	55.55	3	4	1	22.22
Peter	22.22	22.22	33.33	38.89	27.78	33.33	33.33	33.33	38.89	22.22	38.89	44.44	6	8	2	22.22
Resa	66.67	72.22	83.33	66.67	83.33	83.33	72.22	72.22	72.22	61.11	72.22	83.33	6	2	10	16.66
Toffel	61.11	66.67	66.67	66.67	33.33	50	55.55	50	50	55.55	50	61.11	5	4	4	16.66
Klaus	5.55	5.55	5.55	0	5.55	0	11.11	5.55	5.55	0	5.55	5.55	5	8	1	11.11
Rooks																
Brain	33.33	33.33	27.78	33.33	38.89	16.67	16.67	38.89	27.78	5.55	5.55	44.44	4	7	1	27.77
Kafka	83.33	66.67	83.33	66.67	72.22	55.55	33.33	55.55	61.11	22.22	16.67	66.67	7	4	7	50
Merlin	61.11	61.11	66.67	55.55	44.44	50	33.33	44.44	38.89	11.11	16.67	50	4	4	2	27.77
Osiris	50	37.5	50	50	43.75	50	62.5	62.5	43.75	18.75	25	31.25	2	2	1	31.25
Hooded crows																
Gertrude	72.22	77.78	66.67	77.78	77.78	72.22	77.78	72.22	72.22	83.33	72.22	72.22	5	1	10	11.11
Nino	66.67	83.33	55.55	61.11	72.22	61.11	66.67	72.22	44.44	61.11	44.44	88.88	5	4	7	44.44
Ravens																
Hugin	61.11	61.11	72.22	55.55	50	33.33	33.33	38.89	50	44.44	5.55	72.22	4	4	2	38.89
Rumo	61.11	12	10	11	11	8	13	12	7	10	8	14	5	9	1	54.11

Note: Individual score obtained by each subject in each scenario is computed as follows: we assume that the observations of a subject are independent Bernoulli trials with a 50% probability of exchanging, then, a score of 1 is recorded for each lottery if the exchange rate is in accordance with the scenario and zero is recorded for all other cases. In other words, for an average exchanging rate of x%, we count 1 for x ≥ 66.7% (i.e., 12 out of 18), if exchanging (E) is expected, 1 for x ≤ 33.3% (i.e., 6 out of 18) if no exchanging (NE) is expected, or 1 for 33.3% < x < 66.7% if indifference (I) is expected. The maximum score is 12 (equal to the total number of lotteries). The last column (range %) summarises the maximum range in the exchange rate when considering all lotteries except lotteries #10 and #11. It is calculated by considering the difference between the largest and smallest values of exchange rate per row of the table (i.e., per individual) excluding lotteries #10 and #11.

FIGURE 2 Percentage of exchange at each lottery in the first 36 trials, last 36 trials and all trials included



score a total of 12 points in the Maximin scenario if he/she exchanged more than 66.7% of the time in lottery #12, exchanged between 33.3% and 66.7% of the time in lotteries #1, #6 and #11 (showing indifference) and less than 33.3% of the time in all other lotteries (no exchange). The higher the score, the more likely it is that an individual is following the decision rule. A score of 10, for example, would mean that individuals' choices correspond 80% to the prediction.

In Table 6, the best decision rule for each subject is highlighted in grey. None of the subjects preferentially used the number of high-quality items to make their decisions. The best score reached for this scenario was seven (out of 12) for a rook. The Maximin strategy was the preferred scenario in five birds but with rather low scores (highest scores ranging from 7 to 9, one rook, three carrion crows, one raven). Three birds had response profiles that were more consistent with the Maximax scenario (highest score ranging from 7 to 10, one carrion crow and two hooded crows) than any other scenario.

Note that the maximal score obtain was 10 (in two birds), and this was only seen in the Maximax heuristic. However, in this heuristic, this score can be easily obtained if individuals exchange at a constant high rate (whatever the lottery), because exchanging more than 66.6% is expected at all but two lotteries (see Gertrude's result for an illustration in Table 6). We investigated this further by checking the range within which each individual exchanged (based on the results reported in table 6), excluding lottery #10 and #11 which, as we know, were discriminated from the others. For all other lotteries, nine birds had an exchange rate within a 30% range (Table 6, for example, shows the lowest exchange rate of 33.33% and a highest exchange rate of 55.55% for Gabi). This included the birds with the best scores in the Maximax and Maximin heuristics. Exchanging at a constant level (except for lottery #10 and #11) has proven to be the dominant strategy in corvids.

4 | DISCUSSION

The present study shows corvids' behavioural responses to a situation in which they were asked to exchange an initial food reward for

another piece of food, which could be of higher, lower or equal quality than the initial food. With the exception of the two lotteries where no high-quality rewards were offered, the corvids did not discriminate significantly between lotteries and most individuals exchanged at a rate that varied little from one lottery to another. This contrasts the results of primate species using a similar set-up (Broihamme et al., 2018). Indeed, primates used a Maximax heuristic, generally exchanging as soon as at least one high-value reward was available and taking into account the odds of the outcomes. In addition, compared to non-human primates, the average exchange rate for corvids was considerably lower (44.96% of all trials compared to 74.1% for non-human primates).

Several hypotheses may explain these differences. First, the low exchange rates of corvids could be indicative of risk-aversion. Corvids could prefer certainty to variability in the delivery of rewards, which would lead them to overestimate the value of the initial item over lotteries (including advantageous ones). It is known that some non-human animals prefer constant options to variable options (Bateson & Kacelnik, 1995; Heilbronner, Rosati, Stevens, Hare, & Hauser, 2008; Reboreda & Kacelnik, 1991) but, as in humans, risk-aversion is sensitive to contextual effects (Bateson, 2002; Caraco, 1981, 1980, 1983; Caraco et al., 1980; Hayden et al., 2008; Heilbronner & Hayden, 2013; Kacelnik & Bateson, 1996; Long et al., 2009; McNamara, 1996; O'Neill & Schultz, 2010; So & Stuphorn, 2010, 2012; Watson et al., 2009). Further work should seek to determine if risk-aversion in corvids is context-dependant or whether it is a constant and stable feature of their decision-making process. It might be worth mentioning that corvids often exhibit neophobia towards new objects and foods (Greggor, Clayton, Fulford, & Thornton, 2016). This may explain a general reluctance to risk losing a certain food. However, we found no evidence of a decrease in risk-aversion, which could be expected if neophobia decreased throughout the test. Thus, exposure to a new type of task cannot explain the lower exchange rates, compared to non-human primate species.

Another difference from studies in non-human primates is the type of reward used. In primates, rewards differed according to

their quantity and not according to their quality (Broihanne et al., 2018). Here, we used rewards of different quality to ensure that birds would be motivated to exchange. Indeed, previous work has shown that corvids fail to maximise reward income when they can exchange a small amount of food for a larger amount of the same food (Hillemann et al., 2014; Wascher et al., 2012). We do not expect this difference in methodology to have affected our results, but it does limit the type of analysis that can be performed on the data and further work may be required to investigate this aspect.

The lower exchange rate could also be due to lower self-control and, consequently, the inability to give away the food item birds already had in their possession. This could be true for one or two individuals which almost never exchanged in the experiment, although they did so successfully during the training (at least in Phase 1), but it is probably not the case for the others. In addition, it has already been shown that corvids are able to overcome impulsivity and cope with delay of gratification (Dufour et al., 2011; Hillemann et al., 2014; Wascher et al., 2012). Corvids also engage in scatter-hoarding, which means that they regularly give up food for later use (Glutz von Blotzheim, 1985). To do this, they need to cope with temporary losses and give up items they already own. Thus, a lack of self-control is unlikely to explain their reluctance to exchange.

Alternatively, corvids may lack the cognitive capacity to compute information about odds (i.e., frequency of rewards). We investigated different scenarios based on simple decision rules. None of the birds preferred the first scenario (a scenario based on the frequency of high-value rewards over low-value rewards) over the other. Four birds showed a preference for the Maximax heuristic (two of them with high scores), and five birds behaved according to Maximin heuristics predictions (albeit with rather low scores). However, an alternative decision rule was to exchange at a constant rate (either low or 'high'—i.e., still below 80% on average) regardless of the lottery. In previous work, we have shown that non-human primates mostly favoured Maximax heuristics with some inter-individual differences (Broihanne et al., 2018). This means that they first considered (ranked) the maximum outcome and did not avoid the minimum outcome (ignoring potential loss). In addition, the evaluation of odds also influenced their decision. Here, the corvids responded differently from the primates. A constant exchange rate could mean that they did not discriminate between lotteries because they did not understand that the content of the cups could contain information about the odds of the outcomes. However, we know that they paid attention to the content of the cups, because they exchanged generally less when there was nothing to win (lottery #10 and #11). They noticed the lack of potential high-quality rewards. Note that using heuristics or simple decision rules does not mean that individuals cannot estimate odds. Such rules are used to make decisions more quickly (avoiding complex cognitive calculation). Here, corvids may have used this rule to simply avoid complex cognitive calculations. Further studies are needed to assess whether corvids indeed disengaged from the task or whether such calculations are cognitively out of their reach. We would have expected the birds to learn about the probability to win or lose in each lottery from their experience and modify their exchange behaviour accordingly. However,

at the end of the study, individuals discriminated even less between lotteries than at the beginning of the study. This lack of discrimination suggests that, if birds paid attention to the odds of each lottery at the beginning, they gave up doing in the course of the study.

In addition to the 'exchange at a constant rate' strategy, the outcome accumulated from the beginning of the session also influenced the willingness to exchange at a given trial in the crows and the hooded crows. Crows were less likely to exchange if more gains had been accumulated since the beginning of the session. Hooded crows showed the reverse pattern, exchanging more as they accumulated more gains. These results are similar to some results in primates but also in human studies, where different decision biases influenced by previous outcomes have been described. The 'gambler's fallacy' describes a situation where the willingness to take risks decreases after the gains (Croson & Sundali, 2005). In contrast, the 'hot hand' and 'house money' effects describe situations in which a series of gains increases the willingness to take future risks (Thaler & Johnson, 1990; Tversky & Kahneman, 1971). Considerations on the underlying mechanisms of these differences in response to outcome at the species level would only be purely speculative, especially since these results in the hooded crow are based on the response of only two individuals. In addition, there was no main effect of species on the exchange rate, and rooks, contrary to what was predicted, did not perform better than other corvids. Larger sample sizes are needed to detect potential species differences and underlying mechanisms. However, it seems safe to say that individual differences can be found in the willingness to exchange in general. In previous experiments applying the exchange paradigm in crows, large individual differences were found and were not necessarily correlated between tasks (Dufour et al., 2011; Wascher, 2015). These results suggest that, in addition to species differences in response to a gamble, individual differences must also be taken into account.

Our results indicate that corvids failed or chose not to evaluate the odds of winning or losing at each new trial. When each decision required a cognitive effort, most corvids chose a single course of action that they maintained constant in most lotteries. Further studies now need to assess whether a similar course of action is detected in decisions about other contexts such as social interactions, predator avoidance while travelling, etc. Alternatively, corvids may only deploy the full potential of their cognitive skills in decisions involving more specialised contexts, that is time-related or cache-related, as the debate regarding the domain-specific versus generalised cognition is still an ongoing issue in these species (Amodio, Jelbert, & Clayton, 2018; Byrne & Bates, 2007; Shettleworth, 2010).

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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REFERENCES

- Amodio, P., Jelbert, S. A., & Clayton, N. S. (2018). The interplay between psychological predispositions and skill learning in the evolution of tool use. *Current Opinion in Behavioral Sciences*, 20, 130–137. <https://doi.org/10.1016/j.cobeha.2018.01.002>
- Bateson, M. (2002). Recent advances in our understanding of risk-sensitive foraging preferences. *Proceedings of the Nutrition Society*, 61, 1–8. <https://doi.org/10.1079/PNS2002181>
- Bateson, M., & Kacelnik, A. (1995). Preference for fixed and variable food sources: Variability in amount and delay. *Journal of the Experimental Analysis of Behavior*, 63, 313–329.
- Bateson, M., & Kacelnik, A. (1997). Starlings' preferences for predictable and unpredictable delays to food. *Animal Behaviour*, 53, 1129–1142. <https://doi.org/10.1006/anbe.1996.0388>
- Bateson, M., & Kacelnik, A. (1998). Risk-sensitive foraging: Decision making in variable environments. In R. Dukas (Ed.), *Cognitive ecology: The evolutionary ecology of information processing and decision making*. Chicago, IL: University of Chicago.
- Bird, C. D., & Emery, N. J. (2009). Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Sciences*, 106(25), 10370–10375. <https://doi.org/10.1073/pnas.0901008106>
- Blanchard, T. C., Wolfe, L. S., Vlaev, I., Winston, J. S., & Hayden, B. Y. (2014). Biases in preferences for sequences of outcomes in monkeys. *Cognition*, 130(3), 289–299. <https://doi.org/10.1016/j.cognition.2013.11.012>
- Brandstätter, E., Gigerenzer, G., & Hertwig, R. (2006). The priority heuristic: Making choices without trade-offs. *Psychological Review*, 113, 409–432. <https://doi.org/10.1037/0033-295X.113.2.409>
- Brandstätter, E., & Gussmack, M. (2013). The cognitive processes underlying risky choice. *Journal of Behavioral Decision Making*, 26, 185–197. <https://doi.org/10.1002/bdm.1752>
- Brito-e-Abreu, F., & Kacelnik, A. (1999). Energy budgets and risk-sensitive foraging in starlings. *Behavioral Ecology*, 10, 338–345. <https://doi.org/10.1093/beheco/10.3.338>
- Bröder, A. (2000). Assessing the empirical validity of the "take-the-best" heuristic as a model of human probabilistic inference. *Journal of Experimental Psychology, Learning, Memory and Cognition*, 26, 1332–1346. <https://doi.org/10.1037/0278-7393.26.5.1332>
- Bröder, A., & Schiffer, S. (2003). Bayesian strategy assessment in multi-attribute decision making. *Journal of Behavioral Decision Making*, 16, 193–213. <https://doi.org/10.1002/bdm.442>
- Broihanne, M.-H., & Dufour, V. (2018). Risk-taking in children and primates in a comparable food gambling game. In *Advances in psychology research*, vol. 134. ISBN: 978-1-53613-948-8
- Broihanne, M.-H., Romain, A., Call, J., Thierry, B., Wascher, C. A. F., De Marco, A., ... Dufour, V. (2018). Monkeys (*Sapajus apella* and *Macaca tonkeana*) and great apes (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan paniscus* and *Pan troglodytes*) play for the highest bid. *Journal of Comparative Psychology*, 133(3), 301–312. <https://doi.org/10.1037/com0000153>
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*, 33, 261–304. <https://doi.org/10.1177/0049124104268644>
- Byrne, R. W., & Bates, L. A. (2007). Sociality, evolution and cognition. *Current Biology*, 17(16), R714–R723. <https://doi.org/10.1016/j.cub.2007.05.069>
- Caraco, T. (1980). On foraging time allocation in a stochastic environment. *Ecology*, 61, 119–128. <https://doi.org/10.2307/1937162>
- Caraco, T. (1981). Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). *Behavioral Ecology and Sociobiology*, 8, 213–217. <https://doi.org/10.1007/BF00299833>
- Caraco, T. (1983). White-crowned sparrows (*Zonotrichia leucophrys*): Foraging preferences in a risky environment. *Behavioral Ecology and Sociobiology*, 12, 63–69. <https://doi.org/10.1007/BF00296934>
- Caraco, T., Martindale, S., & Whittam, T. S. (1980). An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour*, 28, 820–831. [https://doi.org/10.1016/S0003-3472\(80\)80142-4](https://doi.org/10.1016/S0003-3472(80)80142-4)
- Chen, M. K., Lakshminarayanan, V., & Santos, L. R. (2006). How basic are behavioral biases? Evidence from capuchin monkey trading behavior. *Journal of Political Economics*, 114, 517–537. <https://doi.org/10.1086/503550>
- Crosron, R., & Sundali, J. (2005). The gambler's fallacy and the hot hand: Empirical data from casinos. *Journal of Risk and Uncertainty*, 30, 195–209.
- De Petrillo, F., Ventricelli, M., Ponsi, G., & Addessi, E. (2015). Do tufted capuchin monkeys play the odds? Flexible risk preferences in *Sapajus* spp. *Animal Cognition*, 18, 119–130. <https://doi.org/10.1007/s10071-014-0783-7>
- Dhami, M. K. (2003). Psychological models of professional decision making. *Psychological Science*, 14, 175–180. <https://doi.org/10.1111/1467-9280.01438>
- Dufour, V., Wascher, C. A. F., Braun, A., Miller, R., & Bugnyar, T. (2011). Corvids can decide if a future exchange is worth waiting for. *Biology Letters*, 8(2), 201–204. <https://doi.org/10.1098/rsbl.2011.0726>
- Emery, N. J., & Clayton, N. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science*, 306, 1903–1907. <https://doi.org/10.1126/science.1098410>
- Emery, N. J., Seed, A. M., von Bayern, A. M. P., & Clayton, N. S. (2007). Cognitive adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society B*, 362, 489–506. <https://doi.org/10.1098/rstb.2006.1991>
- Glutz von Blotzheim, U. N. (1985). *Handbuch der Vögel Mitteleuropas*. Wiesbaden, Germany: Aula-Verlag.
- Greggor, A. L., Clayton, N. S., Fulford, A. J., & Thornton, A. (2016). Street smart: Faster approach towards litter in urban areas by highly neophobic corvids and less fearful birds. *Animal Behaviour*, 117, 123–133. <https://doi.org/10.1016/j.anbehav.2016.03.029>
- Güntürkün, O., & Bugnyar, T. (2016). Cognition without cortex. *Trends in Cognitive Sciences*, 20(4), 291–303. <https://doi.org/10.1016/j.tics.2016.02.001>
- Hayden, B. Y., Heilbronner, S. R., Nair, A. C., & Platt, M. L. (2008). Cognitive influences on risk-seeking by rhesus macaques. *Judgment and Decision Making*, 3, 389–395.
- Heilbronner, S. R., & Hayden, B. Y. (2013). Contextual factors explain risk-seeking preferences in rhesus monkeys. *Frontiers in Neurosciences*, 7, 7. <https://doi.org/10.3389/fnins.2013.00007>
- Heilbronner, S. R., Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters*, 4, 246–249. <https://doi.org/10.1098/rsbl.2008.0081>
- Hillemann, F., Bugnyar, T., Kotrschal, K., & Wascher, C. A. (2014). Waiting for better, not for more: Corvids respond to quality in two delay maintenance tasks. *Animal Behaviour*, 90, 1–10. <https://doi.org/10.1016/j.anbehav.2014.01.007>
- Kacelnik, A., & Bateson, M. (1996). Risky theories—The effects of variance on foraging decisions. *American Zoologist*, 36, 402–434. <https://doi.org/10.1093/icb/36.4.402>
- Knight, F. (1921). *Risk, uncertainty, and profit*. Boston, MA: Hart, Schaffner and Marx.

- Lakshminarayanan, V. R., Chen, M. K., & Santos, L. R. (2011). The evolution of decision-making under risk: Framing effects in monkey risk preferences. *Journal of Experimental Social Psychology*, 47(3), 689–693. <https://doi.org/10.1016/j.jesp.2010.12.011>
- Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, 69(1), 1–33. <https://doi.org/10.18637/jss.v069.i01>
- Long, A. B., Kuhn, C. M., & Platt, M. L. (2009). Serotonin shapes risky decision making in monkeys. *Social Cognitive and Affective Neuroscience*, 4, 346–356. <https://doi.org/10.1093/scan/nsp020>
- Luce, R. D., & Raiffa, H. (1957). *Games and decisions: Introduction and critical survey*. New York, NY: Dover Publications.
- Marsh, B., & Kacelnik, A. (2002). Framing effects and risky decisions in starlings. *Proceedings of the National Academy of Science*, 99, 3352–3355. <https://doi.org/10.1073/pnas.042491999>
- Massen, J. J. M., Ritter, C., & Bugnyar, T. (2015). Tolerance and reward equity predict cooperation in ravens (*Corvus corax*). *Scientific Reports*, 5, 1–11. <https://doi.org/10.1038/srep15021>
- McNamara, J. (1996). Risk-prone behaviour under rules which have evolved in a changing environment. *American Zoologist*, 36, 484–495. <https://doi.org/10.1093/icb/36.4.484>
- Monosov, I. E., & Hikosaka, O. (2013). Selective and graded coding of reward uncertainty by neurons in the primate anterodorsal septal region. *Nature Neuroscience*, 16, 756–762. <https://doi.org/10.1038/nn.3398>
- Müller, J. J. A., Massen, J. J. M., Bugnyar, T., & Osvath, M. (2017). Ravens remember the nature of a single reciprocal interaction sequence over 2 days and even after a month. *Animal Behaviour*, 128, 69–78. <https://doi.org/10.1016/j.anbehav.2017.04.004>
- Newell, B. R., Weston, N. J., & Shanks, D. R. (2003). Empirical tests of a fast-and-frugal heuristic: Not everyone 'takes-the-best'. *Organizational Behavior and Human Decision Processes*, 91, 82–96. [https://doi.org/10.1016/S0749-5978\(02\)00525-3](https://doi.org/10.1016/S0749-5978(02)00525-3)
- O'Neill, M., & Schultz, W. (2010). Coding of reward risk by orbitofrontal neurons is mostly distinct from coding of reward value. *Neuron*, 68, 789–800. <https://doi.org/10.1016/j.neuron.2010.09.031>
- Paglieri, F., Addessi, E., De Petrillo, F., Laviola, G., Mirolli, M., Parisi, D., ... Adriani, W. (2014). Nonhuman gamblers: Lessons from rodents, primates, and robots. *Frontiers in Behavioral Neurosciences*, 8, 33. <https://doi.org/10.3389/fnbeh.2014.00033>
- Payne, J. W., Bettman, J. R., & Johnson, E. J. (1993). *The adaptive decision maker*. Cambridge, UK: Cambridge University Press.
- Payne, J. W., Bettman, J. R., & Luce, M. F. (1996). When time is money: Decision behavior under opportunity-cost time pressure. *Organizational Behavior and Human Decision Processes*, 66, 131–152. <https://doi.org/10.1006/obhd.1996.0044>
- Pelé, M., Broihanne, M.-H., Thierry, B., Call, J., & Dufour, V. (2014). To bet or not to bet? Decision-making under risk in non-human primates. *Journal of Risk and Uncertainty*, 49, 141–166. <https://doi.org/10.1007/s11166-014-9202-3>
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Reboreda, J. C., & Kacelnik, A. (1991). Risk sensitivity in starlings: Variability in food amount and food delay. *Behavioral Ecology*, 2, 301–308. <https://doi.org/10.1093/beheco/2.4.301>
- Rieskamp, J., & Hoffrage, U. (1999). When do people use simple heuristics and how can we tell? In G. Gigerenzer, & P. M. Todd (Eds., the ABC Group) *Simple heuristics that make us smart* (pp. 141–167). New York, NY: Oxford University Press.
- Schkade, D. A., & Johnson, E. J. (1989). Cognitive processes in preference reversals. *Organizational Behavior and Human Decision Processes*, 44, 203–231. [https://doi.org/10.1016/0749-5978\(89\)90025-3](https://doi.org/10.1016/0749-5978(89)90025-3)
- Shettleworth, S. J. (2010). *Cognition, evolution, and behavior*. New York, NY: Oxford University Press.
- So, N.-Y., & Stuphorn, V. (2010). Supplementary eye field encodes option and action value for saccades with variable reward. *Journal of Neurophysiology*, 104, 2634–2653. <https://doi.org/10.1152/jn.00430.2010>
- So, N.-Y., & Stuphorn, V. (2012). Supplementary eye field encodes reward prediction error. *Journal of Neuroscience*, 32, 2950–2963. <https://doi.org/10.1523/JNEUROSCI.4419-11.2012>
- Tabachnick, B. G., & Fidell, L. S. (2007). *Using multivariate statistics*, 5th ed. Boston: Pearson Education.
- Thaler, R. H., & Johnson, E. J. (1990). Gambling with the house money and trying to break even: The effects of prior outcomes on risky choice. *Management Science*, 36, 646–660. <https://doi.org/10.1287/mnsc.36.6.643>
- Tversky, A., & Kahneman, D. (1971). Belief in the law of small numbers. *Psychological Bulletin*, 76, 105–110. <https://doi.org/10.1037/h0031322>
- Tversky, A., & Kahneman, D. (1974). Judgment under uncertainty: Heuristics and biases. *Science*, 185, 1124–1131. <https://doi.org/10.1126/science.185.4157.1124>
- Tversky, A., & Kahneman, D. (1981). The framing of decisions and the psychology of choice. *Science*, 211, 452–458. <https://doi.org/10.1126/science.7455683>
- Tversky, A., & Kahneman, D. (1986). Rational choice and the framing of decisions. *Journal of Business*, 59, S251–S278. <https://doi.org/10.1086/296365>
- Wascher, C. A. (2015). Individual performance in socio-cognitive tasks predicts social behaviour in carrion crows. *Behaviour*, 152(5), 615–634. <https://doi.org/10.1163/1568539X-00003245>
- Wascher, C. A. F., & Bugnyar, T. (2013). Behavioral responses to inequity in reward distribution and working effort in crows and ravens. *PLoS ONE*, 8(2), e56885. <https://doi.org/10.1371/journal.pone.0056885>
- Wascher, C. A. F., Dufour, V., & Bugnyar, T. (2012). Carrion crows cannot overcome a delay of gratification in a quantitative exchange task. *Frontiers in Comparative Psychology*, 3, 118.
- Watson, K. K., Ghodasra, J. H., & Platt, M. L. (2009). Serotonin transporter genotype modulates social reward and punishment in rhesus macaques. *PLoS ONE*, 4(1), e4156. <https://doi.org/10.1371/journal.pone.0004156>
- Watzek, J., & Brosnan, S. F. (2018). (Ir)rational choices of humans, rhesus macaques, and capuchin monkeys in dynamic stochastic environments. *Cognition*, 178, 109–117. <https://doi.org/10.1016/j.cognition.2018.05.019>
- Yamada, H., Tymula, A., Louie, K., & Glimcher, P. W. (2013). Thirst-dependent risk preferences in monkeys identify a primitive form of wealth. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 15788–15793. <https://doi.org/10.1073/pnas.1308718110>

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