

Ravens remember the nature of a single reciprocal interaction sequence over 2 days and even after a month



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To explain reciprocity, direct or indirect, several proximate mechanisms have been proposed, yet little attention has been given to the specific underlying cognitive mechanisms. Regardless of what proximate rules underlie reciprocity, some kind of memory would be paramount. Corvids in general, and ravens, *Corvus corax*, specifically, have been shown to possess an array of sophisticated cognitive mechanisms involved in memory. In this study, we tested the memory of nine ravens in an exchange paradigm where they could exchange a low-quality for a high-quality food item. Specifically, we tested whether they remembered who was a reliable ‘fair’ experimenter and who would not reliably exchange (the ‘unfair’ experimenter), and whether they would subsequently choose to interact with the former when given the choice. In addition, we tested whether ravens that observed the initial seeding of information about who was ‘fair’ or ‘unfair’ could transform bystander information into first-person interactions, i.e. also preferring to interact with the ‘fair’ experimenter when given the choice. The results show that ravens with first-hand experience were more likely to interact with experimenters with whom they had had a positive previous experience, and that this memory lasted at least 1 month. In contrast, observers did not distinguish between the experimenters when given the choice to interact with them. Previous first-hand experience with the paradigm, however, seemed to help observers to be more successful in solving the task, albeit not significantly above chance. In sum, this study shows memory for direct reciprocity in ravens, and tentatively suggests memory for indirect reciprocity. Accordingly, these results provide hints for the underlying mechanism of memory in raven social interactions.

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Reciprocal altruism (Trivers, 1971) has proven a powerful theory explaining the evolution of repeated prosocial interactions between individuals. In such repeated interactions individuals may exchange different goods and commodities with each other (Hemelrijk & Ek, 1991; Kappeler & van Schaik, 2006; Sachs, Mueller, Wilcox, & Bull, 2004). For example, there is ample evidence that primates exchange grooming (meta-analyses on 22 primate species: Schino & Aureli, 2008), as well as agonistic support in conflicts (Schino, 2007; Smith et al., 2010), and that they interchange both commodities (meta-analysis on 14 primate species: Schino, 2007). A similar picture has recently started to emerge in birds such as

corvids that form long-term social bonds (Emery, Seed, von Bayern, & Clayton, 2007). Ravens, *Corvus corax*, for instance, were found to exchange coalitionary support among each other as well as interchanging the avian equivalent of grooming (preening) for support, and do so most with those individuals with whom they share a bonded relationship (Fraser & Bugnyar, 2010, 2012). Moreover, ravens have been shown to stop cooperating when their partner cheats (Massen, Ritter, & Bugnyar, 2015). Both rooks, *Corvus frugilegus*, and ravens cooperate better with affiliates (Seed, Clayton, & Emery, 2008), and ravens even actively choose to cooperate with friends when given a choice between different partners (Asakawa-Haas, Schiestl, Bugnyar, & Massen, 2016).

Several hypotheses have been proposed for the underlying proximate mechanisms of reciprocation. Calculated reciprocity refers to the active scorekeeping of the value and amount of what has been given and received (de Waal & Luttrell, 1988), a mechanism so far only shown in orang-utans, *Pongo abelii* (Dufour, Pelé, Neumann,

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Thierry, & Call, 2009). Attitudinal reciprocity, which was shown in capuchin monkeys, *Cebus apella* (de Waal, 2000), describes a mechanism in which the choice to cooperate depends on the attitude the interaction partner has recently shown towards the subject (Brosnan & de Waal, 2002; de Waal, 2000). Emotionally mediated reciprocity is related, but stresses the emotions derived from a long-term series of interactions and has been investigated by studying the time frame of the reciprocal exchange of grooming and agonistic support in Japanese macaques, *Macaca fuscata* (Schino, Polizzi di Sorrentino, & Tiddi, 2007). Finally, symmetry-based reciprocity suggests that the initiation and maintenance of reciprocal relations is solely based on the symmetrical features of two individuals (de Waal & Luttrell, 1988). Brosnan and de Waal (2002) argued that many examples of animal altruism might depend on symmetry-based reciprocity (e.g. Wilkinson, 1984, 1988). However, a recent modelling study revealed that this is not an evolutionarily stable strategy to maintain reciprocity in a group (Campenni & Schino, 2016). In addition to direct forms of reciprocation, there is indirect reciprocity, where A helps B because B has the reputation of being cooperative, as A observed B helping C in the past (Nowak & Sigmund, 2005). This has, for example, been shown in dogs, *Canis lupus familiaris* (Chijiwa, Kuroshima, Hori, Anderson, & Fujita, 2015), capuchin monkeys (Anderson, Kuroshima, Takimoto, & Fujita, 2013) and squirrel monkeys, *Saimiri sciureus* (Anderson, Bucher, Kuroshima, & Fujita, 2016). In contrast, in generalized or upstream reciprocity receiving something leads to a good 'feeling' which in turn creates a higher propensity to give something to a third party (Boyd & Richerson, 1989; Nowak & Roch, 2007), which has, for example, been shown in rats, *Rattus norvegicus* (Rutte & Taborsky, 2007).

Calculated reciprocity, as an example, has been considered cognitively too demanding for nonhuman species (Schino & Aureli, 2010; Stevens & Hauser, 2004; but see Dufour et al., 2009). However, little attention has been given to those cognitive skills that nonhuman animals purportedly lack for the different forms of reciprocity. Some emphasis has been put on the time frame of reciprocation to distinguish attitudinal from emotional systems (Schino et al., 2007), but it does not pinpoint specific traits. Apart from symmetry-based reciprocity and generalized reciprocity, however, all proposed mechanisms rely on some sort of memory, and more specifically on memories of what happened to you in an interaction with a specific individual, or in the indirect case, of interactions between others. Therefore, the aims of this study were to analyse whether ravens can remember (1) who acted cooperatively or defectively in a single session, and (2) an experience of third-party interactions of cooperation or defection. The required memories may rely on numerous cognitive systems working in concert, and it has previously been shown that corvids have several of these systems.

A central memory skill for reciprocity is the recall of someone's identity. Face recognition is an integral part of such recollection. The ability to recognize faces is a conserved skill, found not only in mammals, such as primates and sheep (Tate, Fischer, Leigh, & Kendrick, 2006), but, for example, also in American crows, *Corvus brachyrhynchos* (Marzluff, Walls, Cornell, Withey, & Craig, 2010) and honeybees, *Apis mellifera* (Dyer, Neumeyer, & Chittka, 2005). Naturally, interspecies face recognition does not rely on specific predispositions for recognizing faces of members of other species. Rather, much of the recognition results from configural processing of the elements from which a face is constructed, which is a process used by bees as well as humans (Avarguès-Weber, Portelli, Benard, Dyer, & Giurfa, 2010). Face recognition does not suffice, however, if one must remember the cooperativeness of an individual. At the very least, one needs positive or negative emotions associated with the identity. American crows have been shown to make such emotional associations in identity

recognition, using neurobiological mechanisms similar to those of mammals (Marzluff, Miyaoka, Minoshima, & Cross, 2012). It has further been shown that ravens can remember the valence of their relationship with conspecifics over years and respond to their calls accordingly (Boeckle & Bugnyar, 2012).

Remembering single events of reciprocal interactions would, arguably, contribute substantially to more economical behaviour in future interactions between the same individuals. There is evidence that large-billed crows, *Corvus macrorhynchos*, remember the dominance status of another individual, in relation to themselves, after single event interactions (Izawa & Watanabe, 2008; Nishizawa, Izawa, & Watanabe, 2011). It has also been shown that American crows will remember the face of a dangerous human (a trapper of crows) for several years after only one interaction (Marzluff et al., 2010). Moreover, ravens and western scrub jays, *Aphelocoma californica*, remember which of their group mates was watching them during a single caching event (Bugnyar, 2011; Dally, Emery, & Clayton, 2006).

Memories of single events are often attributed to the workings of an episodic memory system. Episodic-like memories have been exhibited, in relation to different caching contexts, by western scrub jays (for a review see de Kort, Dickinson, & Clayton, 2005). However, so-called one-shot learning in animals is an ill-understood and debated phenomenon (Osvath, 2015). Nevertheless, some studies have provided evidence that chimpanzees, *Pan troglodytes*, orang-utans and humans share some core features of their memory systems to recall personal experiences from the past (Martin-Ordas, Berntsen, & Call, 2013). Single event learning can, however, be supported by different mechanisms; for example innate defence behaviours and so-called preparedness (Bolles, 1970; Seligman, 1971). The above examples of single event memories in corvids are related either to dominance, fear or caching contexts, domains of great importance for corvids. Regardless of the specific mechanisms underlying their memories, however, we wanted to investigate whether ravens can extend this single-event-memory skill to reciprocal interactions.

Finally, we also wanted to investigate whether ravens can remember and act upon a single interaction sequence of third-party interactions. Indirect reciprocity is generally regarded as cognitively more demanding than direct reciprocity (Nowak & Sigmund, 2005). Among other things, one must be able to form memories of interactions between others, and attribute valence to the actions. However, it has been shown that ravens are capable of representing and remembering the relationships between others, without even having interacted with any of the observed individuals (Massen, Pašukonis, Schmidt, & Bugnyar, 2014), and they also seem to keep track of such third-party relationships over time (Massen, Szípl, Spreafico, & Bugnyar, 2014) suggesting at least some sort of third-party knowledge and memory. Given such extraordinary capabilities in corvids in general and ravens in particular, one could hypothesize that many reciprocal behaviours in corvids also rely on elaborate memory systems. Therefore, we predicted that ravens are able to remember the identity of certain experimenters and their characteristic behaviour (cooperate, defect), and that they prefer interacting with the 'fair' experimenter when given the choice at a later stage. Moreover, we predicted ravens would have third-person event memory, expressed by a transfer to a first-person interaction. Consequently, observing birds should show the same behaviour (preference) and exchange rates as the first-hand experienced birds when given the choice at a later test phase. Finally, given the complex fission–fusion dynamics in raven nonbreeding flocks (Loretto, Reimannf, Schuster, Graulich, & Bugnyar, 2016; Loretto, Schuster, & Bugnyar, 2016) that allow for long-term separations of known conspecifics, we predicted that these memories could also last a long time, i.e. from 2 days to a month.

METHODS

Subjects and Housing

The study was conducted at Haidlhof Research Station, Bad Vöslau, Austria. Nine captive bred, hand-raised ravens served as subjects (for detailed information of individuals see Table 1). The birds were kept in a large aviary complex (15 × 15 m and 5 m high) separated into four parts. Each part was equipped with trees, perches, different playing devices, and pools with water for bathing and drinking. The experimental compartment (7 × 4 m and 3 m high) was directly connected to the aviary and could be split into six smaller areas. During the study, normal feeding routines were upheld. Water was available *ad libitum* in both living and test compartments. Some of the birds had experience with experimental tests of prosociality, using either a token exchange paradigm (Massen, Lambert, Schiestl, & Bugnyar, 2015) or prosocial choice task (Lambert, Massen, Seed, Bugnyar, & Slocombe, 2017), and/or with tests on cooperation using a loose-string paradigm (Asakawa-Haas et al., 2016; Massen, Ritter, et al., 2015). However, none of these tests were performed parallel to our study period, and since the paradigms were different, we did not expect any influence of the birds' experience on our results.

Ethical Note

The birds were never forced to participate and were not tested if they did not want to come into the test compartment. Moreover, when they showed distress or unwillingness during a test, we terminated the test. As our tests were dependent on specific time frames (2 days and approximately 1 month), we therefore could not always test all birds. Consequently, the sample sizes per time frame vary (see Table 3 in the Results). Furthermore, this study was noninvasive and consequently complied with Austrian law. The study design was evaluated and approved by the ethical board of

the behavioural research group at the Faculty of Life Sciences, University of Vienna (case number: 2015-003) and meets the latest ASAB/ABS ethical guidelines (www.sciencedirect.com/science/article/pii/S0003347215004613).

Experimental Design and Set-up

We used an exchange paradigm, in which the ravens had the opportunity to exchange a low-quality food (bread) for a high-quality food (cheese) from a human experimenter (E). We know that ravens prefer cheese over bread from our day-to-day experience with the birds when they are being fed both types of food, and this was corroborated during the training phase in which all ravens happily exchanged bread for cheese. Nevertheless, the exchange entailed an initial cost for the bird, as it had to give the low-quality food away. In the training, the cost was always outweighed by the gain of a better reward; however, in the experiment, the ravens experienced that giving food away bears the risk of getting nothing in return.

Before the experiment started, all ravens were trained in exchanging bread for cheese. Seven of nine ravens involved in this study were already trained in exchanging tokens for a reward (Massen, Lambert, et al., 2015); the other two were naïve to the paradigm. The request for exchange was done by presenting the empty palm of the right hand while a piece of cheese was held up between two fingers of the left hand. Once a bird had exchanged the bread it got from one trainer (J.M.) for the cheese from a second familiar trainer sitting next to J.M., we increased, step by step, the distance between the trainers, until they stood on opposite sides outside the test compartment. This was the initial situation. For later seeding sessions, the second trainer was replaced by novel unknown experimenters (Fig. 1). The birds only participated in the study when they passed the criterion, i.e. without a vocal request performing eight of 10 exchanges successfully in two consecutive sessions.

The experiment consisted of a seeding phase and two test phases that were conducted, respectively, 2 days and approximately 1 month (range 26 days–40 days; mean: 31 days) later. The seeding phase featured the encounters the ravens had to encode in their memories. During seeding, each raven faced two novel experimenters in two different exchange sessions 3 h apart. In one session, they encountered an experimenter (the 'fair' exchange partner) who always exchanged bread for cheese. In the other session, they interacted with an experimenter who would accept the bread but then eat the cheese herself (the 'unfair' exchange partner). All exchange partners were female and the ravens had no previous social experience with any of them. Whether the subjects started with a fair or an unfair exchange partner was counter-balanced. The roles of the human partners were also counter-balanced between the dyads, but remained the same for each individual/dyad during the study.

Table 1
Name, sex, age, origin and relatedness of participating subjects

Name	Sex	Age (years)	Origin	Kinship
Tom	♂	3	Germany	Group 1
Laggie	♂	3	Germany	Group 1
Horst	♂	3	Sweden	Group 2
Louise	♀	3	Sweden	Group 2
Nobel	♀	3	Sweden	Group 2
George	♂	3	Sweden	Group 2
Paul	♂	3	Austria	Group 3
Joey	♀	5	Germany	Group 4
Rocky	♂	3	Czech Republic	Group 5

Table 2
Overview of the dyads of first-hand experienced birds and observers in rounds 1 and 2

Round 1		Round 2	
First-hand experienced	Observer	First-hand experienced	Observer
Laggie	Tom	Tom	Laggie
Nobel	George	George	Nobel
Horst	Louise	Joey	Rocky
Rocky	Joey	Nobel [†]	Paul
Paul	Horst [*]	Louise [‡]	—

* When Paul was tested as a first-hand experienced bird it was already round 2 for Horst, who was tested as observer in that session.

† After Nobel finished the experiment in round 2 as observer, she served as demonstrator in the seeding phase for Paul, but was not tested again.

‡ Louise was tested much later than the other birds and, therefore, she did not have an observing partner.

Table 3
Number of first-hand experienced and observing birds that chose the fair, the unfair or the neutral experimenter in their first choice

	2 days			±1 month		
	Fair	Unfair	Neutral	Fair	Unfair	Neutral
First-hand experienced	6 (7)	0	1	7 (8)	1	1
Observer	3 (4)	3 (4)	2	5	2	1*
Observers without experience	0 (1)	1 (2)	2	1	1	1
Observers with experience	3	2	0	4	1	0

Since the neutral experimenter gave the piece of bread back and the bird could choose again, numbers in parentheses represent the number of birds that chose the fair and the unfair experimenter after exchanging with the neutral one.

* This bird did not choose another experimenter after choosing the neutral one.

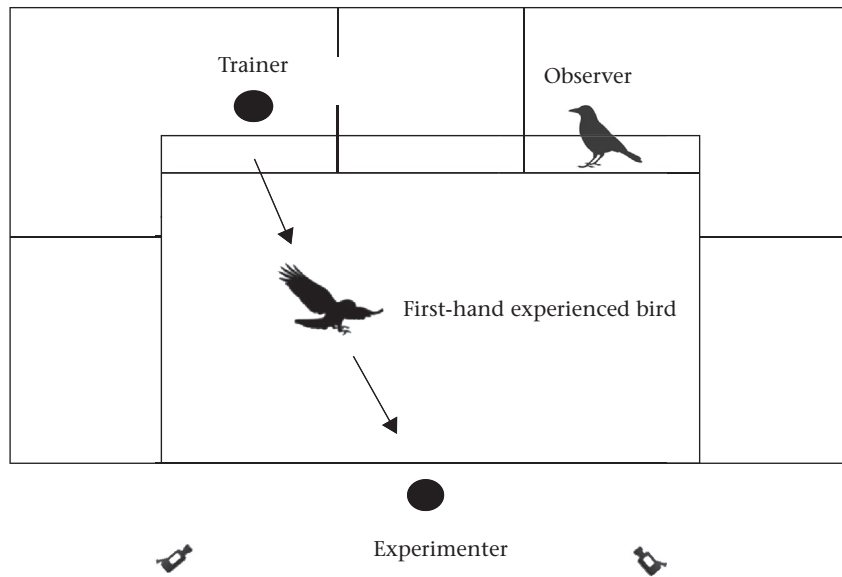


Figure 1. Set-up for seeding the experience.

During seeding sessions, two ravens were present in the experimental area: the exchanger and the observer (Table 2). While the former could get first-hand experience by interacting with the human experimenters, the latter could observe these interactions from an adjacent compartment, separated from the experimental room by wire mesh (Fig. 1). In each seeding session, a familiar trainer called the exchanging bird to get the piece of bread on a board placed at the same height as that on which the observing individual was sitting. With the bread in its beak the exchanging bird could then fly down to the experimenter on the other end of the compartment for the exchange (Fig. 1). Observers could watch these exchanges but had no means to intervene. Each seeding session included a maximum of 15 exchanges, depending on how often the exchanging individual continued and took a new piece of bread. When the bird did not retrieve a new piece of bread for 3 min, the session was ended before all possible 15 exchanges were done. This choice of a maximum 15 exchanges was determined arbitrarily with the ulterior motive to give the observing birds a realistic chance to watch and remember the interaction. Repeated exchanges within the single interaction sequences with the fair and the unfair experimenters were thought to give an accurate summary of the experimenters' trustworthiness (Volstorf, Rieskamp, & Stevens, 2011).

We created dyads of exchanging and observing birds by putting together socially affiliated birds. Affiliation between birds was determined by regular behavioural observations (cf. Lambert et al., 2017). The arrangement of the birds had practical reasons because affiliated birds were easier to separate, and more willing to 'work' while the other one was watching. After one round (round 1) of testing was completed, i.e. after the test approximately 1 month after seeding, we switched the positions of observers and exchangers to test all individuals ($N = 9$) both as first-hand experienced and as observing birds (round 2). Consequently, some birds had first-hand experience with the paradigm when they became observers. This experience, though, referred to the paradigm and not to the specific experimenters, as these were different across the two rounds.

As a final step, we tested the ravens individually, first-hand experienced birds and observers alike, for their ability to recall which of the experimenters had cooperated in the past. The birds were offered a choice between the 'fair' and the 'unfair'

experimenter, as well as a third and unknown neutral person (Fig. 2). This third experimenter was meant to be a control for novelty and spontaneous preferences, and as she was unfamiliar to the birds, she should be without any valence to them and thus chosen more often than the unfair experimenter but less often than the fair experimenter.

The tested bird received a piece of bread from the trainer sitting on the ground in the middle of the compartment (to preclude side bias; Fig. 2), and could then choose to exchange it with either of the three experimenters on the other side of the compartment. All three experimenters were asking for exchange by presenting the empty palm of the right hand and offering a piece of cheese in their left hand. As in the seeding phase, the fair experimenter exchanged the cheese but the unfair experimenter ate the cheese after receiving the bread. When the neutral experimenter was selected, she gave the bread back, and the raven thus got another option to exchange. All birds received 15 consecutive trials per test session. Tests were conducted twice, 2 days and 1 month after seeding. The side position of the fair and the unfair experimenters (left, right) were counterbalanced over the birds and per bird over the test sessions (i.e. 2 days or 1 month after seeding); the position of the neutral experimenter (middle) remained the same.

Video and Statistical Data Analysis

All seeding and test interactions with the human experimenters were videorecorded for later analysis (see [Supplementary videos](#) for an example). We scored the birds' first exchange decisions, and the frequency of choosing which experimenter per test session. The videos of the observing birds were analysed for attentiveness by measuring the time the observer was sitting in front of a window from which the exchange events could be watched. A second independent experimenter coded 20% of the videos on observer's attentiveness for inter-rater reliability, which showed perfect agreement (Spearman rank correlation: $r = 1.00$, $N = 4$, $P < 0.001$).

We ran statistical analyses with IBM SPSS Statistics 21 (IBM Corp., Armonk, NY, U.S.A.), assuming $\alpha = 0.05$. To test whether one experimenter was chosen first (i.e. in the first trial) by significantly more birds we conducted chi-square tests. As the birds could

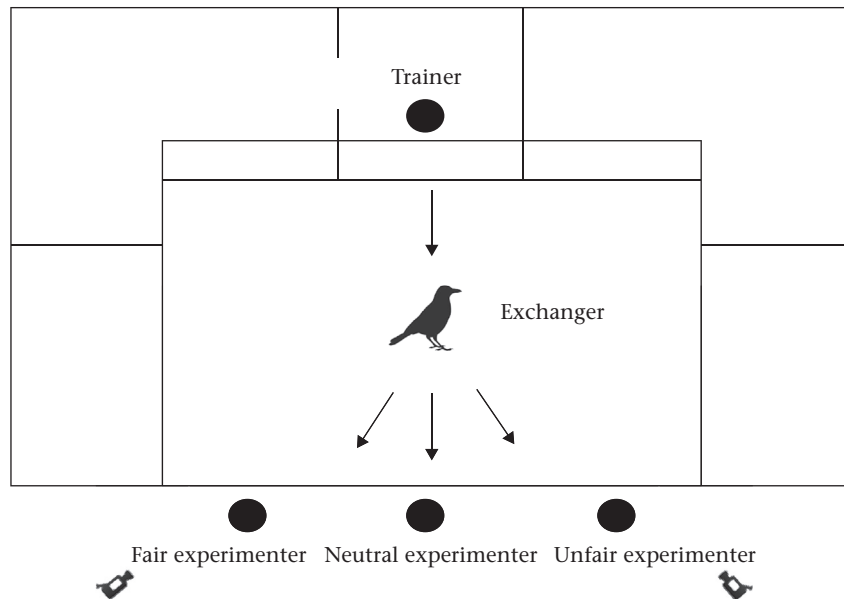


Figure 2. Set-up for the test 2 days and ± 1 month after seeding the experience.

choose again after exchanging with the neutral experimenter, we compared first choices for the two conditions ‘fair’ and ‘unfair’ only. We ran these tests separately for first-hand experienced birds and for observers. Additionally, chi-square tests were done to measure whether there was a significant difference between the first choices of first-hand experienced birds and observers. Finally, we tested whether having experience as a subject would affect choices when observer. Therefore, we compared the first choices of observer birds with and without experience with the paradigm, again using chi-square tests.

To investigate whether first-hand experienced or observing birds chose the fair experimenter over multiple trials significantly above chance, we used the Wilcoxon signed-rank test to compare the ratio of choices for the fair experimenter with random choices. Moreover, to compare the frequencies of choices between observer birds that had experience with the paradigm with those that did not, we used Mann–Whitney U tests.

RESULTS

During seeding sessions, first-hand experienced birds exchanged significantly more often with the fair experimenter than with the unfair one ($T^+ = 41$, $N = 9$, $P = 0.026$); i.e. on average \pm SE 11 ± 3.8 pieces of bread with the fair experimenter and 7 ± 1.9 with the unfair one. Albeit the birds could not exchange the piece of bread successfully with the unfair experimenter, they did not interrupt the session significantly earlier ($T^+ = 34$, $N = 9$, $P = 0.172$); although seeding sessions took on average \pm SE 4.1 ± 1.6 min with the fair and 5.6 ± 2.5 min with the unfair experimenter, this difference was not significant. Consequently, observing birds had similar amounts of time to observe interaction sequences with both the fair and unfair experimenter.

First-hand Experienced Birds

Two days after seeding, six of the seven first-hand experienced birds chose to exchange first with the fair experimenter and one bird chose the neutral experimenter first (see [Table 3](#)), which constitutes a significant preference for the fair experimenter

compared to a chance level of 0.33 (mean = 8.9, $N = 7$, $P = 0.012$). However, since the neutral experimenter served as a control and gave the piece of bread back, we concentrated on the comparison of the choices for either the fair or the unfair experimenter. After being given back the piece of bread the one bird that did choose the neutral experimenter first subsequently also chose to exchange with the fair experimenter, and thus all seven first-hand experienced birds significantly preferred the fair over the unfair experimenter 2 days after seeding the experience (mean = 7, $N = 7$, $P = 0.008$; [Fig. 3a](#)). When comparing the frequency of choices for the ‘fair’ experimenter versus random choices, we found that 2 days after seeding the experience, first-hand experienced birds chose the fair experimenter significantly more often than chance ($T^+ = 28$, $N = 7$, $P = 0.018$; [Fig. 4a](#)). Approximately 1 month after seeding the experience, seven of the nine first-hand experienced birds chose the fair experimenter first, one the unfair and one the neutral experimenter, again constituting a significant preference for the fair experimenter compared to a chance level of 0.33 (mean = 8, $N = 9$, $P = 0.018$). After being given back the piece of bread the one bird that did choose the neutral experimenter first subsequently chose to exchange with the fair experimenter, and thus eight of nine birds chose the fair over the unfair experimenter (mean = 5.44, $N = 9$, $P = 0.02$; [Fig. 3b](#)). When comparing the frequency of choices for the ‘fair’ experimenter versus random choices, we found after approximately 1 month a nonsignificant trend for birds to choose the fair experimenters more often than chance level ($T^+ = 31$, $N = 9$, $P = 0.068$; [Fig. 4b](#)), which may be an artefact of our small sample size.

Observing Birds

Unlike in the first-hand experienced birds, we found no significant difference in the first choice of observers ([Table 2](#)) 2 days after the seeding (mean = 0.00, $N = 8$, $P = 1.00$) and approximately 1 month after the seeding (mean = 1.286, $N = 7$, $P = 0.257$; [Fig. 3a](#)); 2 days after seeding the experience four birds chose the fair and four the unfair experimenter, and 1 month after seeding five birds chose the fair experimenter, and only two birds chose the unfair one ([Table 3](#)). Consequently, the number of first-hand experienced birds

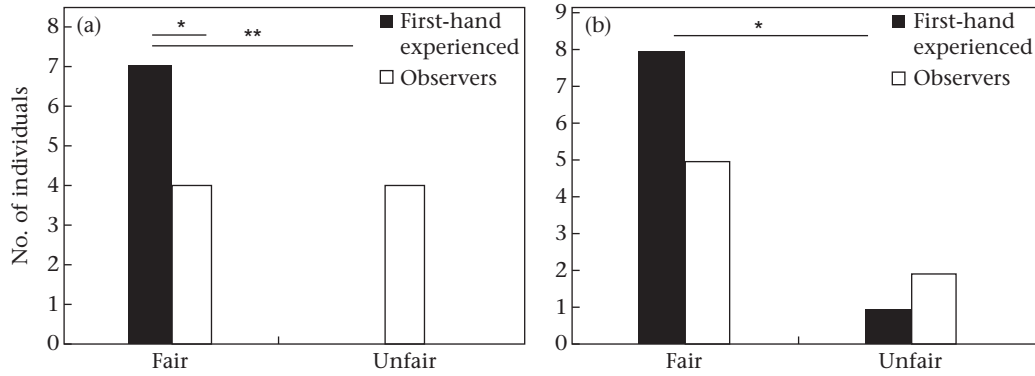


Figure 3. First decision for the two conditions (fair and unfair) of first-hand experienced birds and observers (a) 2 days after seeding and (b) ± 1 month after seeding. * $P < 0.05$; ** $P < 0.01$; chi-square test. In the second round of tests, observers also had some first-hand experience from the first round of tests.

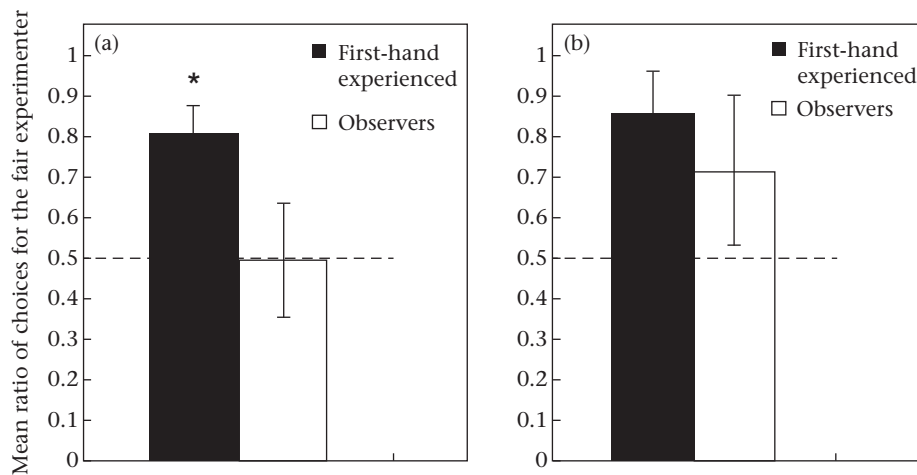


Figure 4. Mean \pm SEM ratio of fair choices compared to random for first-hand experienced birds and observers (a) 2 days after seeding and (b) ± 1 month after seeding. * $P < 0.05$; Wilcoxon-signed rank test.

that chose the fair experimenter was significantly higher than the birds that just observed others interacting (mean = 6.25, $N = 8$, $P = 0.012$; Fig. 3a). These findings indicate that only first-hand experienced birds encoded and remembered the different cooperativeness of the experimenters. Accordingly, when we looked at the frequency of choices for the fair experimenter compared to chance, 2 days after seeding the experience there was no significant difference for observing birds ($T^+ = 11$, $N = 8$, $P = 0.611$; Fig. 4a), and we also did not find a significant difference after approximately 1 month ($T^+ = 20.5$, $N = 7$, $P = 0.270$; Fig. 4b).

Observers Divided by Experience with the Paradigm

Observing birds could be classified into birds without experience with the paradigm (observers in round 1) and birds with experience (observers in round 2), i.e. due to the role change between the two rounds, observers in round 2 were first-hand experienced birds in round 1 and had experienced the set-up in the past. Note, however, that all experimenters (fair, unfair and neutral) were new in the second round. During the first test 2 days after seeding the experience, three birds with experience chose the fair experimenter first, whereas none of the birds without experience did (mean = 4.00, $N_1 = 5$, $N_2 = 4$, $P = 0.046$; Fig. 5a). However, even though more birds with experience chose the fair experimenter first, their preference was not significantly different from chance (mean = 0.2, $N = 5$, $P = 0.655$; Fig. 5a). Regarding the ratio

of choices for the fair versus the unfair experimenter, 2 days after seeding, there was no significant difference between birds with and without experience ($U = 9.5$, $N_1 = 5$, $N_2 = 3$, $P = 0.546$; Fig. 6a).

The first test enabled all birds, whether they had experience with the paradigm or not, to gain more experience. One month after seeding the experience, four instead of three birds with experience chose the fair experimenter, whereas of the five birds without experience only one chose the fair experimenter first (mean = 9.00, $N = 5$, $P = 0.003$; Fig. 5b). However, when comparing the first choices of birds with experience of either the fair or the unfair experimenter with a random distribution, we found no significant difference (mean = 1.80, $N = 5$, $P = 0.180$; Fig. 5b). Regarding the ratio of choices for the fair versus unfair experimenter compared to chance, we did not find significant differences for birds with or without experience ($U = 6.5$, $N_1 = 5$, $N_2 = 2$, $P = 0.571$; Fig. 6b).

Observer's Attentiveness

To analyse whether observer birds that paid more attention would also remember better, we determined the attentiveness of observing birds via head direction, exclusively when the bird was sitting in front of a window facing the compartment. Observers solving the task successfully (i.e. choosing the fair experimenter first) spent on average \pm SE 7.40 \pm 6.34 min watching, whereas observers failing the task spent 4.99 \pm 1.71 min watching. This difference, however, was not significant ($U = 6$, $N_1 = 4$, $N_2 = 4$, $P = 1.00$).

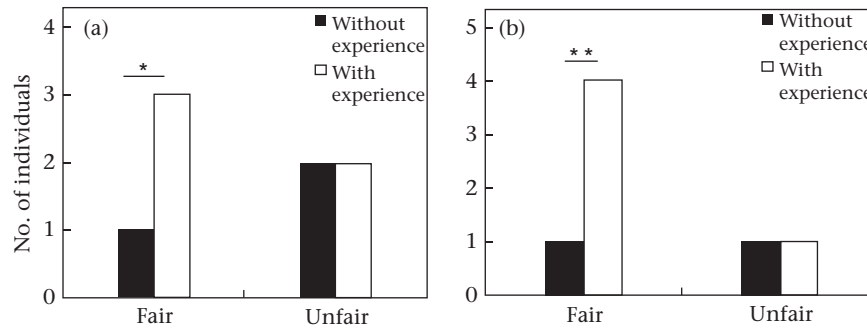


Figure 5. First decision for the two conditions (fair and unfair) of observer birds without and with experience (a) 2 days after seeding and (b) ± 1 month after seeding. * $P < 0.05$; ** $P < 0.01$; chi-square test.

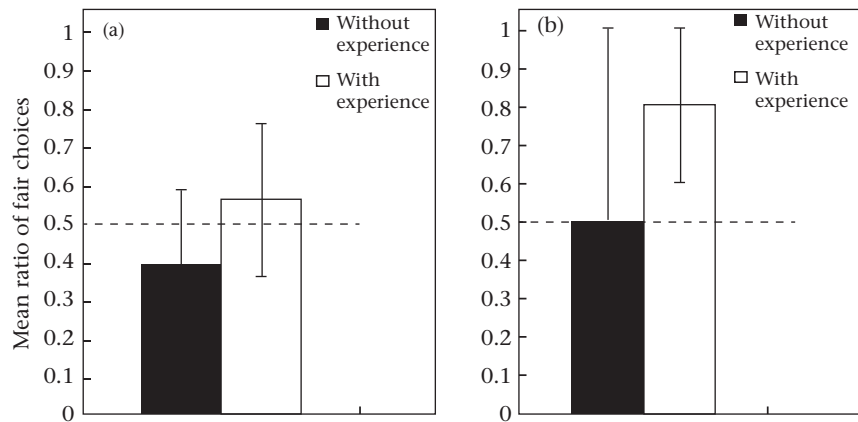


Figure 6. Mean \pm SEM ratio of fair choices compared to random of observer birds without and with experience (a) 2 days after seeding and (b) ± 1 month after seeding.

DISCUSSION

Our results show that ravens can remember, after a single interaction sequence, who is worth cooperating with in the future. First-hand experienced birds remembered who acted cooperatively in the past, as they acted accordingly in a future direct reciprocity task, be it after 2 days or even after a month, i.e. most of the time they chose the fair experimenter first, and chose to exchange with that fair experimenter more often. This suggests that for direct reciprocity ravens can rely on their memory from one interaction sequence only.

Getting First-hand Experience

Since first-hand experienced birds acted according to our prediction by choosing the experimenter who was cooperative in the past, we have shown experimental evidence for direct reciprocity (Nowak & Sigmund, 2005; Roberts, 2008) in ravens after a single interaction sequence in the past. Our findings corroborate past studies that also showed experimental evidence for direct reciprocity in birds and mammals (e.g. Hauser, Chen, Chen, & Chuang, 2003; Krams, Krama, Igaune, & Mänd, 2008; Rutte & Taborsky, 2008; reviewed by Carter, 2014) and correlational work on ravens (Fraser & Bugnyar, 2012). In this study, however, we showed successful reciprocal interactions of ravens with a human experimenter, rather than with a conspecific. Presumably, these interactions did not rely on dominance or fear (because of the clear behavioural instructions to the experimenters) and they were not related to domain-specific tasks such as food caching, in which corvids are renowned to excel. Therefore, we can exclude single

event learning based on innate defence behaviours and so-called preparedness (Bolles, 1970; Seligman, 1971). In general, however, the existence of direct reciprocity in animals is still controversial because of the complex cognitive abilities and adequate memory that are supposedly required (see Freidin, Carballo, & Bentosela, 2015 for a review).

We can only speculate about the type of memory mechanisms underlying the performance of the ravens. The birds had only one encounter with the experimenter. This encounter consisted of a maximum of 15 trials with the experimenter, and the bird had no interactive experience with the experimenters beforehand. It is unlikely, therefore, that the memory was semantic or rule based. To exceed the limit of short-term or working memory, which in humans is roughly no longer than 30 s to 1 min (e.g. Baddeley, 1990), we let the shortest retention interval be 2 days. The memories could have been episodic because the birds had to recall a single experience. However, the memories might also have had only an attitudinal or emotional base (Schino et al., 2007; de Waal, 2000), without containing details of the event, except of the individual (which does not have to be episodic in character). The birds may simply have remembered the positive and negative emotions in relation to the different individuals. To try to tease apart whether the birds responded to the particularities of the interaction sequences or the associated emotions, we also tested the memory of observers that witnessed these interaction sequences yet did not experience a positive or negative exchange themselves. Whereas the negative results of the observers do seem to hint in the direction of some sort of attitudinal or emotionally based mechanisms, they do not allow us to make any meaningful conclusions on such a distinction. Future research could, alternatively, test whether the

ravens distinguish between different activities with the same individual, particularly where the same individual is cooperative in one context but not in a distinctly different one.

Note that in our second memory test after approximately 1 month, ravens could use their experience from two encounters: the seeding and the first test. However, these two events differed in structure and complexity, i.e. birds interacted with one experimenter at a time during seeding, whereas they were simultaneously presented with three experimenters in the test. The gain of first-hand experience through the first test might explain the slight improvement in the observers' choices for the fair experimenter; i.e. in the first test, 2 days after seeding, observers were allowed to interact with the experimenters themselves, and when tested again approximately 1 month later they improved across trials, albeit only marginally and they still were not significantly more likely to choose the fair experimenter first.

Observing Others' Interactions from a Bystander Perspective

We did not get distinct hints that observing birds were able to remember the fair experimenter. We expected downstream indirect reciprocity, that is, the birds would choose the experimenter who acted cooperatively to somebody else in the past (Nowak & Sigmund, 2005). Therefore, observers were required to differentiate between individuals that had or had not acted cooperatively in the past (Nowak & Sigmund, 1998). Consequently, our results provide no evidence for indirect reciprocity in ravens. This contrasts with recent findings in dogs, capuchin monkeys and squirrel monkeys (Anderson et al., in press; Anderson et al., 2016; Anderson et al., 2013; Chijiwa et al., 2015), although in these studies the animals observed interactions between two humans rather than between a conspecific and a human, and these were tested immediately after witnessing the event rather than after 2 days or approximately 1 month, which may require the use of different memory systems. This finding also contrasts with recent findings that ravens do understand the relationships of others based on observations only (Massen, Pašukonis, et al., 2014; Massen, Szpl, et al., 2014), can keep track of these relationships, and interfere in them when they become threatening for themselves (Massen, Pašukonis, et al., 2014; Massen, Szpl, et al., 2014).

The fact that observers did not solve the task could have had more than one cause. One would be that observers could not transform third-person event memory into a first-person interaction. Another possible explanation would be that observing birds did not understand that watching and being attentive was important for them to solve the task. Although we did check whether attention had an effect based on head orientation, the bilateral position of the eyes of ravens makes it particularly difficult to distinguish what they are paying attention to. Alternatively, memory studies with humans have shown that self-performed actions are easier to recall than actions that were only observed (Engelkamp & Zimmer, 1997; Hornstein & Mulligan, 2001), and a lack of such memory-for-action may explain the failure of the observers. A further possibility would be that observing birds extracted some information from the seeding sessions, but did not transfer this experience to their own test. In fact, the daily routine of our experimental work with the ravens involved selective treatment of subjects (e.g. those that finished a test were not rewarded for entering the experimental room again, whereas those that had not finished were rewarded). Hence, observing a person not exchanging with a given raven did not mean for a bystander raven that this person would always act like this. In addition, the relationship A has with B does not have to reflect the relationship between oneself and B, an explanation that also reconciles the fact that ravens do understand the relationships of others (Massen,

Pašukonis, et al., 2014; Massen, Szpl, et al., 2014) and keep track of these relationships over time (Massen, Pašukonis, et al., 2014; Massen, Szpl, et al., 2014). Nevertheless, alternative study designs are needed to test the reason for the failure of the observers in this test, excluding the possibilities one by one.

The fact that observers with experience with the paradigm performed significantly better than those without such experience hints that observers had to learn to transfer the information gained during seeding to their own test. Although these experienced birds did not perform significantly above chance at the group level, this lack of significance is probably due to the small sample size (only five of nine birds experienced with the paradigm could be tested). That experience with the paradigm may be necessary to solve the task from the observer's perspective is in line with findings from caching studies, which show that ravens need experience through social interactions to judge the behaviour of potential competitors (Bugnyar, Stöwe, & Heinrich, 2007).

Finally, it can be questioned whether the birds understood the meaning of 'fair' and 'unfair' treatment, regarding the experimenters' actions, within this study. We could rule out the possibility that the birds expected a cumulated bigger reward after continuing exchanging, given that the unfair experimenter ate the piece of high-quality reward herself. Indeed, first-hand experienced birds appeared to react in a 'frustrated' way to the behaviour of the unfair experimenter. They started vocalizing, showed increased activity and cached or ate the remaining pieces of the low-quality reward. We assumed these behavioural expressions were confirmation of an unfair experience, and hence a validation of our paradigm.

To conclude, we could show that ravens can remember from a single interaction sequence who acted cooperatively in the past and that they subsequently prefer to exchange reciprocally with this person, rather than with someone who acted uncooperatively in the past. Moreover, we showed that this memory can last at least 1 month. In contrast, we could not find any proof that ravens that observed interactions of others could remember who was fair or unfair and transfer this third-party knowledge into first-person action. However, it did seem that experience with the paradigm increased the proficiency of observers. As such we consider the exchange paradigm a promising avenue for the study of direct and indirect reciprocity. Whether it can help us to truly distinguish episodic memory from alternative explanations, however, needs further examination with larger sample sizes.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2017.04.004>.

References

- Anderson, J. R., Bucher, B., Chijiwa, H., Kuroshima, H., Takimoto, A., & Fujita, K. (2017). Third-party social evaluations of humans by monkeys and dogs. *Neuroscience and Biobehavioral Reviews*. <http://dx.doi.org/10.1016/j.neurobiorev.2017.01.003> (in press).
- Anderson, J. R., Bucher, B., Kuroshima, H., & Fujita, K. (2016). Evaluation of third-party reciprocity by squirrel monkeys (*Saimiri sciureus*) and the question of mechanisms. *Animal Cognition*, 19(4), 813–818. <http://dx.doi.org/10.1007/s10071-016-0980-7>.
- Anderson, J. R., Kuroshima, H., Takimoto, A., & Fujita, K. (2013). Third-party social evaluation of humans by monkeys. *Nature Communications*, 4, 1561. <http://dx.doi.org/10.1038/ncomms2495>.
- Asakawa-Haas, K., Schiestl, M., Bugnyar, T., & Massen, J. J. M. (2016). Partner choice in raven (*Corvus corax*) cooperation. *PLoS One*, 11(6), e0156962. <http://dx.doi.org/10.1371/journal.pone.0156962>.
- Avargues-Weber, A., Portelli, G., Bernard, J., Dyer, A., & Giurfa, M. (2010). Configural processing enables discrimination and categorization of face-like stimuli in honeybees. *Journal of Experimental Biology*, 213(4), 593–601. <http://dx.doi.org/10.1242/jeb.039263>.
- Baddeley, A. (1990). *Human memory: Theory and practice*. Boston, MA: Allyn & Bacon.
- Boeckle, M., & Bugnyar, T. (2012). Long-term memory for affiliates in ravens. *Current Biology*, 22(9), 801–806. <http://dx.doi.org/10.1016/j.cub.2012.03.023>.
- Bolles, R. C. (1970). Species-specific defense reactions and avoidance learning. *Psychological Review*, 77(1), 32–48. <http://dx.doi.org/10.1016/j.ajog.2010.07.025>.
- Boyd, R., & Richerson, P. J. (1989). The evolution of indirect reciprocity. *Social Networks*, 11, 213–236.
- Brosnan, S. F., & de Waal, F. B. M. (2002). A proximate perspective on reciprocal altruism. *Human Nature*, 13(1), 129–152.
- Bugnyar, T. (2011). Knower-guesser differentiation in ravens: Others' viewpoints matter. *Proceedings of the Royal Society B: Biological Sciences*, 278(1705), 634–640. <http://dx.doi.org/10.1098/rspb.2010.1514>.
- Bugnyar, T., Stöwe, M., & Heinrich, B. (2007). The ontogeny of caching in ravens, *Corvus corax*. *Animal Behaviour*, 74(1C), 757–767. <http://dx.doi.org/10.1016/j.anbehav.2006.08.019>.
- Campenni, M., & Schino, G. (2016). Symmetry-based reciprocity: Evolutionary constraints on a proximate mechanism. *PeerJ*, 4, e1812. <http://dx.doi.org/10.7717/peerj.1812>.
- Carter, G. (2014). The reciprocity controversy. *Animal Behavior and Cognition*, 1(3), 368–386. <http://dx.doi.org/10.12966/abc.08.11.2014>.
- Chijiwa, H., Kuroshima, H., Hori, Y., Anderson, J. R., & Fujita, K. (2015). Dogs avoid people who behave negatively to their owner: Third-party affective evaluation. *Animal Behaviour*, 106, 123–127. <http://dx.doi.org/10.1016/j.anbehav.2015.05.018>.
- Dally, J. M., Emery, N. J., & Clayton, N. S. (2006). Food-caching western scrub-jays keep track of who was watching when. *Science*, 312(June), 1662–1666.
- Dufour, V., Pelé, M., Neumann, M., Thierry, B., & Call, J. (2009). Calculated reciprocity after all: Computation behind token transfers in orang-utans. *Biology Letters*, 5(2), 172–175. <http://dx.doi.org/10.1098/rsbl.2008.0644>.
- Dyer, A. G., Neumeyer, C., & Chittka, L. (2005). Honeybee (*Apis mellifera*) vision can discriminate between and recognise images of human faces. *Journal of Experimental Biology*, 208(Pt 24), 4709–4714. <http://dx.doi.org/10.1242/jeb.01929>.
- 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 of London. Series B, Biological Sciences*, 362(1480), 489–505. <http://dx.doi.org/10.1098/rstb.2006.1991>.
- Engelkamp, J., & Zimmer, H. D. (1997). Sensory factors in memory for subject-performed tasks. *Acta Psychologica*, 96(1–2), 43–60. [http://dx.doi.org/10.1016/S0001-6918\(97\)00005-X](http://dx.doi.org/10.1016/S0001-6918(97)00005-X).
- Fraser, O. N., & Bugnyar, T. (2010). Do ravens show consolation? Responses to distressed others. *PLoS One*, 5(5). <http://dx.doi.org/10.1371/journal.pone.0010605>.
- Fraser, O. N., & Bugnyar, T. (2012). Reciprocity of agonistic support in ravens. *Animal Behaviour*, 83(1), 171–177. <http://dx.doi.org/10.1016/j.anbehav.2011.10.023>.
- Freidin, E., Carballo, F., & Bentosela, M. (2015). Direct reciprocity in animals: The roles of bonding and affective processes. *International Journal of Psychology*, 1–9. <http://dx.doi.org/10.1002/ijop.12215>.
- Hauser, D. M., Chen, M. K., Chen, F., & Chuang, E. (2003). Give unto others: Genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society B: Biological Sciences*, 270(1531), 2363–2370. <http://dx.doi.org/10.1098/rspb.2003.2509>.
- Hemelrijk, C. K., & Ek, A. (1991). Reciprocity and interchange of grooming and 'support' in captive chimpanzees. *Animal Behaviour*, 41(6), 923–935. [http://dx.doi.org/10.1016/S0003-3472\(05\)80630-X](http://dx.doi.org/10.1016/S0003-3472(05)80630-X).
- Hornstein, S. L., & Mulligan, N. W. (2001). Memory of action events: The role of objects in memory of self-and other-performed tasks. *American Journal of Psychology*, 114(2), 199–217. <http://dx.doi.org/10.2307/1423515>.
- Izawa, E. I., & Watanabe, S. (2008). Formation of linear dominance relationship in captive jungle crows (*Corvus macrorhynchos*): Implications for individual recognition. *Behavioural Processes*, 78(1), 44–52. <http://dx.doi.org/10.1016/j.beproc.2007.12.010>.
- Kappeler, P. M., & van Schaik, C. P. (2006). *Cooperation in primates and humans: Mechanisms and evolution*. New York, NY: Springer.
- de Kort, S. R., Dickinson, A., & Clayton, N. S. (2005). Retrospective cognition by food-caching western scrub-jays. *Learning and Motivation*, 36(2 special issue), 159–176. <http://dx.doi.org/10.1016/j.lmot.2005.02.008>.
- Krams, I., Krama, T., Igaune, K., & Mänd, R. (2008). Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*, 62(4), 599–605. <http://dx.doi.org/10.1007/s00265-007-0484-1>.
- Lambert, M. L., Massen, J. J. M., Seed, A. M., Bugnyar, T., & Slocumbe, K. E. (2017). An 'unkindness' of ravens? Measuring prosocial preferences in *Corvus corax*. *Animal Behaviour*, 123, 383–393. <http://dx.doi.org/10.1016/j.anbehav.2016.11.018>.
- Loretto, M.-C., Reimann, S., Schuster, R., Graulich, D. M., & Bugnyar, T. (2016). Shared space, individually used: Spatial behaviour of non-breeding ravens (*Corvus corax*) close to a permanent anthropogenic food source. *Journal of Ornithology*, 157, 439–450. <http://dx.doi.org/10.1007/s10336-015-1289-z>.
- Loretto, M. C., Schuster, R., & Bugnyar, T. (2016). GPS tracking of non-breeding ravens reveals the importance of anthropogenic food sources during their dispersal in the Eastern Alps. *Current Zoology*, 62(4), 337–344. <http://dx.doi.org/10.1093/cz/zow016>.
- Martin-Ordas, G., Berntsen, D., & Call, J. (2013). Memory for distant past events in chimpanzees and orangutans. *Current Biology*, 23(15), 1438–1441. <http://dx.doi.org/10.1016/j.cub.2013.06.017>.
- Marzluff, J. M., Miyaoka, R., Minoshima, S., & Cross, D. J. (2012). Brain imaging reveals neuronal circuitry underlying the crow's perception of human faces. *Proceedings of the National Academy of Sciences of the United States of America*, 109(39), 15912–15917. <http://dx.doi.org/10.1073/pnas.1206109109>.
- Marzluff, J. M., Walls, J., Cornell, H. N., Withey, J. C., & Craig, D. P. (2010). Lasting recognition of threatening people by wild American crows. *Animal Behaviour*, 79(3), 699–707. <http://dx.doi.org/10.1016/j.anbehav.2009.12.022>.
- Massen, J. J. M., Lambert, M., Schiestl, M., & Bugnyar, T. (2015). Subadult ravens generally don't transfer valuable tokens to conspecifics when there is nothing to gain for themselves. *Frontiers in Psychology*, 6, 885. <http://dx.doi.org/10.3389/fpsyg.2015.00885>.
- Massen, J. J. M., Pašukonis, A., Schmidt, J., & Bugnyar, T. (2014). Ravens notice dominance reversals among conspecifics within and outside their social group. *Nature Communications*, 5, 3679. <http://dx.doi.org/10.1038/ncomms4679>.
- Massen, J. J. M., Ritter, C., & Bugnyar, T. (2015). Tolerance and reward equity predict cooperation in ravens (*Corvus corax*). *Scientific Reports*, 5, 15021. <http://dx.doi.org/10.1038/srep15021>.
- Massen, J. J. M., Szapl, G., Spreafico, M., & Bugnyar, T. (2014). Ravens intervene in others' bonding attempts. *Current Biology*, 24(22), 2733–2736. <http://dx.doi.org/10.1016/j.cub.2014.09.073>.
- Nishizawa, K., Izawa, E. I., & Watanabe, S. (2011). Neural-activity mapping of memory-based dominance in the crow: Neural networks integrating individual discrimination and social behaviour control. *Neuroscience*, 197, 307–319. <http://dx.doi.org/10.1016/j.neuroscience.2011.09.001>.
- Nowak, M. A., & Roch, S. (2007). Upstream reciprocity and the evolution of gratitude. *Proceedings of the Royal Society B: Biological Sciences*, 274(1610), 605–610. <http://dx.doi.org/10.1098/rspb.2006.0125>.
- Nowak, M. A., & Sigmund, K. (1998). Evolution of indirect reciprocity by image scoring. *Nature*, 393(6685), 573–577. <http://dx.doi.org/10.1038/31225>.
- Nowak, M. A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, 437(7063), 1291–1298. <http://dx.doi.org/10.1038/nature04131>.
- Osvath, M. (2015). Putting flexible animal prospection into context: Escaping the theoretical box. *Wiley Interdisciplinary Reviews: Cognitive Science*, 7(1), 5–18. <http://dx.doi.org/10.1002/wics.1372>.
- Roberts, G. (2008). Evolution of direct and indirect reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, 275(1631), 173–179. <http://dx.doi.org/10.1098/rspb.2007.1134>.
- Rutte, C., & Taborsky, M. (2007). Generalized reciprocity in rats. *PLoS Biology*, 5(7), 1421–1425. <http://dx.doi.org/10.1371/journal.pbio.0050196>.
- Rutte, C., & Taborsky, M. (2008). The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): Direct vs generalised reciprocity. *Behavioral Ecology and Sociobiology*, 62(4), 499–505. <http://dx.doi.org/10.1007/s00265-007-0474-3>.
- Sachs, J. L., Mueller, U. G., Wilcox, T. P., & Bull, J. J. (2004). The evolution of cooperation. *Quarterly Review of Biology*, 79(2), 135–160. <http://dx.doi.org/10.1086/516403>.
- Schino, G. (2007). Grooming and agonistic support: A meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, 18(1), 115–120. <http://dx.doi.org/10.1093/beheco/arl045>.
- Schino, G., & Aureli, F. (2008). Grooming reciprocation among female primates: A meta-analysis. *Biology Letters*, 4, 9–11. <http://dx.doi.org/10.1007/BF00303714>.
- Schino, G., & Aureli, F. (2010). Primate reciprocity and its cognitive requirements. *Evolutionary Anthropology: Issues, News, and Reviews*, 19(4), 130–135. <http://dx.doi.org/10.1002/evan.20270>.
- Schino, G., Polizzi di Sorrentino, E., & Tiddi, B. (2007). Grooming and coalitions in Japanese macaques (*Macaca fuscata*): Partner choice and the time frame of reciprocity. *Journal of Comparative Psychology*, 121, 181–188.
- Seed, A. M., Clayton, N. S., & Emery, N. J. (2008). Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society B: Biological Sciences*, 275, 1421–1429. <http://dx.doi.org/10.1098/rspb.2008.0111>.
- Seligman, M. E. P. (1971). Phobias and preparedness. *Behavior Therapy*, 47(5), 577–584.
- Smith, J. E., Van Horn, R. C., Powning, K. S., Cole, A. R., Graham, K. E., Memenis, S. K., et al. (2010). Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology*, 21(2), 284–303. <http://dx.doi.org/10.1093/beheco/arp181>.
- Stevens, J. R., & Hauser, M. D. (2004). Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences*, 8(2), 60–65. <http://dx.doi.org/10.1016/j.tics.2003.12.003>.

- Tate, A. J., Fischer, H., Leigh, A. E., & Kendrick, K. M. (2006). Behavioural and neurophysiological evidence for face identity and face emotion processing in animals. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 361(1476), 2155–2172. <http://dx.doi.org/10.1098/rstb.2006.1937>.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, 46(1), 35–57. <http://dx.doi.org/10.1017/CBO9781107415324.004>.
- Volstorf, J., Rieskamp, J., & Stevens, J. R. (2011). The good, the bad, and the rare: Memory for partners in social interactions. *PLoS One*, 6(4). <http://dx.doi.org/10.1371/journal.pone.0018945>.
- de Waal, F. B. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, 60(2), 253–261. <http://dx.doi.org/10.1006/anbe.2000.1471>.
- de Waal, F. B. M., & Luttrell, L. M. (1988). Mechanisms of social reciprocity in three primate species: Symmetrical relationship characteristics or cognition? *Ethology and Sociobiology*, 9, 101–118.
- Wilkinson, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature*, 308(5955), 181–184. <http://dx.doi.org/10.1038/308181a0>.
- Wilkinson, G. S. (1988). Reciprocal altruism in bats and other mammals. *Ethology and Sociobiology*, 9, 85–100.