**Crows and common ravens do not reciprocally exchange tokens with a conspecific to gain food rewards**

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**Abstract**

Human economic transactions are based on complex forms of reciprocity, which involve the capacities to share and to keep track of what was given and received over time. Animals too engage in reciprocal interactions but mechanisms, such ascalculated reciprocity have only been shown experimentally in few species. Various forms of cooperation, *e.g.* food and information sharing, are frequently observed in corvids and they can engage in exchange interactions with human experimenters and accept delayed rewards. Here, we tested whether carrion crows and common ravens would reciprocally exchange tokens with a conspecific in an exchange task. Birds received a set of three different types of tokens, some valuable for themselves, *i.e.* they could exchange them for a food reward with a human experimenter, some valuable for their partner, and some without value. The valuable tokens differed between the birds, which means that each bird could obtain more self-value tokens from their partner’s compartment. We did not observe any active transfers, *i.e.* one individual giving a token to the experimental partner by placing it in its beak. We only observed 6 indirect transfers, *i.e.* one individual transferring a token into the compartment of the partner (3 no-value, 1 partner-value and 2 self-value tokens) and 67 ‘passive’ transfers, *i.e.*, one subject taking the token lying in reach in the compartment of the partner. Individuals took significantly more self-value tokens compared to no-value and partner-value tokens. This indicates a preference for tokens valuable to focal individuals. Significantly more no-value tokens compared to partner-value tokens were taken, likely to be caused by experimental partners exchanging self-value tokens with the human experimenter, and therefore more no-value tokens being available in the compartment. Our results presently do not provide empirical support for reciprocity in crows and ravens, most likely caused by them not understanding the potential roles of receiver and donor. We therefore suggest further empirical tests of calculated reciprocity to be necessary in corvids.

**Keywords:** carrion crows, common ravens,cooperation, corvids, reciprocity, token exchange

**Introduction**

Human societies show a high propensity of cooperation between unrelated individuals (Fehr & Fischbacher, 2003) and the inherent evolutionary instability of cooperation inspires a great amount of interest in researching these cooperative behaviours (Axelrod & Hamilton, 1981), because individuals are not expected to invest in a cooperative enterprise without a guarantee of net fitness returns. To date, the most prominent theory explaining human cooperation is reciprocal altruism, based on the idea of individuals engaging in actions that are costly for themselves expecting future returns (Maynard Smith, 1983; Trivers, 1971). The relationship between interaction partners plays a significant role regarding the complexity of cooperation. In symmetry-based cooperation, interactions without equivalent returns balance out over time between kin and long-term partners (Berghänel et al., 2011; Dunbar, 1980). In contrast, calculated reciprocity requires keeping a mental record of the debts owed and the favours given (de Waal & Luttrell, 1988), based on the expectancy of a return for every costly favour given. Emotions may as well modulate cooperative interactions. Attitudinal reciprocity has been suggested to take the partner’s general social attitude into account (de Waal, 2000) and emotionally based bookkeeping allows long-term tracking of reciprocity without involving complex cognitive skills (Schino et al., 2007). Therefore, different forms of cooperative behaviour in nonhuman animals are expected to be based upon different cognitively challenging mechanisms depending on the complexity of the social system.

Despite the growing research effort on cooperation in animal societies in the recent decades, it is still unclear if and to what degree, some non-human animals are also capable of cooperative interactions based on reciprocal altruism (Taborsky, 2013). Observational studies, particularly in primates, suggest reciprocity in grooming (Barrett et al., 1999; Gomes et al., 2009; Majolo et al., 2012; Molesti, 2017; Schino et al., 2007), grooming for food (de Waal, 1997), agonistic support (Watts, 2001), grooming for agonistic support (Carne et al., 2011), food sharing (Wilkinson, 1984) and allonursing (Engelhardt & Weladji, 2015).

Surprisingly few experimental studies test for direct reciprocity in non-human animals. In a token exchange task, individuals had to exchange tokens useless to themselves but valuable to an experimental partner, in order to exchange the token valuable to them for food with the experimenter. Two orangutans (*Pongo pygmaeus abelii*) actively gave numerous tokens valuable to the experimental partner and one of the orangutans routinely used gestures to request tokens while the other complied with such requests (Dufour et al., 2009). Similarly, requests for help in a reciprocal exchange paradigm have also been discussed in Norway rats (Schweinfurth & Taborsky 2018). A number of other primate species (Capuchin monkeys (*Sapajus apella*), Tonkean macaques (*Macaca tonkeana),* gorillas *(Gorilla gorilla),* bonobos *(Pan paniscus),* and chimpanzees *(Pan troglodytes))* tested in a similar token exchange paradigm compared to the study in orangutans, failed to actively exchange tokens and if exchanges occurred, they were mostly of ‘passive’ nature, *i.e.* a subject brings a token near the common mesh wall and tolerates the partner to take it or ‘indirect’ exchanges, *i.e.* an individual places a token in the partner’s compartment without physical contact with the partner (Pelé et al., 2009; Pelé et al., 2010). In different experimental setups, *e.g.* instrumental cooperation tasks, food exchange or predator mobbing, rats, pied flycatchers (*Ficedula hypoleuca*), zebra finches (*Taeniopygia guttata*), vampire bats (*Desmodus rotundus*), chimpanzees and working dogs (*Canis familiaris*) cooperated more with previous cooperators compared to defectors (Gfrerer & Taborsky, 2018; Krams et al., 2008; Melis et al. , 2008; Rutte & Taborsky, 2008; St-Pierre et al., 2009), however direct reciprocity still requires to be studied in different species in order to gain further insight in the social and ecology requirements facilitating the evolution of reciprocal altruism in the wild (Taborsky 2013).

In the present study, we examined if two species of corvids, carrion crows (*Corvus corone corone*) and common ravens (*Corvus corax*) were able to engage in calculated reciprocity using the paradigm already used in several primate species (Dufour et al., 2009; Pelé et al., 2009; Pelé et al., 2010). Various forms of naturally occurring cooperation can be observed in different corvid species (*e.g.* coalition formation: (Heinrich, 1999), social support: (Emery et al. , 2007), resource or information sharing: (Bugnyar & Kotrschal, 2001; de Kort et al., 2006), and cooperative breeding: (Baglione et al., 2003; Woolfenden & Fitzpatrick, 1985). Cooperative propensities vary not only between but also within species, depending on socio-ecological factors (Clayton & Emery, 2007). Particularly in costly interactions (*e.g.* food sharing, agonistic encounters) corvids are very selective in choosing a certain partner (Emery et al., 2007; Fraser & Bugnyar, 2010), which hints at reciprocity. In corvids, long-term relationships are frequent, which makes symmetry-based reciprocity likely. But also, short-term cooperative interactions exist (Fraser & Bugnyar, 2011), which could be based on calculated reciprocity. Experimental studies on cooperative behaviour in corvids are scarce and it remains unclear whether mutualism or reciprocal altruism is involved (Massen et al., 2015b; Scheid & Noë, 2010; Seed et al., 2008). Subadult ravens and crows fail to transfer valuable tokens to conspecifics, when there is nothing to gain for themselves (Massen et al., 2015a; Horn et al. unpublished data) and food sharing in pinyon jays (*Gymnorhinus cyanocephalus*) is not based on short-term or long-term reciprocity (Duque & Stevens, 2016). In cooperative contexts, ravens have been shown to memorise the outcome of an interaction with human experiments after a single interaction (Müller et al., 2017). In a prisoner’s dilemma task, blue jays (*Cyanocitta cristata*) failed to behave reciprocally (Clements & Stephens, 1995). This is of special interest as the blue jay’s inability to cope with a delay of gratification causes its failure to reciprocate (Stephens et al., 2002). Recently, this cognitive prerequisite of reciprocity has been successfully shown in crows and ravens (Dufour et al., 2012; Hillemann et al., 2014). Crows have also demonstrated to be sensitive to inequity in reward distribution and working effort (Wascher & Bugnyar, 2013) and learn to differentiate between reliable and unreliable cooperation partners (Massen et al., 2015b; Mueller et al., 2015; Wascher et al., 2015). This shows that corvids do possess cognitive abilities necessary for reciprocal altruism and this makes them ideal candidates to test this form of cooperation. Further, individuals responding stronger to unequal treatment initiate less affiliative behaviour in a group context (Wascher, 2015), indicating cognitive skills in crows facilitating cooperative behaviours.

In the present study, we expected the crows and ravens to learn to attribute different value of tokens for different individuals and to adapt their behaviour accordingly. By monitoring the occurrence of transfers, the value of tokens exchanged and the alternation of roles between individuals, we aimed to assess the extent to which crows and ravens may purposefully engage in reciprocal behaviours.We expect individuals to preferentially exchange self-value tokens with the human experimenter. Further, we expect crows and ravens to preferentially manipulate self-value and partner-value tokens, compared to no-value tokens. If crows and ravens engage in reciprocal altruism, we expect experimental partners to transfer partner-value tokens in a reciprocal way with each other. Further, if focal individuals fully understand the value of different types of tokens, they might preferentially cache partner-value tokens for future use.

**Methods**

*Study subjects and housing*

Subjects were 6 captive crows (5 carrion crows, *Corvus corone corone, 1 hooded crow, Corvus corone cornix*) at the Konrad Lorenz Forschungstelle (KLF), Austria and 2 captive ravens (*Corvus corax*) at Edinburgh Zoo, RZSS, UK. Birds were held in large outdoor aviaries, equipped with wooden perches, natural vegetation and rocks. An enriched diet consisting of fruit, vegetables, bread, meat and milk products was provided on a daily basis. Water was available *ad libitum*. For testing, subjects were voluntarily, *i.e.* they entered the experimental compartment on their own, separated in a familiar compartment.

*Tokens*

In the present experiment we used three different types of tokens. Tokens differed in form, material and colour, and some could be exchanged for food in the experiment. Tokens used were a triangle cut out of a blue plastic bottle screw-top, with the sides being about 1 cm long, a metal screw nut, about 1 cm in diameter and a wooden triangle, with sides approximately 2 cm long. In the experiment, subjects were initially given sets of 36 tokens, consisting of 12 items of each of the three types of tokens. In an initial training phase, tokens were associated as either (a) ‘self-value’ tokens, which the subject could exchange for a food reward with a human experimenter, (b) ‘partner-value’ tokens were

valuable to the experimental partner and valueless to the subject, and (c) ‘no-value’

tokens were not valuable to any individual within an experimental dyad. Table 1 gives

information about each subject’s self-value tokens. Self-value tokens were associated semi-randomly for individuals, however experimental dyads were considered, *i.e.* individuals of a dyad had to have different self-value tokens. The wooden triangle was assigned as the no-value token for all dyads.

*Training Procedure*

All the birds were trained to exchange an item against a food reward with a human experimenter and participated in different experiments applying this paradigm (Dufour et al., 2012; Wascher et al., 2012; Wascher & Bugnyar, 2013). The present experiments have been conducted by two human experimenters, TF and CAFW. At the beginning of each training session, 12 items of each token type were placed in the experimental compartment (Figure 1). A training session started with the experimenter requesting tokens by holding an open hand, with palm up, next to the fence and showing the reward in the other hand*.* Rewards were either mealworms or greaves, *i.e.* deep-fried pig grease, depending on the personal preference of the birds. When a subject gave a self-value token to the human experimenter, it received one piece of food reward, but did not receive a reward when transferring a partner-value or no-value token to the human experimenter. When receiving a token from the subject, the human experimenter placed the self-value tokens in one container and the partner-value and no-value token in a different container, to illustrate the difference in value to the subject. Once the bird had returned its 12 self-value tokens, the training session was over. A subject was considered trained when they succeeded in giving at least 90 % of the correct tokens first, during three consecutive sessions.

*Testing Procedure*

Testing took place in the same room as the training, divided into two testing compartments by a wire mesh through which subjects could interact and transfer tokens with each other. In testing phase 1 (full set phase), we placed the same set of 36 tokens (12 self-value tokens for subject, 12 partner-value tokens, and 12 no-value tokens) in each compartment. In the first part of a session, partners had the possibility to exchange self-value tokens with the experimenter. Once both individuals had exchanged all 12 self-value tokens, the experimenter left the room for 3 minutes (min) to not influence interactions and possible transfers of tokens between subjects. After 3 min, the experimenter came back for a minimum duration of 3 min to give birds the opportunity for further exchanges. A session ended 3 min after the last interaction, *e.g.* begging or token manipulation. During the entire session, subjects could interact through the mesh. Each dyad received twelve sessions, with a maximum of two sessions per day. We tested all possible pairs of individuals (3 crow dyads, 1 raven dyad), with the limitation that only individuals with different self-value tokens could be tested together. Testing phase 2 (reduced set phase) was similar to phase 1 except individuals received 12 partner-value and 12 no-value tokens but no self-value tokens. Here, food could only be gained at a trial if some transfers of valuable token had occurred between partners. We expected this to motivate individuals to interact with their partner as the only self-value tokens available for them were in the partner’s compartment. Two crow and one raven dyad were tested in this phase. Testing phase 3 (re-motivation phase) was similar to phase 2, but the set of tokens comprised three self-value tokens in addition to the 12 partner-value and 12 no-value tokens. This was done to increase motivation of subjects to participate in the session. In addition, the experimenter did not leave individuals on their own after all self-value tokens have been exchanged, but stayed for three minutes after the last interaction with any token. Eight crow dyads were tested in this phase. Different test phases have been designed to increase motivation to exchange tokens between experimental partners, *e.g.* by reducing the number of self-value tokens.

*Video Processing*

Test sessions have been video-recorded and were analysed using Solomon Coder version beta 17.03.22 (©András Péter, [www.solomoncoder.com](http://www.solomoncoder.com/)). The behaviours recorded during testing sessions were (a) exchange with experimenter: a subject passes a token through the mesh to the experimenter; (b) transfer with partner: a subject obtains a token that was originally in its partner’s compartment; we distinguished between ‘passive transfer’, *i.e.* one subject taking the token from the compartment of the partner, facilitated by the experimental partner dislocating the tokens closer to the wire mesh, *e.g.* by stepping on them or moving them through beak movement. ‘Indirect transfer’, *i.e.* a token is placed in the partner’s compartment and ‘active transfer’, *i.e.* a token is placed directly into the partner’s beak; (c) manipulation of tokens: a subject is manipulating a token with its beak or feet. (d) caching of tokens: a subject cached a token somewhere in its own compartment. The frequency of all these behaviours were recorded.

*Data analysis*

All data were analysed using R version 3.5.3 (R Core Team 2015). We conducted Friedman and Wilcoxon signed-rank tests to calculate whether subjects showed an initial preference returning a specific token type more than others in the first training session. Results of all tests are given two-tailed and significance was set to α = 0.05. In order to investigate how frequency of behaviour was affected by phase of the experiment and type of token, we conducted four generalized linear mixed models (GLMMs) with poisson error distribution. Models were calculated using the glmmADMB package (Skaug et al., 2013). The response variables were exchanges with the human experimenter (GLMM1), passive transfers between individuals (GLMM2), frequency of token manipulations (GLMM3) and frequency of caching a token (GLMM4). Experimental phase (1, 2 and 3), type of token (self-value, partner-value, no-value), and the interaction between phase and type of token was included as fixed factors. In models where the interaction between phase and type of token was non-significant it was subsequently removed from the model (Engqvist, 2005). For each model, we fitted individual identity as a random term to control for the potential dependence associated with multiple samples from the same individual.

**Results**

*Initial training phase*

Crows needed on average (± standard deviation) 7.66 ± 2.65 sessions and ravens on average 11.5 ± 3.53 sessions to reach the discrimination criterion, *i.e.* preferentially returning their self-value token to the human experimenter.

*Exchange with experimenter and partner*

Individuals gave more no-value tokens to the human experimenter compared to partner-value tokens in phase 3, but not the other experimental phases (Table 2; Figure 2).

In our experiment, we did not observe any active transfers, *i.e.* one individual giving a token to the experimental partner by placing it in its beak. We only observed 6 indirect transfers, *i.e.* one individual transferring a token into the compartment of the partner (3 no-value, 1 partner-value and 2 self-value tokens) and 67 ‘passive’ transfers, *i.e.*, one subject taking the token from the compartment of the partner. More passive transfers occurred in phase 1 compared to phase 2, but not significantly different between phase 2 and 3 and phase 1 and 3. Individuals took significantly more self-value tokens compared to no-value and partner-value tokens and significantly more partner-value tokens compared to no-value tokens (Table 2, Figure 3). Most of the transfers (indirect and passive) were observed by one individual (Klaus taking tokens from the other compartment in 56 out of 73 occasions).

*Manipulation and caching of tokens*

In order to investigate whether focal subjects showed a preference for a specific token type, we investigated whether they cached or manipulated certain types of tokens more than others. Individuals manipulated tokens more in phase 1 compared to phase 2, but no significant difference was found in frequency of manipulation between phase 2 and 3 as well as between phase 1 and 3. Individuals manipulated self-value tokens more often compared to partner-value and no-value tokens and no-value tokens more often compared to partner-value tokens (Table 2). Individuals cached no-value tokens more often compared to self-value tokens, but not significantly different to partner-value tokens and partner-value tokens compared to self-value tokens. Individuals cached significantly more in phase 1 compared to phase 3, but no significant difference was detected between phase 1 and 2 as well as between phase 2 and 3 (Table 2; Figure 4).

**Discussion**

Both, ravens and crows learned to distinguish their self-value tokens among three different types of tokens. They preferentially exchanged those tokens with the experimenter. The number of sessions required to reach the criterion for being considered trained is comparable to those found in primates (Pelé et al., 2009; Pelé et al., 2010). We recorded no active transfers between experimental partners and only a very limited number of indirect transfers. Most of the transfers were passive transfers, so one individual taking a token from the compartment of the partner, which was only possible for those tokens placed close to the wire mesh. Our results are comparable to previous results in monkeys and apes, except orangutans, which show calculated reciprocity in exchanges of tokens (Dufour et al., 2009; Pelé et al. 2009; Pelé et al., 2010). Therefore, it has to be considered, although orangutans exchanged tokens in a reciprocal way, the presented experimental design might be too complicated for other species of non-human animals, as it requires understanding of different values of tokens. The use of alternative paradigms, such as instrumental cooperation tasks (Gfrerer & Taborsky, 2018; Rutte & Taborsky, 2007), might be preferable. We further recommend future studies applying the token exchange paradigm to consider introducing an additional training phase, during which the experimental partners are trained to exchange tokens amongst themselves, as most species tested in the paradigm until now, did not spontaneously start exchanging tokens amongst themselves.

Passive transfers were facilitated by the experimental partner dislocating the tokens closer to the wire mesh, *e.g.* by stepping on them or moving them through beak movement. Displacements have been accidental and no intend to move the tokens closer to the experimental partner could be identified. Most of these passive transfers have been conducted by one individual (Klaus; 56 out of 73 occasions), further supporting the view that the observed passive transfers do not reflect a general pattern of one individual giving tokens to an experimental partner. We suggest that rather than showing purposeful manipulation of the tokens valuable to their partners near the common mesh so that they could benefit from them, a parsimonious hypothesis is that the potential roles of

receiver and donor in our experiment have not been understood by subjects. However, one interesting aspect regarding the passive transfers is the fact that the experience of being able to acquire valuable tokens from the compartment of the experimental partner, did not elicit any further behavioural interactions between subjects. Although in very low numbers, five out of nine experimental dyads experienced indirect transfers and three out of nine dyads experienced passive transfers. Therefore, more than half of the dyads had opportunities to learn about the possibility to exchange tokens between experimental partners. Common ravens previously have shown to memorise the outcome of cooperative interactions with human experiments after a single interaction (Müller et al., 2017), therefore it could have been expected that our crows and ravens learn to exchange with an experimental partner after a limited amount of interactions.

We did not find evidence for our crows and ravens to develop a preference, shown by transferring, exchanging, manipulating or caching more partner-value tokens compared to no-value tokens. A preference for specific type of tokens has previously been shown in primate studies, which describe subjects to attribute more value to types of tokens which have been observed to be valuable to other individuals (Brosnan & Waal, 2004; Pelé et al., 2009; Pelé et al., 2010). Object manipulation in common ravens has been previously shown to be socially facilitated, *i.e.* individuals to manipulate objects more which have been previously manipulated by a social partner (Schwab et al., 2008), therefore we would have expected crows and ravens in the present study to develop a stronger preference to manipulate partner-value tokens more. Previous studies in ravens suggest enhanced social facilitation between affiliated individuals (Schwab et al., 2008). Due to the small sample size, we did not consider affiliation status between experimental pairs in the present study. In the first training session, we did find an initial preference for no-value tokens (wooden triangles) compared to any other token type and generally the number of interactions with tokens, *i.e.* manipulation, caching, passive transfers, did decrease in the course of the experiment, indicating the crows and ravens do lose interest.

The absence of active transfers makes it difficult to evaluate whether partners understood the potential value of the token to their experimental partner. Great apes, previously have been observed to engage in solicitation or the use of begging behaviours, such as pointing and holding-out-hand gestures (Dufour et al., 2009; Pelé et al., 2009; Yamamoto et al., 2009). We could not identify specific solicitation or begging behaviours in our focal individuals. Occasionally, we have observed individuals approaching their experimental partner and looking at the partner’s tokens, however these behaviours were difficult to identify and did not occur regularly enough to be systematically analysed.

To summarise, although cooperative behaviours including the sharing of food has been described in corvids (de Kort et al., 2003; Emery et al., 2007) in our experiment, crows and ravens did not exchange tokens with each other. Similar experiments have previously shown that crows and juvenile ravens do not exchange tokens with experimental partners, when there is nothing to gain for themselves (Horn et al. unpublished data; Massen et al., 2015a). A limited amount of indirect and passive transfers provided learning opportunities for individuals, however they did not result in an increase in active and indirect transfers. More studies are required to further examine the ability of corvids to engage in reciprocal actions.

Conflict of Interest: The authors declare that they have no conflict of interest

**References**

Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, *211*, 1390–1396.

Baglione, V., Canestrari, D., Marcos, J. M., & Ekman, J. (2003). Kin selection in cooperative alliances of carrion crows. *Science*, *300*(5627), 1947–1949.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B: Biological Sciences*, *266*, 665–670.

Berghänel, A., Ostner, J., Schröder, U., & Schülke, O. (2011). Social bonds predict future cooperation in male Barbary macaques, Macaca sylvanus. *Animal Behaviour*, *81*(6), 1109–1116. https://doi.org/10.1016/j.anbehav.2011.02.009

Brosnan, S. F., & de Waal, F. B. M. (2004). Socially Learned Preferences for Differentially Rewarded Tokens in the Brown Capuchin Monkey (*Cebus apella*), *118*(2), 133–139.

Bugnyar, T., & Kotrschal, K. (2001). Movement coordination and signalling in ravens (*Corvus corax*): an experimental field study. *Acta Ethologica*, *3*(2), 101–109.

Carne, C., Wiper, S., & Semple, S. (2011). Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology*, *73*(11), 1127–1133.

Carter, G. G., Wilkinson, G. S., & Carter, G. G. (2013). Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B*, *280*. https://doi.org/https://doi.org/10.1098/rspb.2012.2573

Clayton, N. S., & Emery, N. J. (2007). The social life of corvids. *Current Biologyiology*, *17*(16), R652-656.

Clements, K. C., & Stephens, D. W. (1995). Testing models of non-kin cooperation: mutualism and the Prisoner’s dilemma. *Animal Behaviour*, *50*(2), 527–535.

Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature*, *462*, 51–57.

de Kort, S. R., Emery, N. J., & Clayton, N. S. (2003). Food offering in jackdaws (*Corvus monedula*). *Naturwissenschaften*, *90*, 238–240.

de Kort, S. R., Emery, N. J., & Clayton, N. S. (2006). Food sharing in jackdaws, *Corvus monedula*: what, why and with whom? *Animal Behaviour*, *72*(2), 297–304.

de Waal, F. B. M. (1997). The chimpanzee’s service economy: food for grooming. *Evolution and Human Behavior*, *18*, 375–386.

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.

de Waal FB. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, *60*(2), 253–261.

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.

Dufour, V., Wascher, C. A. F., Braun, A., Miller, R., & Bugnyar, T. (2012). Corvids can decide if a future exchange is worth waiting for. *Biology Letters*, *8*(2), 201–204.

Dunbar, R. I. M. (1980). Determinants and evolutionary consequences of dominance among female gelada baboons. *Behavioral Ecology and Sociobiology*, *7*(4), 253–265.

Duque, J. F., & Stevens, J. R. (2016). Voluntary food sharing in pinyon jays: the role of reciprocity and dominance. *Animal Behaviour*, *122*, 135–144. https://doi.org/10.1016/j.anbehav.2016.09.020

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.

Engelhardt, S. C., & Weladji, R. B. (2015). Evidence of reciprocal allonursing in reindeer, Rangifer tarandus. *Ethology*, *121*, 245–259.

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, *70*(4), 967–971.

Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, *425*(6960), 785–791.

Fraser, O. N., & Bugnyar, T. (2010). The quality of social relationships in ravens. *Animal Behaviour*, *79*(4), 927–933. https://doi.org/10.1016/j.anbehav.2010.01.008

Fraser, O. N., & Bugnyar, T. (2011). Ravens reconcile after aggressive conflicts with valuable partners. *PloS One*, *6*(3), e18118.

Gfrerer, N., & Taborsky, M. (2018). Working dogs transfer different tasks in reciprocal cooperation. *Biology Letters*, *14*, 20170460.

Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1657), 699–706.

Heinrich, B. (1999). *Mind of the raven*. New York: Harper Collins.

Hillemann, F., Bugnyar, T., Kotrschal, K., & Wascher, C. A. F. (2014). Waiting for better, not for more: Corvids respond to quality in two delay maintenance tasks. *Animal Behaviour*, *90*, 1–10.

Horn, L., Bugnyar, T., & Massen, J. J. M. No proof for prosocial preferences in carrion/hooded crows’ when tested in a token exchange paradigm. *Ethology*, submitted.

Koenig, W. D. (1988). Reciprocal altruism in birds: A critical review. *Ethology and Sociobiology*, *9*(2–4), 73–84.

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.

Majolo, B., Schino, G., & Aureli, F. (2012). The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges. *Animal Behaviour*, *83*(3), 763–771.

Massen, J. J. M., Lambert, M., Schiestl, M., & Bugnyar, T. (2015a). Subadult ravens generally don’t transfer valuable tokens to conspecifics when there is nothing to gain for themselves. *Frontiers in Comparative Psychology*, *6*, 885.

Massen, J. J. M., Ritter, C., & Bugnyar, T. (2015b). Tolerance and reward equity predict cooperation in ravens (Corvus corax). *Scientific Reports*, *5*, 1–11.

Maynard Smith, J. (1983). Game theory and the evolution of cooperation. In D. S. Bendall (Ed.), *Evolution from Molecules to Men* (pp. 445–456). Cambridge: Cambridge University Press.

Melis, A. P., Hare, B., & Tomasello, M. (2008). Do chimpanzees reciprocate received favours? *Animal Behaviour*, *76*(3), 951–962.

Molesti, S. (2017). Evidence of direct reciprocity , but not of indirect and generalized reciprocity , in the grooming exchanges of wild Barbary macaques (*Macaca sylvanus*). *Americal Journal of Primatology*, *79*, e22679.

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.

Pelé, M., Dufour, V., Thierry, B., & Call, J. (2009). Token transfers among great apes (*Gorilla gorilla, Pongo pygmaeus, Pan paniscus*, and *Pan troglodytes*): Species differences , gestural requests, and reciprocal exchange. *Journal of Comparative Psychology*, *123*(4), 375–384.

Pelé, M., Thierry, B., Call, J., & Dufour, V. (2010). Monkeys fail to reciprocate in an exchange task. *Animal Cognition*, *13*(5), 745–751.

R Core Team (2015). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

Rutte, C., & Taborsky, M. (2007). The influence of social experience on cooperative behaviour of rats (Rattus norvegicus): direct vs generalised reciprocity. *Behavioral Ecology and Sociobiology*, *62*(4), 499–505.

Scheid, C., & Noë, R. (2010). The performance of rooks in a cooperative task depends on their temperament. *Animal Cognition*, *13*(3), 545–553.

Schino, G., di Sorrentino, E. P., & Tiddi, B. (2007). Grooming and coalitions in Japanese macaques (Macaca fuscata): partner choice and the time frame reciprocation. *Journal of Comparative Psychology*, *121*(2), 181–188.

Schwab, C., Bugnyar, T., Schloegl, C., & Kotrschal, K. (2008). Enhanced social learning between siblings in common ravens, Corvus corax. *Animal Behaviour*, *75*(2), 501–508.

Seed, A. M., Clayton, N. S., & Emery, N. J. (2008). Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings. Biological Sciences / The Royal Society*, *275*(1641), 1421–1429.

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A., & Bolker, B. (2013). Generalized Linear Mixed Models using AD Model Builder.

St-Pierre, A., Larose, K., & Dubois, F. (2009). Long-term social bonds promote cooperation in the iterated Prisoner’ s dilemma. *Proceedings of the Royal Society B*, *276*, 4223–4228.

Stephens, D. W., McLinn, C. M., & Stevens, J. R. (2002). Discounting and reciprocity in an Iterated Prisoner’s Dilemma. *Science*, *298*(5601), 2216–2218.

Schweinfurth, M., & Taborsky, M. (2018). Norway rats (Rattus norvegicus) communicate need, which elicits donation of food. *Journal of Comparative Psychology*, *132*(2), 119–129.

Taborsky, M. (2013). Social evolution: Reciprocity there is. *Current Biology*, *23*(11), R486–R488.

Team, R. D. C. (2015). R: a language and environment for statistical computing. R foundation for statistical computing. Retrieved from http://www.r-project.org/

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, *46*(1), 35–57.

Wascher, C. A. F. (2015). Individual performance in socio-cognitive tasks predicts social behaviour in carrion crows. *Behaviour*, *152*, 615–634.

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.

Wascher, C. A. F., Dufour, V., & Bugnyar, T. (2012). Carrion crows cannot overcome impulsive choice in a quantitative exchange task. *Frontiers in Comparative Psychology*, *3*, 1–6.

Wascher, C. A. F., Hillemann, F., Canestrari, D., & Baglione, V. (2015). Carrion crows learn to discriminate between calls of reliable and unreliable conspecifics. *Animal Cognition*, *18*(5).

Watts, D. P. (2001). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, *139*, 343–370.

Wilkinson, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature*, *308*(8), 181–184.

Woolfenden, G. E., & Fitzpatrick, J. W. (1985). *The Florida Scrub Jay. Demography of a Cooperative-Breeding Bird*. New Jersey: Princeton University Press.

Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees help each other upon request. *PLoS ONE*, *4*(10), e7416.

Table 1: Subjects sex (M = male, F = female), age (year of hatching), self-value token and experimental partners in each experimental phase.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Subject | Sex | Age | Species | Self-value token | Dyads (phase 1) | Dyads (phase 2) | Dyads (phase 3) |
| Baerchen | M | 2008 | Carrion crow | blue plastic | Peter | NA | Resa, Peter, Gabi |
| Gabi | F | 2007 | Carrion crow | screw nut | Klaus | Klaus | Klaus, Baerchen |
| Gertrude | F | 2011 | Hooded crow | blue plastic | NA | NA | Resa, Peter |
| Klaus | M | 2009 | Carrion crow | blue plastic | Resa, Gabi | Resa, Gabi | Resa, Peter, Gabi |
| Peter | F | 2007 | Carrion crow | screw nut | Baerchen | NA | Gertrude, Baerchen, Klaus |
| Resa | F | 2009 | Carrion crow | screw nut | Klaus | Klaus | Klaus, Getrude, Baerchen |
| Hugo | M | 2003 | Common raven | screw nut | Manon | Manon | NA |
| Manon | F | 1990 | Common raven | blue plastic | Hugo | Hugo | NA |

NA: individual did not participate in this testing phase

Table 2 Results of the generalized mixed linear model investigating factors affecting exchange behaviour with human experimenter. Significant values (*p*≤0.05) are highlighted in bold.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Parameters | Estimate ± SE | *Z* | *p* |
| Exchange with | **Intercept** | **1.98 ± 0.35** | **5.53** | **<0.001** |
| human | **Type of token** | **-0.98 ± 0.19** | **-5.1** | **<0.001** |
| experimenter | Phase 2 | -18.44 ± 2116 | -0 | 0.993 |
|  | Phase 3 | -0.01 ± 0.23 | -0.08 | 0.934 |
|  | Type of token\*phase 2 | 16.89 ± 211 | 0 | 0.993 |
|  | **Type of token\*phase 3** | **-1.21 ± 0.47** | **-2.56** | **0.01** |
| Passive | Intercept | -0.71 ± 0.53 | -1.33 | 0.182 |
| transfers | **Type of token (partner-value)** | **-1.86 ± 0.64** | **-2.88** | **0.003** |
|  |  |  |  |  |
|  | **Type of token (self-value)** | **0.92 ± 0.28** | **3.27** | **0.001** |
|  | **Phase 2** | **-2.1 ± 0.47** | **-4.46** | **<0.001** |
|  | Phase 3 | -14.22 ± 140.9 | -0.1 | 0.919 |
| Frequency of | Intercept | -0.71 ± 0.53 | -1.33 | 0.182 |
| manipulation | **Type of token (partner-value)** | **-1.86 ± 0.64** | **-2.88** | **0.003** |
|  | **Type of token (self-value)** | **0.92 ± 0.28** | **3.27** | **0.001** |
|  | **Phase 2** | **-2.1 ± 0.47** | **-4.46** | **<0.001** |
|  | Phase 3 | -14.22 ± 140.9 | -0.1 | 0.919 |
| Frequency of | Intercept | 0.86 ± 0.45 | 1.9 | 0.056 |
| caching | Type of token (partner-value) | -0.1 ± 0.16 | -0.64 | 0.516 |
|  | **Type of token (self-value)** | **-1.8 ± 0.37** | **-4.78** | **<0.001** |
|  | Phase 2 | 0.18 ± 0.18 | 0.98 | 0.322 |
|  | **Phase 3** | **-1.1 ± 0.23** | **-4.73** | **<0.001** |

Figure 1: Layout of the experimental set-up. Two testing subjects were separated by a common mesh (vertical dashed line). In the training and phase 1 of the experiment, each subject had the same number of tokens, 12 self-values, 12 partner-values and 12 no-values that were placed in each compartment out of reach of the partner. Tokens could be transferred through the wire mesh or exchanged with the human experimenter through an hole in the wire mesh (horizontal dashed line).

Figure 2: Number of tokens ± standard deviation and actual data points, given to the experimenter in different experimental phases by each focal individual of a dyad. Dots represent individual data points and darker colours indicate overlapping data points.

Figure 3: Sum of tokens taken by subjects from their partner’s compartment (passive transfers) in each experimental phase ± standard deviation.

Figure 4: Frequency of caching depending on token type and experimental phase ± standard deviation.