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„Prosocial Behavior in Carrion Crows: Effects of Relationship Status and Quality "

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Abstract

Prosocial behavior, a voluntary behavior that benefits others with no or little cost to the actor, is especially prominent in humans. Research in non-human animals has focused mainly on primates but also members of the corvid family are an interesting group to investigate prosociality, as these species show complex socio-cognitive skills. Additionally, they form long-term monogamous pair bonds, which makes them ideal to study effects of relationships on prosociality. I here tested four pairs of carrion crows (*Corvus corone*) in two food sharing and in a token transfer experiment. In Food-Sharing Experiment 1, each pair had access to several food pieces. In Food-Sharing Experiment 2, the donor crow was separated and received all pieces, which could be shared with a recipient crow. The set-up in the Token Transfer Experiment was the same as in food sharing experiment 2, but the donor crow received tokens instead of food pieces. Additionally, I measured the relationship quality of each pair to identify possible effects on prosocial behavior. No food or token transfer were observed in any of the experiments. Even though differences in relationship quality were found, they did not significantly influence the crows' prosocial behaviour in the experiments. Interestingly, more food caches were made in the presence of a pair partner than a non-partner, suggesting that the crows tolerated pilfering of their partner. This could indicate that carrion crows do not share food actively in these paradigms but express their prosocial tendencies through tolerated theft particularly in case of the pair partner.

Zusammenfassung

Prosoziales Verhalten, jenes freiwilliges Verhalten das anderen nützt und nur mit wenig oder keinen Kosten für den Ausführenden verbunden ist, ist besonders ausgeprägt bei Menschen. Die Forschungen an Tieren konzentrieren sich hauptsächlich auf Primaten, aber auch Mitglieder der Corviden Familie eignen sich gut, um dieses Verhalten zu untersuchen, da sie komplexe kognitive Fähigkeiten besitzen. Außerdem formen sie Langzeit monogame Paarbindungen und eignen sich daher gut, um Effekte von Paarbeziehungen auf Prosozialität zu untersuchen. Deshalb habe ich vier Paare von Krähen (*Corvus corone*) in zwei Futterteilexperimenten und in einem Token Transfer Experiment getestet. In Futterteilexperiment 1 erhielt jedes Paar mehrere Futterstücke. In Futterteilexperiment 2 wurde die „Spender"-Krähe separiert und erhielt alle Futterstücke, welche sie mit einer „Empfänger"-Krähe teilen konnte. Der Versuchsaufbau des Token Transfer Experiments war ähnlich zu Futterteilexperiment 2, nur erhielt die „Spender"-Krähe Token anstelle von Futterstücken. Zusätzlich wurde die Beziehungsqualität gemessen, um mögliche Effekte dieser auf prosoziales Verhalten zu identifizieren. Weder Futter noch Token Transfere wurde in einem der Experimente beobachtet. Weiters wurden Unterschiede in der Beziehungsqualität gefunden, diese beeinflussten jedoch nicht signifikant die Prosozialität. Interessanterweise wurden mehr Stücke versteckt, wenn der Paarpartner anwesend war als ein Nicht-Paarpartner, welches vermuten lässt, dass Krähen den Diebstahl ihres Partners tolerierten. Dies könnte darauf hindeuten, dass Krähen ihre Prosozialität eher durch Tolerieren eines Diebstahles ausdrücken als durch aktives Futter teilen, besonders bei ihrem Paarpartner.

Introduction

Prosocial behavior is defined as any voluntary behavior that benefits another individual but with no or little costs to the actor (Marshall-Pescini et al., 2016), such as sharing, helping, informing, or comforting (Jensen, 2016). This behavior is especially prominent in humans and can be seen in our everyday life, in, for example, something as simple as holding a door open for other people (Jensen et al., 2014). For a long time, it was believed that prosocial behavior is a unique feature of humans (Burkart et al., 2007). However, more and more studies have been focusing on prosociality in animals, especially in non-human primates, and found evidence that strongly disagrees with this theory (chimpanzees: Horner et al., 2011; wolves: Dale et al., 2019; rats: Hernandez-Lallement et al., 2015; African grey parrots: Brucks and von Bayern, 2020; azured-winged magpies: Horn et al., 2016).

There are a lot of different experimental paradigms that have been used to test animals for prosociality. However, they can be narrowed down to three major paradigms: prosocial choice, instrumental helping, and food sharing paradigms (Marshall-Pescini et al., 2016). In the prosocial choice task subjects could usually choose between two options: a selfish and a prosocial option. While the selfish choice only delivers food to the subject, the prosocial choice also delivers food to a partner. Therefore, if a subject is aware of the partner`s welfare it should choose the prosocial option over the selfish choice (e.g. capuchin monkeys: Lakshminarayanan and Santos, 2008; ravens: Di Lascio et al., 2012). However there has been some criticism, that a positive result might not necessarily infer an understanding of the task, but rather come from an overtraining (Marshall-Pescini et al., 2016). In the instrumental helping paradigm, a subject can help another individual to achieve a certain goal, which the individual alone could not attain. This could be done by, for example, handing over an object that is out of reach (Warneken and Tomasello, 2006; Yamamoto et al., 2009). Especially common are hereby token transfers. In this form of instrumental helping, animals are trained to exchange a non-valuable object, a token, for food with an experimenter. In a further step two individuals are separated from each other. One has access to tokens but cannot exchange them with an experimenter, while the other individual could do so but has no tokens. A transfer of tokens therefore would be seen as a form of prosocial act. (e.g. capuchin monkeys: Skerry at al., 2011). In the last paradigm, food sharing, most setups provide a group of individuals with easy to monopolize food pieces to observe interactions between the subjects. Sharing is thereby defined as a transfer of a food item from one subject to another subject (Marshall-Pescini et al., 2016), although sometimes also tolerated

theft and foraging together with a partner is included in this term (Stevens and Gilby 2004). De Kort et al. (2006) provided each individual of a group of jackdaws with the same amount of food and measured the frequency of food transfers as well as who initiated the transfer. Although all of these paradigms have been frequently used in studies on non-human animals, there have hardly ever been any studies that combined multiple paradigms within the same study.

Many studies have focused on exploring prosociality in non-human primates as our closest relatives. However, more and more studies also begin to focus on avian species, where parrots and corvids are especially outstanding in respect to their cognitive abilities (Lambert et al., 2019). Members of the corvid family are interesting species to investigate prosociality, as they show advanced socio-cognitive skills that are comparable to apes (Güntürkün and Bugnyar, 2016). They also possess large brains (Jacobs et al., 2014) and display cognitive abilities, such as imagination, flexibility, causal reasoning, and prospection, which are claimed to be the foundation for a complex cognition (Emery and Clayton, 2004). In addition, corvids live relatively long, form long-term monogamous bonds, and have altricial offspring (Emery, 2006; Emery et al., 2007). When a pair has formed in young rooks and ravens, for example, they engage in long episodes of bill holding, allopreening and they even support each other during or after fights (Clayton and Emery, 2007; Fraser & Bugnyar, 2010). It can enhance a pairs' dominance status when the pair partners support each other in agonistic conflicts with others (Clayton an Emery, 2007; Braun & Bugnyar, 2012), although most corvid pairs are also characterized through a dominance relationship between the partners (the male being dominant over the female, e.g.: carrion crows: Chiarati et al., 2010; rooks: Scheid et al., 2008).

Relationships are defined as especially valuable between individuals, when partners spend a lot of time in proximity to each other, exchange friendly behaviors like allopreening, show hardly any agonistic conflicts and support their partner in conflicts with others (van Schaik and Aureli, 2000). Fraser and Bugnyar (2010) showed that the relationship quality in ravens can be separated into three main components, whereby the component defined as "value" is of particular interest for how the partners exchange services and resources. It consists of contact sitting, allopreening and agonistic support. Additionally, food sharing is another behavior to express affiliation between individuals (Emery et al., 2007). In monogamous bird species, it is common to feed the partner (Scheid et al., 2008). For instance, in corvids food sharing occurs more often than in many primate species (Duque & Stevens 2016). Food sharing can also play an important role in the formation of pair bonds (rooks: Scheid et al., 2008).

The identity of the partner has been shown to have an influence on a prosociality in birds. African grey parrots´ strength of a pair's affiliation affected prosocial transfers in a token transfer paradigm (Brucks and von Bayern, 2020). Also, ravens preferentially chose affiliated individuals over non-affiliated birds in a string-pulling paradigm (Asakawa-Haas et al., 2016). Furthermore, mesotocin, the bird's homologue to oxytocin, was linked to increased prosociality in pinion jays (Duque et al, 2019) and a recent study in ravens found higher levels of mesotocin during the breeding season in spring, compared to the mating season in winter (Stocker et al, 2021). Thus, corvids are ideal to investigate the effects of relationship quality and breeding season on prosocial behavior, as both could be factors of influence.

Carrion crows are a promising species for investigating prosociality as they can be cooperative breeders, where care for the offspring is not only provided by their parents but also by other individuals (Baglione et al., 2002a). They also have been shown to share food in other contexts. For example, Chiarati et al. (2011) discovered that males share food with conspecifics, although they allow offspring to feed even longer than non-kin. Crows are a monogamous species and pairs stay together year-round in their territory (Baglione et al., 2002b). Therefore, prosocial behavior between pair-partner might be more pronounced, than between non-paired conspecifics. Carrion crows have already been shown to be prosocial in a group service paradigm where they could provide other group members with food through landing on a perch (Horn et al., 2020). However, so far they did not show this behavior in a token transfer paradigm in a group setting, where donor crows could transfer tokens to their group members, who in turn could exchange them for food (Horn et al., 2021).

In this study, I conducted three sharing experiments with differing levels of constraints and training requirements with four pairs of carrion crows. Using three different experiments should increase the level of control imposed on the crows by the set-up. In the Food-Sharing Experiment 1, the crows received several food pieces together as a pair to provide an unrestricted setting, in which the crows could share food. In Food-Sharing Experiment 2, the pairs were separated and only one crow, the donor, received all food pieces which it could share with the recipient. The set-up in the Token Transfer Experiment was the same as in Food Sharing Experiment 2, but the donor crow received tokens instead of food pieces. Note that I used the set-up developed by Massen et al. (2015) for ravens, but I included tokens with different values, to draw attention to the token and not to the act of exchanging. The donor thus received tokens, for which some were rewarded, while others were not. However, the donor himself could not exchange them for food, but a partner in an adjacent compartment could. In

Food-Sharing Experiment 2 as well as the token transfer, I tested the crows with their pair partner and with a non-pair partner. In addition to this I assessed each pair´s relationship quality to make possible effects of the identity of the partners visible. Since Stevens and Gilby (2004) also included tolerated theft in their definition of food sharing, I also monitored food caches and their pilferages in the experiment. Lastly, I planned to assess whether prosociality was more pronounced in the breeding season then during the rest of the year.

I predicted that:

1) Carrion crows show prosocial behavior in all three experiments, since they have been shown to share food in naturalistic settings and provide food to their group members in the groups service paradigm (Chiarati et al., 2011; Horn et al., 2020)

2) Food or token transfers occur more often between pair-partners then between crows that are not pair-partners in all three experiments. Furthermore, I expected less caches to be made in the presence of a pair partner, since I assumed that they are more interested in sharing with partners.

3) Pairs with a longer pair bond duration to have a better relationship quality. Therefore, pairs with a better relationship quality should have more equal access to food in Food-Sharing Experiment 1 and should act more prosocial towards one another then other pairs in Food-Sharing Experiment 2 and in the Token Transfer Experiment. Additionally, I predicted that caches are placed nearer to the pair partner, as a result of higher proximity to each other and that pilferages are more tolerated in pairs with higher relationship quality.

4) Crows would show more prosocial behavior during the breeding season as mesotocin is especially high in the breeding season and linked to prosocialty in corvids (Stocker et al, 2021; Duque et al, 2019). However, due to the first lockdown caused by the Covid-19 pandemic, part of my study had to be delayed for several months and was conducted well after the breeding season. Therefore, I could not investigate the effect of the breeding season on the crows' food sharing behavior.

Methods and Material

Subjects and Housing

Subjects were 8 adult, hand-reared carrion cows (*Corvus corone*). In terms of appearance, the crows were either carrion crows or hybrids of carrion and hooded crows, reflecting the hybridization belt in Middle Europe. Both types of crows have highly similar life histories and are often considered to be subspecies (Vijay et al., 2016). The crows were housed in pairs at the Haidlhof Research Station in Bad Vöslau, Austria. Each pair consisted of one male and one female crow. Housed together were Saul and Peppi, Willy and Juno, Corbie and Rainer, and Signore and Daisy (see figure 1). Corbie and Rainer have been housed together as a pair since 2014. Saul and Peppi had reached their sexual maturity in 2015 and formed a pair bond soon afterwards while living in a group. They had been housed as a pair since 2019. Signore and Daisy, and Willy and Juno had been housed as pairs since 2019, when Signore and Juno had each lost their respective previous pair-partners. None of the pairs had ever had chicks. The pairs lived in outdoor aviaries, into which they had moved to in the summer of 2019. All birds were mainly housed in their living compartments and had alternating access to the experimental compartments when they were not being tested (see figure 1: compartments with a red frame). Due to the arrangement of the compartments Saul and Peppi, and Willy and Juno were tested in another experimental compartment than the other two pairs.

The birds had ad libitum access to water and were fed twice a day, once in the morning and once in the afternoon. All crows had already participated in studies before. Entering the experimental compartments, and therefore participating on this study, was completely voluntary.

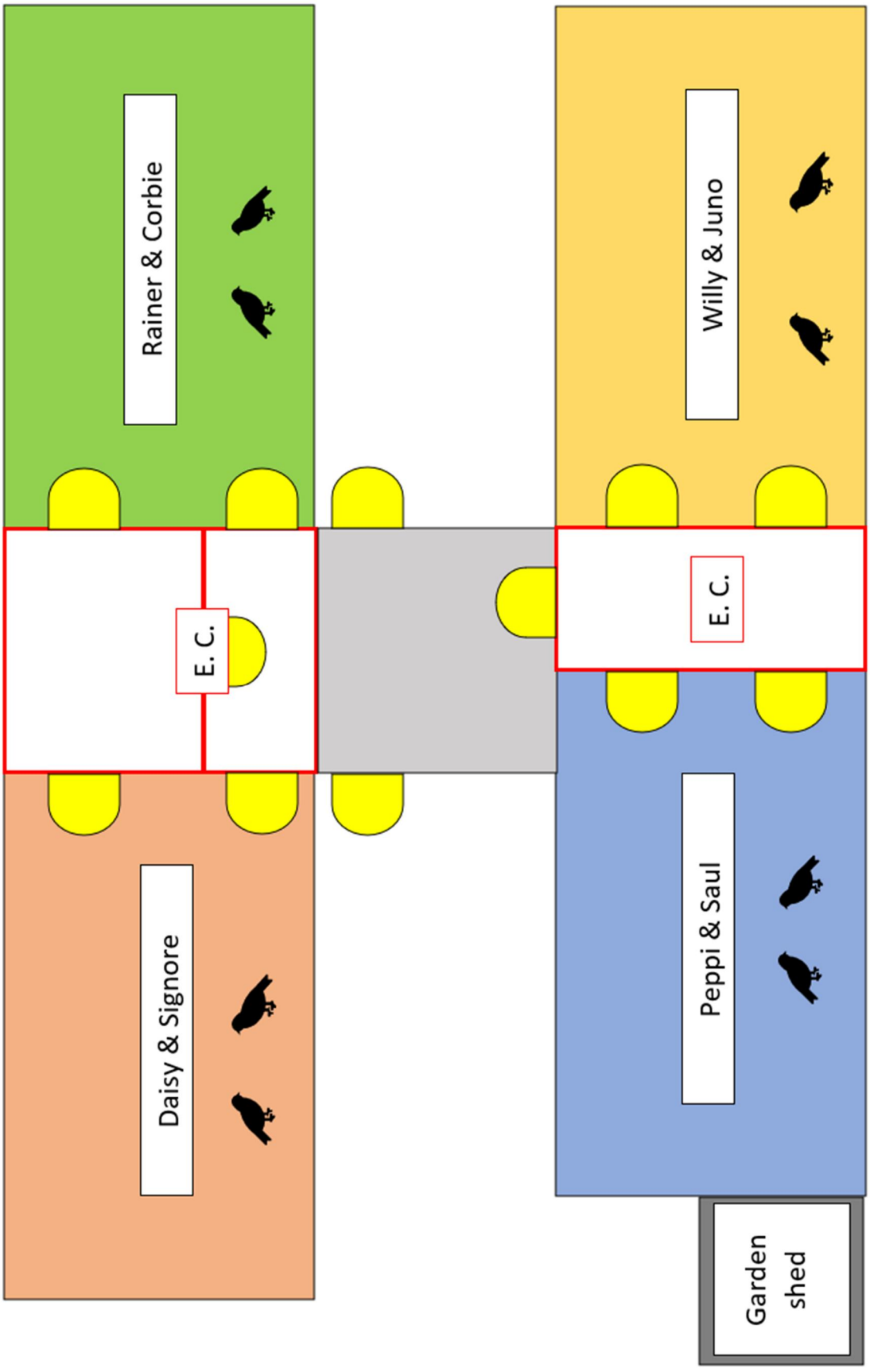

Figure 1 *Map of the crows' aviaries at the Haidlhof Research Station. Boxes with names show the respective compartment of a pair. Compartments with a red frame are the experimental compartments and are therefore labeled with "E. C.". The yellow half circles indicate doors.*

Study Design

My study consisted of two different food sharing experiments, that each consisted of two runs, and a token transfer experiment (see figure 2). In Food-Sharing Experiment 1, I investigated how the pairs behaved when they were in the same compartment and received ten half Frolic® pieces. It was of particular interest who got those pieces and whether sharing between the pair-partners occurred. All pairs were tested in their home-aviaries, half of the time after feeding in the morning and the other half before feeding in the afternoon. Each pair was tested 6 times per run, so at the end every pair participated in 12 sessions. The first run was conducted in October 2019. Since Juno was separated after a surgery during the first run, I conducted Willy and Juno´s first run a month later. The second run took place between June and July 2020 for all birds (see figure 2).

The crucial difference in Food-Sharing Experiment 2 was that the pairs were separated and only the donor crow received ten half pieces of Frolic®, which could be shared through a wire-mesh with a recipient in an adjacent compartment. Again, I was interested whether sharing occurred in this set-up. I tested each crow with their pair-partner and with a crow from another pair, that was the same sex as their partner, to avoid any biases that could potentially be caused by the sexes. Half of the subjects started with their partner and the other half with a non-partner. All crows completed a total of 12 sessions per run, 6 sessions with their partner and 6 with a non-partner. The first run of this experiment was conducted from December 2019 until February 2020 and the second run took place from July until the beginning of October in 2020 (see figure 2).

In the Token Transfer Experiment, I investigated whether crows shared tokens with a partner who could exchange these tokens for food, while the donor itself could not. The setup was the same as in Food-Sharing Experiment 2. This test along with three control conditions was conducted once with the pair-partner and once with a non-partner. The sequence of the conditions was semi-randomized and balanced between subjects. Testing always took place in the morning before feeding. I conducted this experiment in November and December 2020 (see figure 2)

Prior to the experiments I conducted habituation and training sessions (see figure 2). Throughout the duration of my study, I conducted focal observations, which allowed me to assess the pairs' relationship quality (see figure 2).

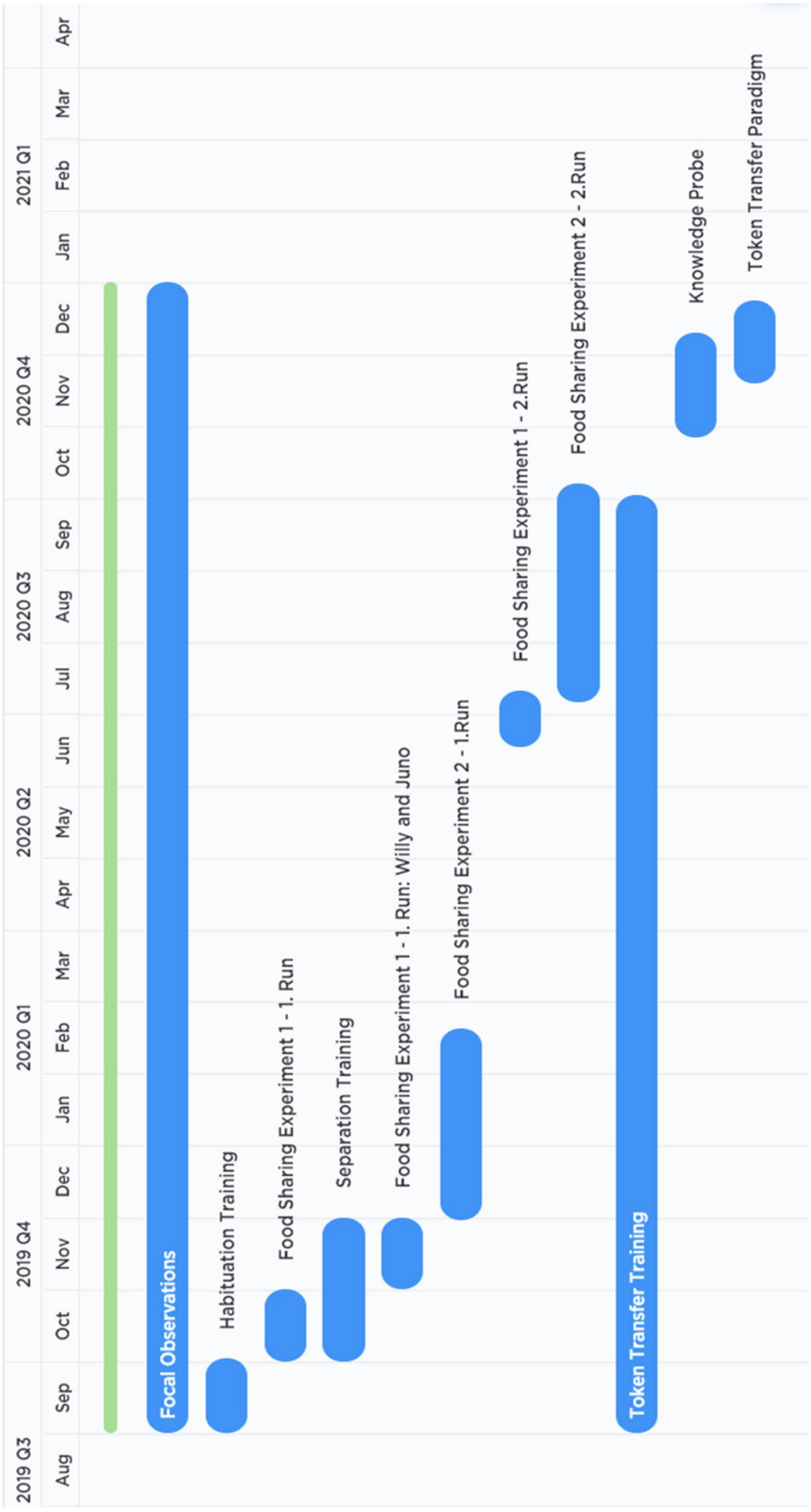

Figure 2 *Timeline of the different experiments and trainings.*

Preliminary Training

Before the experiments could begin, all pairs had to get used to my presence, since corvids are highly neophobic (Greggor et al., 2016). I therefore started spending time with each pair inside the aviary, not giving the birds too much attention at first. When the crows began to feel more comfortable and thus spent more time on the floor than on high branches, I would put small pieces of Frolic® dog food near me or would throw them slightly in one of the crow's direction. With each session the crows should come closer and closer, till finally most of them would even be comfortable with sitting on my legs or arms. In addition to being inside the aviaries, I started to do focal observations at the same time as the habituation training, so that the subjects would get used to me standing in front of the aviary for longer periods. These focal observations conducted before the start of my first experiment were not analyzed in this study. As soon as all individuals were habituated to the experimenter, the Food-Sharing Experiments could be carried out.

For Food-Sharing Experiment 2 and the Token Exchange, the birds had to be trained to be separated into the experimental compartments. Although all crows had this kind of training before, they had to get used to the experimental compartments in the new aviary, as well as to the experimenter. At first the crows were lured inside of the experimental compartment through pieces of dry cat food, until they were comfortable enough to stay inside the compartment in my presence. I then would start moving the door slightly, but not yet close it. When the crows were still calm enough to stay inside the compartment the door was closed, and the birds rewarded. Some individuals preferred to be separated with their partner together at first, before in the next step being separated alone inside the experimental compartment.

Relationship Quality

For the relationship quality, a total of 24 focal observations of each individual was collected: 12 samples during each run, thus 6 during the periods of each Food-Sharing Experiment. Every crow was filmed for 5 minutes with a camera on a tripod. Focal observations were done between feedings in the morning and in the afternoon, in randomized order, so that every time a different pair and a different crow within the pairs started.

Food-Sharing Experiment 1

In Food-Sharing Experiment 1, each pair received a total of 10 half pieces of Frolic®-rings. These pieces were placed inside a bowl outside of the aviary, about 15cm away from the wire-mesh. The bowl with the pieces was clearly visible to the birds. After placing the bowl, I waited for 30 seconds until I started to deliver the first piece of Frolic®, by pushing it through the wire-mesh. I then stepped back, so the cameras had a clear view at the delivery site. After 20 seconds the next piece got delivered. This was repeated till all 10 pieces were inside the aviary. Filming ended 1 minute after the last piece of food had been push through the wire-mesh. At the start of the experiment two cameras were placed in front of the aviary, one focusing on the area where the delivery took place and the other one giving an overview of the aviary. Both cameras were positioned in a way that a large part of the aviary was filmed. Additionally to the filming, I noted which crow got the piece, how many each bird got and if any other noticeable events occurred.

Food-Sharing Experiment 2

In contrast to Food-Sharing Experiment 1, the subjects were separated. Daisy and Signore, and Rainer and Corbie therefore were both in adjacent experimental compartments (red framed boxes on top in figure 1); Peppi and Saul, and Willy and Juno were separated in the experimental compartment between their home aviaries and the other one in the compartment connecting both complexes (red framed box on the bottom and grey box in figure 1). Compartments were separated with a wire-mesh from each other that allowed transfers. The rest of the experimental setup was similar to the previous experiment: Again 10 half pieces of Frolic® were placed in a bowl in front of the aviary and after 30 seconds the first piece got pushed through the wire-mesh. As in the previous experiment each delivery is followed by a 20 second break till all 10 pieces were inside the aviary. Again, 2 cameras on tripods were used: one focused on the donor, that got all the pieces, and the other camera was directed at the recipient. The wire-mesh where a food transfer could take place was visible on both videos. Filming ended 2 minutes after the last delivery. Shares along with attempts and other noticeable events were noted additionally.

Token Transfer Experiment

Material

Tokens were made from a wooden round-bar with a diameter of 1.5cm. Approximately every 0.5cm, pieces were cut from the bar with a saw. Since it was done by hand some of the tokens differed slightly in size. However, all tokens still fitted easily through the wire-mesh. After cutting, the tokens were smoothed with a sandpaper and painted in one out of three colors: green, yellow or red (see figure 3, left picture). The paint that was used, was especially suitable for painting wooden children's toys. Therefore, the paint was in no way toxic for the crows, which was particularly important as the birds would take and exchange the tokens with their beaks. At the start of the training there were a total of 15 tokens, 5 of each color. During the training and the experiment tokens got lost on a regular basis. That was caused, for example, by subjects caching them during the trials that could not be found again after the session. On other occasions the crows were also hiding them in their crop and were thus inaccessible. This led to a frequent production of new tokens. Tokens were also cleaned with a toothbrush after sessions and from time to time repainted, if necessary.

Figure 3 *Tokens with different values (left). Token Exchange Training (right): tokens were placed on colored table with respective rewards and put in front of the testing compartment.*

Another essential item for the token exchange was a small table, where the exchange took place (see figure 3, right picture). The table had a height of about 8.5cm, a length of 40cm and a width of 20cm. To highlight the importance of the colors, the table was painted in all three of them. Thus, the top of the table was divided into three parts: one painted yellow, the middle part green and the last one red. The tokens and their corresponding rewards were placed on the field with the same color as their own.

Training

Token exchange training was done with only 6 individuals. Juno and Rainer were excluded from training because they had no experience with exchanging tokens prior to this experiment. All the others were already trained to exchange tokens with an experimenter for a reward.

At first, subjects were introduced to tokens with 3 different colors: green, yellow and red. Each color resulted in a different reward upon exchange with the experimenter. Green tokens had the highest value. By exchanging one of those, the birds got a small piece of cheese, which is a highly valued food item for them. When the crows exchanged a yellow token, they got a small piece (1/ 32nd) of Frolic® (same size as cheese). This is also quite valued among crows, but not as much as cheese. In addition to the food reward, they also received verbal praise. However, for the exchange of a red token they were not rewarded. If they returned one of those, I would cross my arms and wait for about 10 seconds before exchanging any further tokens.

In the first phase of training, subjects were trained together with their pair-partner. At the beginning I held a token through the fence, which the subjects then took and returned the token into my hand. Only if the token was placed into my hand the birds were rewarded. The returned token was then placed back on the table before the reward was given to them. This step should not only help them to understand the value of each token, but also teach them that an exchange can only take place when the table with the food is present. This was continued till the exchange went fluently. Since subjects kept exchanging every token, no matter if rewarded or not, the pairs received 3 tokens of each color at once and thus could exchange the tokens that were more valuable to them. As this did not work well in pairs and since separation training was already successful at this point, I now started to introduce token-value training for each crow separately. At this training phase, sessions were recorded with a camera and the sequence of the returned tokens was written down afterwards into a table in Microsoft Excel. Since the exchange worked well, the number of tokens was increased to 4 tokens of each color. This training was continued until each crow completed a total of 80 trials.

Knowledge Probe

After 80 trials of training with tokens in three colors, I conducted a knowledge probe, to see whether subjects understood the value of the tokens. I used only two of the three token types: green and red. If the crows understood that the green token resulted in a high-quality food reward, whereas the red token resulted in no food reward at all, it was expected that they would return only green ones or at least exchange them at first. Therefore, each crow received 6 green

and 6 red tokens. A trial consisted either of the exchange of all tokens or of exchanging until the last green token was returned. This choice was made by the crows whether they kept on exchanging or stopped after the valuable ones were already traded. If the birds did not exchange at all for 10 minutes, the session was terminated. The criterion for passing the knowledge probe was reached when the individuals exchanged all green tokens first during 5 consecutive trials (for figures of each individual's` knowledge probe see appendix).

Token Transfer Experiment

The methods of the token transfer experiment were based on an experiment done by Massen et al. (2015). Each session of the token transfer experiment consisted of four trials: a prosocial test and three control conditions (i.e., a social control, a non-social control, and a motivation control condition; see figure 4).

Every trial lasted a maximum of 10 minutes, always followed by a 15-minute break between conditions. Trials were only ended earlier if all green tokens were transferred or exchanged. Every subject had to complete 2 sessions: one with their partner as recipient and one with a crow from another pair. The non-partner was the same for each subject as in Food-Sharing Experiment 2. Every crow went through all test conditions as donor as well as recipient, apart from Rainer and Juno, who were not trained to exchange tokens and therefore participated as recipients only. The sessions were recorded with two Cameras on tripods, that were set-up in the same way as in Food-Sharing Experiment 2.

Test

For the test, donor and recipient were in two adjacent compartments that were separated through a wire-mesh. At the beginning of the trial the donor received 12 token, 6 green and 6 red ones. The donor itself could not exchange the token, but the potential recipient in the other compartment could. In front of the recipient's aviary was the colored table on which only an exchange of the tokens was possible. Thus, if the donor transferred tokens through the fence to the recipient, the recipient could exchange them for food. However, the recipient could only get food if the donor transferred green tokens, since red tokens were not rewarded. The donor himself gained no reward for transferring a token to the recipient and therefore would act prosocial towards him.

Social Control Condition

This condition had a similar set-up as the test condition. The difference here was that the table was not present. An exchange was therefore not possible, neither for the recipient nor for the donor. This was done to test whether a transfer of tokens only occurred as a form of object play and not out of prosociality.

Non-Social Control Condition

No recipient was present in this condition, leaving the adjacent compartment vacant. However, the table, where an exchange could take place, was in front of the empty compartment. In this condition it was tested whether subjects just tried to get the tokens as close as possible to the table.

Motivation Control Condition

Here the table was placed in front of the donor's compartment, who could now exchange the received tokens and get a reward himself. This was done on the one hand to test whether the subjects are at all motivated and on the other hand to keep them still motivated, since they were not able to gain any rewards in the other conditions.

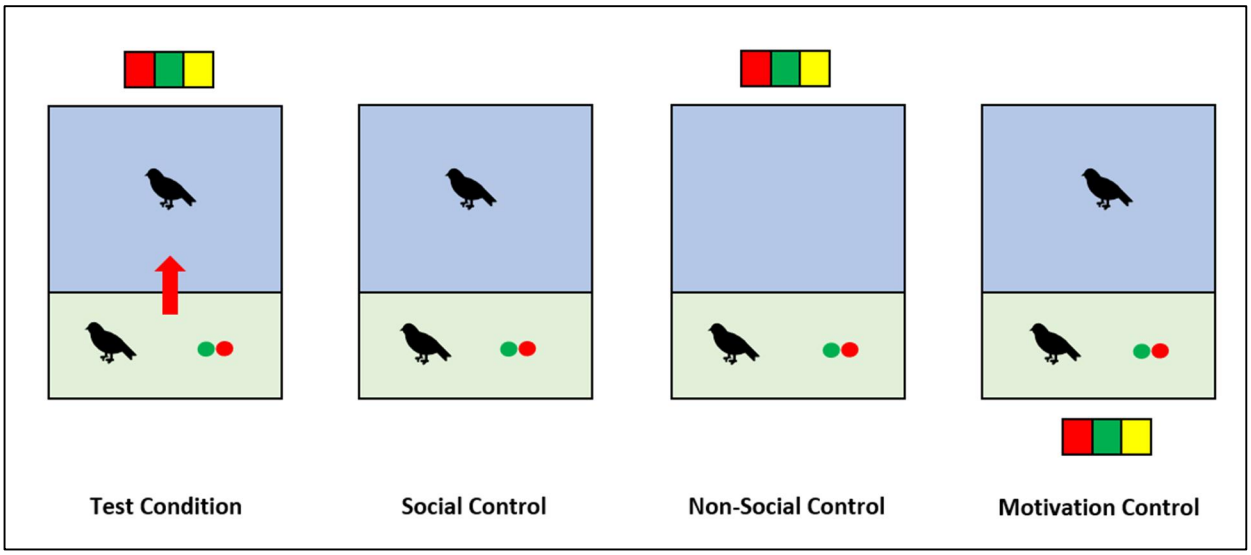

Figure 4 *Token Transfer Conditions: Test Condition, Social Control Condition, Non-Social Control Condition and Motivation Control Condition*

Behavior Scoring and Statistical Analysis

All videos were scored using Solomon Coder (Version 19.08.02; Peter, 2019) and all tests were calculated in SPSS.

Relationship Quality

I coded two of the variables identified to indicate the value of a relationship by Fraser and Bugnyar (2015): contact sitting and allopreening. The third component, agonistic support, was not relevant in my sample, because the crows were not kept in groups. I assessed how many and how long contact sitting and allopreening occurred in every pair. Additionally, I coded whether the focal subjects shared or received food from their partner, as form of natural occurring prosociality. The values were than summed up for each pair. Due to the small sample size of four pairs, I conducted a descriptive comparison between the pairs according to the previous duration of their pair bond.

Food Sharing Experiment 1

After comparing the results from notes and videos, who received which piece in each trial was written down in to an excel sheet for each pair. The results of all trials of both runs were then summed up, to obtain the total amount of pieces that each male and female of a pair received during the whole experiment. Only those pieces that could clearly be assigned to one of the crows were taken into account.

With these variables I calculated whether males and females received on average the same number of frolic-pieces, to see whether the pairs different from one another. Computation was done with a binominal test calculator (Social Science Statistics, 2021).

In addition, I also assessed whether females and males pilfered caches of their partner and if those events were followed by aggressive behavior towards the pilferer. Some pilfers were not visible on camera, but the bird's behavior indicated such action. In these cases, the individuals spent at least 8 seconds in a part of the aviary where their partner cached food earlier, often followed by additional indicators, such as going to the place immediately after their partner left, going straight to the water bowel after "pilfering" or walking quickly towards or away from

their partners cache places. These results, again, are reported descriptively due to the small amount of data.

Food Sharing Experiment 2

I coded the occurrences of food transfers from the donor to the recipient, also attempts of those, when the donor placed food items on the frame of the fence and begging of the recipient. Furthermore, I assessed how often donors placed their caches while the recipient was in close distance (maximum 1 m) to the donor ("caches near partner"). Additionally, all other caches were noted and later summed up with the other cache type, for a total amount of caches. At last, the frequency and the duration of the time that the recipient spent in front of the donor's aviary (max. 1 body length of a crow away) ("presence of recipient") and the time that donor and recipient spent in less than 1 m distance to each other ("time near recipient"), were measured.

To calculate whether the number of total caches differed between trials with their partner and those with a partner of another pair, a Wilcoxon signed ranks test was performed. The same was done for the caches made while the recipient was present. Additionally, the duration of the time spent near each other and of the time when the recipient was present were compared between partner and non-partners.

Token Transfer Experiment

Similar to Food-Sharing Experiment 2, I coded token transfers, attempted transfers and begging of the recipient. Again, tokens that were placed by the donor on the frame of the fence to the recipient´s compartment were considered as attempted transfers. As in the previous experiment I coded whether donors cached while the recipient was in maximum 1 m distance to the donor ("caches near partner"), as well as all other caches placed by the donor ("caches"). Also, duration and frequency of the time recipient and donor spent in proximity to each other (maximum 1 m distance) ("time near partner") and of the time the recipient was maximum 1 body length of a crow away from the donor's compartment ("presence of recipient"). However, coding these variables was only possible for the social control and the test condition. In the non-social condition the only variable that was coded was "caches" since no partner was present in this condition.

For the calculation, I first summed up all caches for each condition, except from the motivation control condition, as no caches were made in this condition. Furthermore, I computed a Friedman test with an additional post hoc test. Afterwards I compared trials where a partner acted as a recipient with those where a non-partner acted the recipient with a Wilcoxon signed ranks test. The same procedure was done with the variables "time near recipient" and "presence of recipient", which were also compared between trials with a partner and a non-partner using a Wilcoxon signed ranks test. At last, all variables ("cache", "time near recipient" and "presence of recipient") were separated into test and social control condition, independent of the recipient's affiliation. With a Wilcoxon signed ranks test each variable was then compared between the two conditions.

Results

Relationship Quality

The two pairs that had long pair bonds (Saul and Peppi; Corbie and Rainer) had relatively long overall durations and bouts of contact sitting and allopreening, whereas these measures were very small or zero in the pairs with short pair bonds (Signore and Daisy; Willy and Juno) (see table 1).

Table 1 *Variables measured for the relationship quality. Pairs in order from highest to lowest quality (from left to right)*

	Pair	**Saul-Peppi**	**Corbie-Rainer**	**Signore-Daisy**	**Willy-Juno**
Contact Sit	Frequency	11	8	6	0
	Duration (s)	1119.3	821.4	197.4	0
	Bout length (s)	101.8	102.7	32.9	0
Allopreening	Frequency	10	3	1	0
	Duration (s)	135.3	18.9	0.7	0
	Bout length (s)	13.53	6.3	0.7	0
Food Transfer	Frequency	1	0	0	0

Food-Sharing Experiment 1

In three out of four pairs, the males obtained significantly more Frolic® pieces than their female partners (see Table 2). Corbie and Rainer were the only pair that did not differ significantly in the number of pieces ($p = 0.426$). On top of that, Rainer was the only female that got more pieces than her male partner during one run.

No transfer of food was observed. However, it could be seen that all females, except Rainer, pilfered caches from their partner. The only male that pilfered his partners cache was Signore. While he stole Daisy´s cache right in front of her, females pilfered when their partner was not near them. None of the pilfers where followed by aggression. Aggression in other contexts than pilfering did only occur in two pairs: Signore and Daisy, and Willy and Juno. In Signore and Daisy there was only one occurrence where Signore displaced Daisy from the place where the

food was delivered. Willy and Juno had 3 aggressive encounters. Two of them took place as Juno wanted to take a piece at the food delivery and one when she was in proximity of one of Willy´s caches.

Table 2 *Total Amount of Frolic®-pieces each crow received in the two runs. The p-value states the equality of the distribution (*p<0.05; **p<0.01; ***p<0.001). Male pilfers indicate the number of times a male pilfered a female's cache, while female pilfers states the number of times a female pilfered a male´s cache. Numbers in square brackets are not directly observed but inferred pilferings.*

Pair	Run	Male	Female	p-Value	Male pilfers	Female pilfers
Peppi-Saul	1.Run	36	17		0	1
	2.Run	33	19		0	1[1]
	Total	69	36	≤0.001***	0	2 [1]
Corbie-Rainer	1.Run	35	24		0	0
	2.Run	24	32		0	0
	Total	59	56	0.426	0	0
Signore-Daisy	1.Run	31	23		1	1
	2.Run	36	23		0	4
	Total	67	46	0.023*	1	5
Willy-Juno	1.Run	49	9		0	2
	2.Run	57	3		0	1 [2]
	Total	106	12	≤0.001***	0	3 [2]

Food-Sharing Experiment 2

During this experiment, no food transfer or attempts of food sharing occurred. Also, none of the recipients ever begged for food. When looking at the number of caches, though, a significant difference was found between the trials with their partner and those with a non-partner as recipient ($z = -1.973$, $p = 0.049$) (see table 3). In contrast to the total number of caches, no difference was found when only the caches near the recipient were compared between partner and non-partner ($z = -1.414$, $p = 0.157$). Overall, this type of cache happened only rarely.

The duration of the time the recipient spent in proximity to the donor`s compartment did not depend on the recipient's affiliation to the donor ($z = -0.84$, $p = 0.401$) Also, when comparing the duration of the time donor and recipient spent close to each other (maximum 1 m distance between donor and recipient), it could not be found that they spent more time together when they were pair-partners ($z = 0$, $p = 1$).

Table 3 *Different types of cache made during the Food-Sharing Experiment 2. Pair partners of the recipients are in bold letters. Total Cache also includes caches made in presence of the recipient ("cache near recipient").*

Subject	Recipient	Caches Near Recipient	Total Number of Caches		
			1.Run	2.Run	Total
Saul	**Peppi**	**1**	**16**	**8**	**24**
	Juno	0	3	15	18
Peppi	**Saul**	**2**	**14**	**23**	**37**
	Willy	0	15	15	30
Corbie	**Rainer**	**0**	**17**	**5**	**22**
	Daisy	1	8	11	19
Rainer	**Corbie**	**0**	**4**	**6**	**10**
	Signore	0	11	2	13
Signore	**Daisy**	**1**	**12**	**16**	**26**
	Rainer	0	8	11	19
Daisy	**Signore**	**1**	**19**	**7**	**28**
	Corbie	0	10	9	19
Willy	**Juno**	**0**	**6**	**12**	**18**
	Peppi	0	4	17	21
Juno	**Willy**	**0**	**1**	**18**	**19**
	Saul	0	0	9	9

Token Transfer Experiment

Knowledge Probe

Despite extensive previous training with three token types, the crows still needed up to 40 trials to pass the knowledge probe where they were required to discriminate between the no-reward token and the high quality-reward token (median = 15.5 trials, min = 7, max = 40).

Token Transfer Experiment

Similar to the other experiments, no transfers or transfer attempts were observed, neither in the test nor in any of the control conditions. Also, like before, no begging of the recipients occurred. When looking at the number of caches, though, a significant difference could be found between the conditions (χ^2 = 6,125, df = 2, p = 0.047; see table 4). After calculating a post hoc test, it was visible that the social control and the non-social control differed most, although the corrected p-value did not indicate a significant difference (p = 0.130). Subjects tended to cache most tokens in the non-social and least in the social control condition. Another interesting fact is that when tokens were cached, it was mostly the green ones, which would have been rewarded

with cheese, and rarely the red ones, which would have not resulted in a food reward. Only Corbie and Daisy cached red tokens too but that only happened rarely (see table 4). However, the number of caches did not depend on whether the individual in the recipient´s compartment was the pair-partner or the non-partner ($z = -0.677$, $p = 0.498$). Also, the time the subjects spent in close proximity to each other did not differ between partner and non-partner ($z = -1.342$, $p = 0.180$). Neither did the duration differ between social control and test condition ($z = -1.604$, $p = 0.109$). As in Food-Sharing Experiment 2, the duration of the recipient's presence was compared between trials with partner and non-partner as recipient. But again, no difference could be found ($z = -1.153$, $p = 0.249$). At last, the presence of the recipients was compared between the test and social control condition, with the same non-significant result ($z = -0.140$, $p = 0.889$).

In the motivation control condition almost all crows started exchanging the tokens immediately, except for Peppi and Saul. Peppi did not exchange at all in this condition, while Saul only did so shortly before the end of the trial. Corbie and Willy were the only birds that exchanged green tokens first in both trials, while Signore did so only in one of them. All others made one error by exchanging a red token before all of the green ones were exchanged. However, even though not all tokens were exchanged in each trial, all six green tokens were always exchanged.

Table 5 *Number of tokens cached in test and control conditions. Numbers in brackets indicate a cache of a red token.*

	Non-Social		Social		Test	
Donors	**No Recipient**	**No Recipient**	**Partner**	**Non-Partner**	**Partner**	**Non-Partner**
Signore	2	1	0	3	3	0
Daisy	2	6(1)	0	0	0	0
Saul	2	2	0	0	0	0
Peppi	0	2	0	0	0	0
Corbie	3	0	0	1	1	4(1)
Willy	1	1	1	0	2	0
Total Caches	10	13	1	4	6	5

Discussion

Although the carrion crows have been tested in two food sharing and in a token transfer paradigm, no food or token transfers, and therefore no prosocial acts, could be found in any of the experiments. Instead, the birds responded with differences in food caching and pilfering. While males tended to get more pieces in Food-Sharing Experiment 1, females compensated with pilfering their mates' caches. Moreover, more caches were made in Food-Sharing Experiment 2, when the pair-partner was the recipient as compared to the non-partner. The training of the token exchange suggested an understanding of the token's values, through passing the knowledge probe before the test. Despite a lack of transfers, a difference in the number of caches could be found, namely that most (green) tokens were hidden in the non-social control.

The ranking of the relationship quality was in line with the duration of the pair bond, meaning that Saul and Peppi, and Corbie and Rainer, who had been together the longest, showed more affiliate behaviors towards one another. Although the duration of pair bonds can have an effect on breeding success in some bird species (Fowler, 1995), no link was found between spending time in proximity to each other and the time a pair has been bonded in other species (e.g. barnacle goose: Black et al. 2007). In addition, it was found in Steller´s jays that a pairs' tenacity remained relatively constant within a pair over time (Gabriel and Black, 2013), indicating that some pairs do have better relationships independent of how long a pair has been bonded. Therefore, since my sample size was quite small, it might have been a coincidence that the pairs that showed more affiliative behavior towards one another had longer pair bond durations.

In Food-Sharing Experiment 1, no food transfer or attempts of those were observed. These results are in line with Emery et al. (2007), who found that food sharing plays an important role in forming a pair bond, whereas the maintenance of an already established pair bond is mainly facilitated through affiliative behaviors. Therefore, pairs that did show more allopreening and contact sitting might not necessarily need to share more food. Overall males got more pieces, supporting the findings of Chiarati et al (2010), that they are dominant over females. However, I found that Corbie and Rainer, a pair with high relationship quality, were the only pair that showed overall no difference in the number of pieces each pair partner got. This is in the contrast to Peppi and Saul, who showed even more affiliative behaviors towards each other than Corbie and Rainer, but showed a clear dominance of the male. Whether there really is an effect of relationship quality on the distribution of the pieces is hard to say, since the sample size is

quite small. Therefore, the distribution might also arise from the individual differences between the pairs (Gabriel and Black, 2012).

Interestingly, Rainer was the only bird that did not pilfer any of her partner`s caches. Since Rainer and Corbie´s number of pieces did not differ significantly from each other, it could have been that there was no need for her to pilfer her partner's caches. However, it could not be observed that the other females pilfered more when they got fewer pieces at the delivery per session.

None of the pilfers were accompanied with aggression from the individual that had cached the food. However, whether the males did not notice being pilfered or did not care, is not clear. In Saul and Peppi, it could be observed that Peppi was pilfering Saul´s caches even though he was near her, suggesting that he tolerated her theft. In fact, it was shown that pilferage between pair partners is often tolerated (Goodwin, 1956). Since Willy often drove Juno away when he saw her near one of his caches (although it is not clear whether she intended to pilfer), it might be that the tolerance of pilfering also depends on the relationship between pair partners.

When looking at the overall caches in Food-Sharing Experiment 2, I expected that they would be placed nearby the recipient or the recipient´s compartment when the recipient was the pair-partner. However, this could not be confirmed. Interestingly, donors tended to cache more when their pair-partner was the recipient. Although this is the contrary from what was expected, it can possibly be explained through tolerated theft. Since donor and recipient were in adjacent compartments, with hardly any places to hide the donors' actions, the recipient could also see where the donor placed his food pieces. In such a situation, some corvids are known to reduce the number of caches (Dally et al, 2006; Clary and Kelly, 2011). But in our setup, reducing caches would also mean that they would lose food pieces, since they could not store them all in their crop. However, the birds could also take into account the identity of the observer in their decision in whether or not to cache food. For instance, Goodwin (1956) noted that female Eurasian jays acted aggressive when other individuals were near their caches, while they tolerated pilfering of their partner. Similar observations were made in ravens, where a mated pair would cache food not far away from each other, so that the food location was often clearly visible to the partner (Heinrich & Pepper, 1998). Thus, donors could be making more caches in the presence of their pair-partner because they tolerate their pilferage. Therefore, it would make more sense to store more pieces inside their crop when the recipient is a non-partner, so that the food is inaccessible to them. This would also match with the pilfer observations in the first experiment, namely that pilfering seemed to depend on the individual's relationship towards

one another. However, no obvious differences between pairs with higher relationship quality could not be found.

So far, token transfer paradigms have been used in different avian species (ravens: Massen et al., 2015; African grey parrots and blue-headed macaws: Brucks and van Bayern, 2020; crows and azure-winged magpies: Horn et al. 2021), but to my knowledge this is the first study that included two sorts of tokens that either had a value or had none. In contrast to the other studies (Massen et al., 2015; Brucks and van Bayern, 2020; Horn et al. 2021), subjects started off with receiving 3 kinds of tokens which were all rewarded differently. Although there have been some individual differences, it could be seen that especially green tokens were exchanged first across all participants. The difference between red and yellow token, on the other hand, was not as clear for all individuals. However, since the training took place at the same time as the Food-Sharing Experiments, they received the same food as reward. This might have caused a lack of motivation in returning the yellow tokens, as the saturation of Frolic® was quite high. Besides, when yellow tokens were left out in the knowledge probe one could see that they did understand at least the values of the other two token, as only few errors were made. Range et al. (2008) showed that ravens learned to discriminate between colored tubes very fast with only few errors and Bogale et al. (2012) reported similar results for jungle crows. However, both studies worked only with two different colors, suggesting that discriminating three colors might have been more difficult for the crows. This would also explain why they reached the criterion quite fast in the knowledge probe, where I reduced the number of token types.

At the beginning of the training, it was also occasionally observed that some crows would put small objects, like stones or sticks, through the wire-mesh in hope of exchanging them for food. This was also observed in other studies (carrion crow and azured-wing magpies: Horn et al., 2021). But interestingly, in my study most subjects stopped that behavior as the training progressed. This might further indicate that they finally understood that only tokens can be exchanged for food. An alternative explanation could be that since they never got rewards in exchange, they eventually stopped trying. That the crows cached mostly green tokens in the Token Transfer Experiment speaks not only for the interpretation that they have learned to put some value to tokens in general but that they can distinguish between tokens of different values.

Although other studies showed at least some token transfers (Horn et al., 2021; Massen et al., 2015), not a single transfer was observed in my study. However, some of the tokens were cached, approximately around 9 % of all tokens. Compared to Massen et al. (2015) where ravens cached about half of the tokens, the carrion crows did only cache little. This is similar

to the findings of Horn et al. (2021) where carrion crows cached around 6 % of the tokens. However, caching in ravens has been found to be more prominent than in crows (Miller et al., 2015), which might explain the lower frequency in the current study.

Interestingly, I did not observe any begging of the recipient that would indicate interest in the tokens. In primates, however, a positive correlation between such begging (a form of harassment) and food sharing was found. Stevens (2004), for example, found that increased harassment also led to increased sharing by a donor in squirrel monkeys and chimpanzees. Similar results were found in jackdaws, where the birds shared more food with an individual to whose begging calls they were exposed to (de Kort et al., 2006). Additionally, Brucks and von Bayern (2020), who found African grey parrots to be prosocial in a token transfer paradigm, also found that parrots were more likely to transfer tokens when the recipient showed attention-getting behaviors like begging, vocalizing and reaching for tokens. On the contrast, neither Horn et al. (2021) nor Massen et al. (2015) found that the recipients paid any special attention to the donor´s actions. However, they also could not find prosociality in form of token transfers. Thus, since recipients showed no interest in the food or tokens in this study, the donors simply might have felt no need to share. The absence of begging behavior towards the donor could be a consequence of the within subject design, as recipients participated as donors also. Hence, it might be that the individuals were not paying too much attention to the pieces, since they knew, they were going to act as donor soon and receive the same number of pieces for themselves anyway. However, if this were the case then more begging would have been expected at the beginning, as long the crows did only participate as recipient, but this did not happen.

Although the crows participated in two food sharing experiments and in a token transfer experiment, I observed no active transfers. One potential problem with the Food Sharing Experiments is that the direct access to food may distract the donor, who consequently pays not much attention to the recipient (Marshall-Pescini et al.,2016). That is why I opted for the Token Transfer Experiment, which was based on a similar setup, but used an artificial symbol (i.e., the token) instead of food. Since this study found at least some evidence of understanding the value of token, it is unlikely that the token as a symbol was cognitively too challenging for the crows (compare Beran and Parrish, 2021). Also, African grey parrots which have similar cognitive abilities to corvids (Lambert et al.,2019), showed token transfers in the same paradigm as in this study (Brucks and von Bayern, 2020).

Although they did not actively share food or tokens in my study, it cannot be excluded that crow are not prosocial in general. For example, in a group service paradigm, the same birds did

provide other group members with food by landing on a perch (Horn et al., 2020). However, landing on a perch is a more passive way of sharing food than the active transfer required in my study. Therefore, it might be easier for crows to provide or share food in a passive way through, for example, tolerated theft. My results on the food caching of the donor hints also in this direction. After all, little is known about prosociality in crows. The results of this study lead to further questions that other studies could focus on, to provide an even better insight in crows' prosociality. Different paradigms could be used and tolerated pilfering as form of food sharing should be explored further.

Limitations

One limitation of this project, which it shares with many other studies in this field, is the low number of test subjects. From testing four pairs of carrion crows, it is hard to make a statement for an entire population. Especially in the token transfer, where only six of the crows could participate. Additionally, the small sample size did not always allow to calculate statistical tests for all the data. Note that some of the results were on the verge of the statistical significance, so that a larger sample size would likely have allowed to draw more robust conclusions.

Another restriction of this study is the timing of the second run. As stated above, the second run should have been conducted in the breeding season. Due to the Covid-19 pandemic, and the resulting lockdown at the beginning of March, the experiment could not be executed as planned. Therefore, the start of the repetition of the experiments was delayed to June, which is already at the end of breeding season. If the experiments would have been conducted as planned, I would have expected higher levels of prosociality in the breeding season, since mesotocin was found to be higher during this time, which is linked to increased prosociality (Stocker et al., 2021). This might be another reason why only limited prosociality was found. Thus, further investigations of the effects of the breeding season might point out differences that could not be detected in this study.

Conclusion

In the Token Transfer Experiment, no token transfers between the donor and the recipient were observed. Although it is argued that the use of tokens might be too complicated for these birds (Beran and Perrish, 2021), evidence was found that crows are likely to distinguish "valuable" from "worthless" tokens after extensive training. Not only did all participating crows pass the knowledge probe, the majority also only cached tokens for which they would have gotten a reward. Furthermore, in Food-Sharing Experiment 2, a more naturalistic form of the token exchange paradigm, as food was directly used instead of only a symbol for it, no food transfers occurred either. However, in this setup donors made slightly more caches when the recipient was their pair-partner. This increase of caches might be linked to a higher tolerance of pilfering from the donor's pair-partner. Therefore, it might be argued that, although, no direct food transfers were observed, the "actual" prosocial act consists of a higher tolerance of the partner´s pilfering. My results suggest that these paradigms might not be suited to show prosocial food sharing behaviors in carrion crows. Although in Food-Sharing Experiment 1 males dominated over their female partners, males from a relationship with high quality seemed to tolerate pilfers more than male of a pair with low quality. However, no significant effects of relationship quality were found in either of the experiments, which is likely due to the small sample size.

Although this study could not show prosocial behavior in form of food transfers, it raises the question whether crows act prosocial in a more "passive way", through tolerated theft. The collected data on caching is not sufficient to make a firm conclusion in this direction, but it provides ideas for an approach in further studies.

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Appendix

Table A1 *Values for relationship quality split up in both runs*

	Pair	**Saul-Peppi**		**Corbie-Rainer**		**Signore-Daisy**		**Willy-Juno**	
	Run	1	2	1	2	1	2	1	2
Contact Sit	Frequency	8	3	2	6	6	0	0	0
	Duration (s)	846	273.3	27.3	794.1	197.4	0	0	0
	Bout length (s)	105.8	91.1	13.7	132.4	32.9	0	0	0
Allopreening	Frequency	7	3	0	3	0	1	0	0
	Duration (s)	129.4	5.9	0	18.9	0	0.7	0	0
	Bout length (s)	18.5	1.97	0	6.3	0	0.7	0	0

Table A2 *Time Recipient was close enough for a food transfer in Food-Sharing Experiment 2*

Subject	**Recipient**	**Presence of recipient**		**Time near recipient**	
		Frequency	**Duration (s)**	**Frequency**	**Duration (s)**
Saul	**Peppi**	52	1669.5	12	111.6
	Juno	34	1669.2	37	394.7
Peppi	**Saul**	102	1582.8	26	245.4
	Willy	58	754.6	13	68.1
Corbie	**Rainer**	44	553.2	10	100.9
	Daisy	44	270.4	5	34.2
Rainer	**Corbie**	16	386.0	2	11.0
	Signore	36	5577.4	8	36.3
Signore	**Daisy**	41	653.9	9	57.4
	Rainer	37	318.5	1	2.5
Daisy	**Signore**	27	299.5	8	33.2
	Corbie	11	266.7	3	12.4
Willy	**Juno**	34	981.4	8	42.0
	Peppi	39	829.9	1	41.8
Juno	**Willy**	59	537.7	12	55.3
	Saul	126	1558.9	53	333.4

Pair partners of the recipients in bold letters

Knowledge probe – Trials till criterion reached:

Green cells indicate exchanges of a green and red cells exchanges of red tokens. Trial cells in green state trials without an error. The “noR” stands for “no reward” as the subjects exchanged them to early (in the exchange break after exchanging a red token) and were therefore not rewarded. Cells that were marked with “sim” indicate that tokens were exchanged at once.

Willy

Trial	1	2	3	4	5	6	7	8	9	10	11	12
T1							/	/	/	/	/	/
T2						noR		/	/	/	/	/
T3							/	/	/	/	/	/
T4							/	/	/	/	/	/
T5							/	/	/	/	/	/
T6							/	/	/	/	/	/
T7							/	/	/	/	/	/

Signore:

Trial	1	2	3	4	5	6	7	8	9	10	11	12
T1												/
T2					Gr cache	/	/	/	/	/	/	/
T3							/	/	/	/	/	/
T4									/	/	/	/
T5							/	/	/	/	/	/
T6									/	/	/	/
T7								/	/	/	/	/
T8							/	/	/	/	/	/

Saul:

Trial	1	2	3	4	5	6	7	8	9	10	11	12
T1												/
T2							Gr cache	R cache				R cache
T3							/	/	/	/	/	/
T4							/	/	/	/	/	/
T5		sim	sim					sim	sim			
T6				sim	sim				/	/	/	/
T7			sim	sim					/	/	/	/
T8	sim	sim			R cache		/	/	/	/	/	/
T9										/	/	/
T10												
T11									/	/	/	/
T12			sim	sim			/	/	/	/	/	/
T13				sim	sim			sim	sim		/	/
T14								/	/	/	/	/
T15		sim	sim	sim	sim		/	/	/	/	/	/

Daisy:

Trial	1	2	3	4	5	6	7	8	9	10	11	12
T1									/	/	/	/
T2							/	/	/	/	/	/
T3							/	/	/	/	/	/
T4								/	/	/	/	/
T5											/	/
T6								/	/	/	/	/
T7				Canceled								
T8								/	/	/	/	/
T9						/	/	/	/	/	/	/
T10							/	/	/	/	/	/
T11								/	/	/	/	/
T12							/	/	/	/	/	/
T13							/	/	/	/	/	/
T14							/	/	/	/	/	/
T15							/	/	/	/	/	/
T16							/	/	/	/	/	/

Peppi:

Trial	1	2	3	4	5	6	7	8	9	10	11	12
T1												
T2												
T3									/	/	/	/
T4								/	/	/	/	/
T5											/	/
T6									/	/	/	/
T7										Canceled		
T8												
T9										/	/	/
T10										/	/	/
T11							/	/	/	/	/	/
T12								/	/	/	/	/
T13							/	/	/	/	/	/
T14								/	/	/	/	/
T15							/	/	/	/	/	/
T16						/	/	/	/	/	/	/
T17										/	/	/
T18												
T19												
T20												/
T21										/	/	/
T22												/
T23									/	/	/	/
T24							/	/	/	/	/	/
T25							/	/	/	/	/	/
T26							/	/	/	/	/	/

Corbie:

Trial	1	2	3	4	5	6	7	8	9	10	11	12
T1						sim	sim			/	/	/
T2									/	/	/	/
T3				sim	sim		/	/	/	/	/	/
T4		Gr cache				sim	sim					/
T5							/	/	/	/	/	/
T6	sim	sim					/	/	/	/	/	/
T7							/	/	/	/	/	/
T8	sim	sim					/	/	/	/	/	/
T9												/
T10						R cache	R cache		/	/	/	/
T11				sim	sim		/	/	/	/	/	/
T12								/	/	/	/	/
T13							/	/	/	/	/	/
T14		/	/	/	/	/	/	/	/	/	/	/
T15					Gr cache	Gr cache		sim	sim	/	/	/
T16						R cache		Gr cache	R cache	/	/	/
T17								/	/	/	/	/
T18	sim	sim					/	/	/	/	/	/
T19							/	/	/	/	/	/
T20										/	/	/
T21	sim	sim				sim	sim					/
T22									/	/	/	/
T23					Gr cache	Gr cache	R cache	/	/	/	/	/
T24												
T25												
T26					sim	sim			/	/	/	/
T27									/	/	/	/
T28							/	/	/	/	/	/
T29							/	/	/	/	/	/
T30									/	/	/	/
T31							/	/	/	/	/	/
T32							/	/	/	/	/	/
T33									/	/	/	/
T34												
T35									/	/	/	/
T36									/	/	/	/
T37							/	/	/	/	/	/
T38					sim	sim	/	/	/	/	/	/
T39							/	/	/	/	/	/
T40								/	/	/	/	/