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„Investigating Prosociality in Corvids – Performance in the Group Service Paradigm in Azure-Winged Magpies (*Cyanopica cyana)*"

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Introduction

Prosocial behavior is usually linked to altruism. However, while altruism is costly to the donor (de Waal 2008), prosociality is defined as "a behavior that benefits others at no or low cost to the actor" (Silk & House, 2011). This unique form of cooperation is commonly found in humans and emerges early in human ontogeny (Burkart et al. 2009). Burkart and colleagues (2014) consider prosociality to be one fundamental mechanism that allowed humans to develop complex cognition and the awareness of morality. They claim that the development of agglomerated cultures and sophisticated technology, as it exists in human civilization, stems fromthat kind of intensive cooperation. However, prosocial tendencies, which have long been considered to be human-specific, appear to exist also in non-human primates (Cronin 2012).

Various hypotheses were formulated to explain the origin of this feature, one of which claims that prosocial behavior arises in the line of primates and is shared by humans and anthropoid primate species (Melis et al. 2010). In support of this, long-tailed macaques (*Macaca fascicularis*) behaved prosocially towards kin in an experimental set up, while dominant individuals were reported to provide food also to non-kin (Massen et al. 2010). Likewise, capuchin monkeys (*Cebus apella*) were shown to prefer prosocial over selfish options in a choice task (de Waal, 2008, Lakshminarayaran & Santos, 2008), as did several other primate species: cottontop tamarins (*Saguinus oedipus*) (Cronin et al. 2010), bonobos (*Pan paniscus*) (Hare & Kwetuenda 2010) and orang-utans (*Pongo pygmaeus*) (Liebal et al. 2014). However, results of our closest relatives the chimpanzees (*Pan troglodytes*) are only partially in line with this hypothesis. While Warneken and colleges (2007) could show that chimpanzees assisted humans to access a desired object, other

studies with conspecifics revealed ambiguous results as soon as food came into play (Silk et al. 2005).

Another hypothesis argues that prosocial acts are more likely to happen between individuals with strong social bonds (Silk et al. 2005, Burkart 2009). The assumption is to find cooperation between strongly bonded dyads; also prosocial behavior could be stronger in such dyads (Burkart et al. 2014). Yet a study testing the preference to give either to a friend or to a non-friend in a triadic choice test could not prove that long-tail macaques acted according to their relationship quality (Massen et al. 2011). One other hypothesis claims that prosocial behavior is facilitated within groups of high social tolerance (Hare et al. 2012). In line with this, Burkart & van Schaik (2013) found social tolerance in primates to be weakly positively correlated with prosocial acts.

One well-known example for strong prosocial tendencies outside of humans was found in the common marmosets (*Callithrix jacchus*) (Burkart et al. 2007), which are cooperative breeders like humans (Burkart & van Schaik 2009). This led the authors to formulate the cooperative breeding hypothesis. It suggests cooperative breeding as a main selective pressure, which enhanced evolution of human cognition. Being such cooperative breeders humans developed not only the understanding of other individuals' situation but also the intention to affect their situation in a positive way (prosociality). This willingness to share did not only include food but also information. Hence prosociality was hypothesized to have paved the way for evolving traits like social learning and teaching, thus the development of cumulative cultures and language. The genuine concern for the welfare of others is defined as proactive prosociality (Burkart & van Schaik 2013). Contrary, when the recipient has to signal its need to the actor to elicit prosociality the authors talk about reactive prosociality. It is motivated by begging or as a response to signals of need of the recipient, while a proactively prosocial individual assists spontaneously without being solicited. Thus the cooperative breeding hypothesis predicts prosocial behavior to arise with the degree of allomaternal care (Burkart et al. 2007), which is the care for offspring provided by group members others than the genetic parents (Hrdy 2009). According to this hypothesis cooperatively breeding primate species, e.g. common marmosets and cottontop tamarins, should out-perform other primates and even our closest relatives the great apes in prosocial tasks (Burkart et al. 2014).

Existing studies are only partially agreeing with the cooperative breeding hypothesis. While common marmosets provide food to kin and non-kin in prosocial choice tasks (Burkart et al. 2007), other prosocial choice studies on cottontop tamarins were not in line with the cooperative breeding hypothesis (Cronin et al. 2009). Cottontop tamarins acted prosocially more often after their mate had provided food to them (reciprocity condition) than when it had not (Cronin et al. 2010).

Aiming to disentangle those seemingly contradictory findings, a comparative study by Cronin (2012) attributed many results to the influence of small contextual features of the different experimental settings. Parameters like the social relation between donor and recipient in the experimentally assigned dyads, their rank or the interest in the reward expressed by the recipient were pointed out to play a crucial role whether subjects behaved prosocially or not. Overall, she concludes that in most studies, prosociality is more commonly reported between closely related animals and from the dominant towards the subordinate individual. She also suggests that separation from the group and a highly cognitive setup influence individual performance negatively. Contrary to expectations, individuals react less prosocially when the recipient shows interest in the reward. Only when the recipient requests assistance from the donor directly than prosocial behavior will increase (Cronin 2012). However this was only found in chimpanzees (Yamamoto 2009a, Melis et al. 2010).

The strongest support for the cooperative breeding hypothesis comes from a large-scale study of Burkart et al. (2014). Different factors potentially influencing prosocial tendencies were looked at, including cognitive abilities (using brain size as a proxy), social tolerance, the need to coordinate behavior in the context of foraging, strong social bonds and allomaternal care. The authors tested twelve primate species and human children by using a standardized set up, the group service paradigm. In this paradigm one individual can provide food to group members while neither being separated from the group, nor being put into an artificial dyadic setting. They identified allomaternal care to be the main predictor of prosocial behavior. Further, social tolerance and pair bonding were weakly positively correlated with prosocial behavior, and brain size was negatively correlated. However a review of the current literature looking at cognitive abilities of cooperative breeders versus non-cooperative breeders finds no evidence to support the cooperative breeding hypothesis (Thornton & McAuliff, 2015). The main problem being brought up is the fact that supporting results come only from closely related primates (i.e. callitrichids), which are, according to the authors, all cooperative breeders and at the same time the only cooperatively breeding non-human primates. Their argument brings up the urgency to look for convergent evolution and to test species not closely related to humans.

A phylogentically distant taxon interesting for investigating socio-cognitive abilities are corvids. Corvids (Corvidae) are songbirds and the group contains a great variety of species, including ravens, crows, magpies and jays. Most corvids live monogamously, however their territoriality during breeding varies greatly between species (Clayton & Emery 2007). Corvids are known to behave cooperatively like recruiting conspecifics in the context of foraging (ravens: Bugnyar et al. 2001) or sharing food (rooks: Scheid et al.

2008). Their socio-ecological environment led to similar cognitive abilities as are known to exist in primates (Emery & Clayton 2004). Regarding their breeding system corvids are found from pair breeding to cooperatively breeding in varying degrees (Clayton & Emery 2007, Baglione et al. 2003). This makes them a suitable non-primate taxon for investigating prosocial concern. To date, studies looking at prosociality in corvids found contradicting results. Jackdaws (*Corvus monedula*) prefer prosocial over selfish choices, although only when this choice is solicited by the recipient's interest in the reward (Schwab et al. 2012). On the other hand, ravens (*Corvus corax*) were found to be indifferent to other regarding preferences in two studies (di Lascio et al. 2012, Massen et al. 2015). Those contrary results of two closely related species may originate from their different socio-ecological background: ravens are strongly territorial once they are adults and pair-bonded, whereas jackdaws breed in colonies, which means that they have to be socially tolerant towards group members (Massen et al. 2015). According to a previous study social tolerance is positively correlated to prosociality (Burkart et al. 2014). However both, ravens and jackdaws are non-cooperative breeders. This makes the cooperatively breeding azure-winged magpie *(Cyanopica cyana)* an interesting species for investigating prosocial behavior. It is a colonial and cooperatively breeding bird living in flocks of up to twenty individuals (Hosono 1989). An observation by Komeda et al. (1987) of three different groups of azure-winged magpies in central Japan revealed that helping by non-parent individuals was regular in this population. Helpers assisted the breeding pair at different stages including nest building, feeding the incubating mother and chicks and removing fecal sacks. The authors showed that birds helped as their first option in the year as well as when their own breeding failed (Komeda et al. 1987). Long-term observational studies of the closely related Iberian magpie (*Cyanopica cooki*), which was until recently believed to be a sub-species of the azure-winged magpie, mainly identified male birds – both adults and offspring from the previous season – as helpers (Valencia et al. 2003). Studies on both species indicate that helping behavior mostly occurred in years with harsh weather conditions (Komeda et al. 1987, Valencia et al. 2003). In addition, Hosono (1989) states that flocks of azure-winged magpies show high social tolerance. According to the species' social system I expected azure-winged magpies to outperform other non-cooperatively breeding species regarding their prosocial concern as well as their social tolerance.

But how can prosocial tendencies be tested in non-human animals? Commonly, prosociality is tested either by a choice task or by an out-of-reach task. In the prosocial choice task one individual (the donor) has the possibility to choose between a selfish option, where it acquires food only for itself, and a prosocial option, where it can additionally provide food to another individual (the recipient). The two individuals are

typically placed in two separate, adjacent compartments. Commonly, this task is tested by allowing the individual to pull one of two trays towards the cage. While, in most experiments, the amount of food slightly differs on each side of both trays, one always represents the prosocial and one the selfish choice. To date it has been tested in several primate species, i.e. chimpanzees (Silk et al. 2005, Jensen et al. 2006, Melis et al. 2010, Yamamoto & Tanaka 2009a, b, Yamamoto et al. 2012), cottontop tamarins (Cronin et al. 2009, 2010), common marmosets (Burkart et al. 2007), and rhesus macaques (Chang et al. 2011) The other way to conduct a prosocial choice task is by providing the individual with two boxes, a prosocial and a selfish box. Again baiting on each side of either box can differ between experiments. So far this has been done with jackdaws (Schwab et al. 2012) and ravens (di Lascio et al. 2012).

The out-of-reach task puts two individuals in a scenario where one (the recipient) needs an instrument to access food, but the instrument is only accessible to a second individual that has no possibility to use the instrument itself (the donor). The donor has the opportunity to hand over the instrument without being rewarded. This out-of-reach task is tested either with tools or with tokens (Cronin 2012). This out-of-reach paradigm has been used with primates including chimpanzees (Pelé et al. 2009, Vonk et al. 2008, Horner et al. 2011), capuchin monkeys (Westergaard et al. 2007, de Waal 2008), orang-utans (Pelé et al. 2009, Dufour et al. 2009) and ravens (Massen et al. 2015).

However, in both of these paradigms, the tested animals are separated from their group and are put in an artificial dyadic setting. To avoid these issues, Burkart and van Schaik (2013) developed the so-called group service paradigm. In this paradigm one individual can provide food to the whole group. The apparatus in a group service paradigm has two sides, a serving side, where food can be provided, but not received, and a receiving side. As soon as food is placed on the apparatus any individual has the possibility to make food available to the group or to receive it, if food has been provided by another group member. Animals can be tested in their home environment and are not separated from the group. Moreover, the mechanism is cognitively not demanding and to ensure that the individuals understand the mechanism they have to pass several learning steps. Further, by including both an empty control where no food is placed on the apparatus and a blocked control where access to the food is blocked, the set-up tests for a possible lack of inhibition control (i.e. whether animals cannot inhibit to use the apparatus as soon as food is placed there) and whether provisioning happens proactively or reactively in response to begging or signaling. True prosocial behavior is considered when high rates of using the apparatus are sustained over time (Burkart & van Schaik 2013). Food provisioning to group members due to lack of inhibition control can be ruled out when individuals show sustained rather than declining provisioning rates during the prosocial test. Social

facilitation can be excluded because group composition is not manipulated in a group service paradigm (Burkart & van Schaik 2013). Other potentially influencing factors as reputation seeking or expectation of reciprocity are cognitively more demanding traits (Stevens et al. 2005), and are unlikely to be responsible for prosocial behavior in most non-human animals (Burkart & van Schaik 2013). However the authors note that this set up does not provide individual data from all group members or from dyad specific constellations. Neither do lower ranking or slower individuals get the chance to provide or to receive food. Testing primates, Burkart & van Schaik (2013) used a board with a handle on one side. If pulled towards the mesh by a serving animal, group members could feed on the other side of the board.

Given these methodological advantages of the group service paradigm, I used it to test the prosocial behavior of the azure-winged magpie. I followed the experimental set up of Burkart and van Schaik (2013), but to meet the needs of a bird I adapted it in two ways. Firstly, instead of a sliding board I used the mechanism of a seesaw, which could be moved by a bird landing on a perch. Secondly I added one habituation phase in the very beginning of the procedure, since birds are known to be more neophobic than primates. The aim of the present study is to test a non-primate but cooperatively breeding species, azure-winged magpies, for their prosocial choices in a group-service paradigm. I expect azure-winged magpies to be highly socially tolerant, as it has been observed in wild living flocks of azure-winged magpies in central Japan (Komeda et al. 1987). According to the cooperative breeding hypothesis, I further hypothesize that azure-winged magpies provide food to group members, hence to act prosocially. If the intention of the bird is to provide food to conspecifics than it should land significantly more often on the serving perch during the prosocial test than during both control conditions (empty and blocked).

Picture: taken by the author

Figure 1: Azure-winged magpie (*Cyanopica cyana)*

Materials and Methods

Subjects

I tested a group of five azure-winged magpies (two females and three males) at the Haidlhof Research Station of the Department of Cognitive Biology (University of Vienna), located near Bad Vöslau, Lower Austria. The birds were tested in their social group in the home cage (ground: 275 x 285 cm, height: 320 cm). The age range at the beginning of the study in April 2015 was between ten and 33 months (*Tab. 1*). All birds were parent-raised in Blijdorp Zoo, Rotterdam, Netherlands and came to Haidlhof Research Station in November 2014.

Table 1: Names, ages, and sex of the five azure-winged magpie group members at Haidlhof research station

Bird	Abbreviation	Age in April 2015 (months)	Sex
Boots	BO	33	male
Yoda	YO	22	male
Obi-Wan Kenobi	OW	10.5	male
Mon Mothmal	MM	10.5	female
Padme	PD	10	female

Apparatus

I used a wooden apparatus with a seesaw mechanism. It consisted of a board on the outside of the home cage's wire mesh and two sticks reaching through the wire mesh into the cage on one side of the board. There was one perch fixed at the end of these two sticks ("serving perch"). On the other side of the board, but not connected to the apparatus' seesaw mechanism, there was a second perch ("attending perch"). The wire mesh was blocked with a clear plastic board to prevent birds from reaching food placed on the apparatus while sitting on the mesh. Like this they had to sit on one of the perches to reach the food (Fig. 2).

The apparatus' seesaw mechanism was balanced so that the serving perch on the inside pointed up and the board on the outside pointed down. When a bird landed on the serving perch, its weight moved the seesaw down. As soon as the bird left the perch, the apparatus automatically moved back to its original position.

There were two positions for putting food on the board: one in front of the serving perch (position 0) and the other in front of the attending perch (position 1), out of reach from the serving perch. A bird landing on the serving perch was able to move a piece of food into reach only if the food was placed in position 0. Food would slide in the channel towards

the wire mesh and would be stopped there by the barrier, where the bird could take it. If the bird left the serving perch, the food would slide back from the mesh out of the bird's reach. If food was placed in position 1, a bird sitting on the attending perch could only obtain food, if another bird moved the seesaw down and stayed on the serving perch long enough for the bird to take the food (*Fig. 2*).

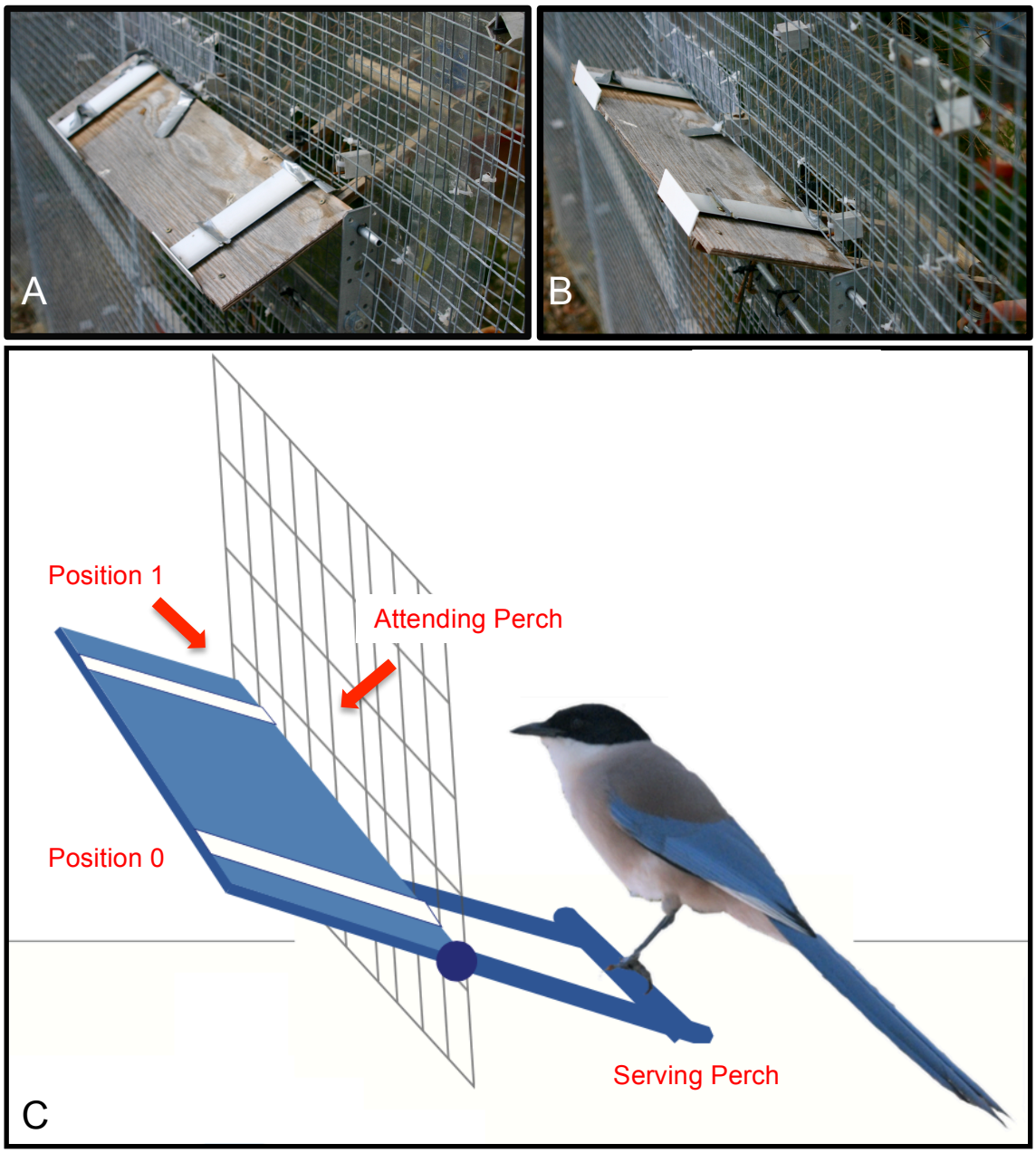

Figure 2: Group service apparatus (seesaw). A: Photo of the apparatus in original position. B: Photo of the apparatus during use. C: Schematic drawing of the apparatus, moved by a bird sitting on the serving perch.

Procedure

The experiment consisted of six consecutive phases. In each phase, all animals had to meet a specific criterion to complete the phase and proceed to the next one (see below).

I. Habituation to the apparatus

To habituate the birds to the apparatus and especially to landing on a moving perch, the apparatus was installed in the home cage in this phase. For one week the seesaw mechanism was not fixed and the apparatus moved freely, but it was not baited with food. After that a food bowl was mounted to the fence in front of the serving perch on the inside of the cage. For each session it was filled up with mealworms and the birds were video recorded for thirty minutes. From the videos I coded the order of birds landing on the apparatus and feeding from it. I considered the birds as being habituated, after each bird had landed on the serving perch and fed from the bowl at least five times.

II. Habituation to the procedure

The aim of phase II was both to train the birds to obtain food through the wire mesh and to habituate them to the procedure of the experimenter approaching the cage and leaving food on the apparatus. In order to better motivate the birds from this phase on I used a more preferred food reward (i.e. deeply frozen crickets). In this phase the apparatus was fixed in a downward position on the inside of the cage, so that a cricket placed on the board would automatically slide to the wire mesh and within the birds' reach. On alternating days crickets were placed either in position 0 or in position 1. Per trial one cricket was placed on the board and attention of the birds was attracted (i.e. calling their names and "look here"). After the birds ate the cricket or after a maximum of two minutes the next trial started and I put another cricket on the board. In this way if birds did not take the food, crickets accumulated on the board. A session ended after 25 trials or when the birds did not land on the apparatus for three consecutive trials. I continued this phase until each bird had obtained at least ten crickets on each perch on a minimum of five days. Birds, which already had fulfilled the criterion, were separated of the group during following sessions. However I started each session training all birds and separated those, who already had passed the criterion during later trials. The total number of one session was still 25 trials.

III. Social tolerance assessment

In phase III the apparatus was still fixed in a downward position on the inside of the cage. To estimate the social tolerance of the group I measured the evenness of distribution of food items. I put 25 crickets onto the apparatus in position 1, one at a time and attracted the birds' attention by calling their names and "look here". After the cricket was taken I immediately placed the next cricket onto the board. Thus if birds did not take the food,

crickets accumulated in the next trials. The session ended after 25 trials. I repeated this session on a second consecutive day.

IV. Apparatus Training

In phase IV the birds learned to move crickets closer to the wire mesh by landing on the serving perch. Food was always placed in front of the serving perch in position 0. To facilitate learning I started to place the crickets at a distance of only one centimeter from the wire mesh. The seesaw mechanism was loosened only partially, so that the serving perch would only move down for about one centimeter when a bird landed on it. In five steps the crickets were placed further away and the seesaw mechanism was loosened more. In the final step the apparatus was completely released and the crickets were placed at a distance of 18 cm from the wire mesh.

Per trial I placed one cricket on the board and called the birds' attention. After the cricket was taken I immediately put the next one in position 0. If no bird had taken the cricket after two minutes, the next trial started and I approached the apparatus, showed the cricket of the previous trial to the birds by picking it up again and calling the birds' attention. This was done because only a single cricket at a time could fit into the channel and slide towards the wire mesh properly. The session ended after 25 trials or when no bird landed on the serving perch for three consecutive trials. The criterion for this phase was reached when each bird had landed on the perch and obtained at least ten food items in the final training step on a minimum of five days. Again, if some birds were faster to reach criterion than others, those individuals were separated of the group during the second half of all following sessions.

V. Prosocial test

In the prosocial test I measured the birds' prosocial tendencies. In the test sessions of this phase the apparatus' seesaw mechanism was completely released, but the cricket was placed in position 1 instead of position 0. Therefore the bird landing on the serving perch was not able to obtain the food, but other birds were able to take the food when landing on the attending perch. To ensure that the animals were still interested in participating, I added one motivation trial with food in position 0 in the very beginning of the session and after every fifth regular trial. Therefore, each session consisted of 25 regular and 6 motivation trials. A trial ended when the cricket was taken or after two minutes had elapsed. If no bird took the cricket I showed the cricket from the previous trial to the birds by picking it up again and calling their attention. In case no bird took the cricket during a regular trial before a motivation trial, the cricket was placed from position 1 to position 0. If no bird landed on the serving perch during three consecutive motivation trials the session was terminated.

The empty control sessions of the prosocial test were identical to the test sessions, except that no food was placed in position 1. I approached the apparatus and pretended to leave a cricket on the board by slightly moving the seesaw and calling the birds' attention.
I ran five test sessions and five empty control sessions on alternating days.
For each trial, I recorded the number of times each bird landed on the serving perch, whether food was successfully provided to another individual and which bird provided and which obtained the food.

VI. Blocked control

In the blocked control I tested if the birds paid attention to whether they provided food to the others or not. The procedure was exactly the same as in the prosocial test (phase V), but I blocked the access to position 1 with a fine-meshed mosquito net. Therefore, despite putting a cricket on the apparatus, no food could be obtained in this position. Position 0 was not blocked, so that the birds could still obtain a cricket in the motivation trials. Again, I ran five regular sessions where I put a cricket in position 1 and five empty blocked control sessions on alternating days. The empty blocked control sessions of this phase were only done to follow the same procedure of the previous phase. It was not used for further calculations. The results of the two final blocked control sessions and the overall results were used to compare them with the results of the previous phase V (prosocial test).

Analysis

All sessions were video recorded with one or two cameras (*Canon LEGRIA HD-camcorder*). The birds' reaction was immediately noted on paper during the experiment and additionally recoded from the videos. Further behavior analyses of the individuals were coded from the videos (see below).
For the social tolerance assessment I used the percentage of food items taken as the dependent variable. Using Excel[2011], I calculated Pilou's evenness index: $J' = \frac{H'}{H'max}$. J' is the measure of the relative abundance of different groups, originally developed to quantify the biological diversity of species. It is expressed in a number between 0 and 1, indicating 0 as maximal inequality and 1 as a perfect equal distribution. H' derived from the Shannon diversity index and H'_{max} is the maximum value of H'. The Shannon diversity index quantifies the entropy in strings of text: $H' = -\sum_{i=1}^{R} pi \ln pi$ (Mulder et al. 2004). I further assessed the percentage of how many food items each bird received and the theoretical equal distribution of food items.
For the prosocial test I distinguished two types of data, data at group level and data at individual level. At group level, the dependent variables were the total number of landings on the serving perch. I conducted a Wilcoxon signed-rank test comparing prosocial test

sessions with empty control sessions and blocked control sessions. At individual level I compared in how many trials landings occurred or not per bird. The dependent variables were the number of trials, in which each bird landed on the serving perch. I used a Fischer's exact test to compare prosocial test sessions with empty control sessions and blocked control sessions for each bird.

Additionally, I coded the following behavior of each individual: First, agonistic behavior, i.e. displacements in position 1 after food deliveries happened. Second, signaling behavior, i.e. reaching attempts of the receiving bird (birds in position 1 reaching with its beak towards food placed on the board) since vocalizing, a more obvious sign for begging did not occur. Further I assessed how often birds landing first in position 1 followed by another bird providing food, which can be argued to be a mild form signaling.

For the main calculation I pooled the numbers of the last two sessions (session 4 and 5) of all conditions, because by than every bird had multiple opportunities to learn about the consequences of using the apparatus. Nevertheless the results of all sessions are shown below. All statistical analyses were performed in SPSS 23.0.

Results

Habituation to the apparatus and to the procedure (Phase I and II)

On average birds needed a median of 7 sessions (min: 1, max: 10 sessions) to reach criterion of phase I (habituation to the apparatus) and a median of 9 sessions (min: 6, max: 11) for the criterion of phase II (habituation to the procedure) (*Tab.: 2*).

Table 2: Number of sessions to reach the criterion of phase I (habituation to the apparatus) and phase II (habituation to the procedure phase) per bird.

Bird	Habituation to the Apparatus	Habituation to the Procedure
Boots	9	9
Yoda	1	6
Obi-Wan Kenobi	5	9
Mon Mothma	7	11
Padme	10	7

Social Tolerance Assessment (Phase III)

The assessment of the social tolerance showed a Pilou's *J'* of an average of 0.72 (STDV = 0.09; day 1 = 0.65; day 2 = 0.78). Two males of the group received 74% of all food items. Yoda 38% (19 crickets) and Obi-Wan Kenobi 36% (18 crickets). Mon Mothma got 20% (10 crickets), Boots 4% (2 crickets) and Padme 0 crickets. One cricket got lost. The theoretical perfect equal distribution were 20% per bird (10 crickets) (*Fig. 3*).

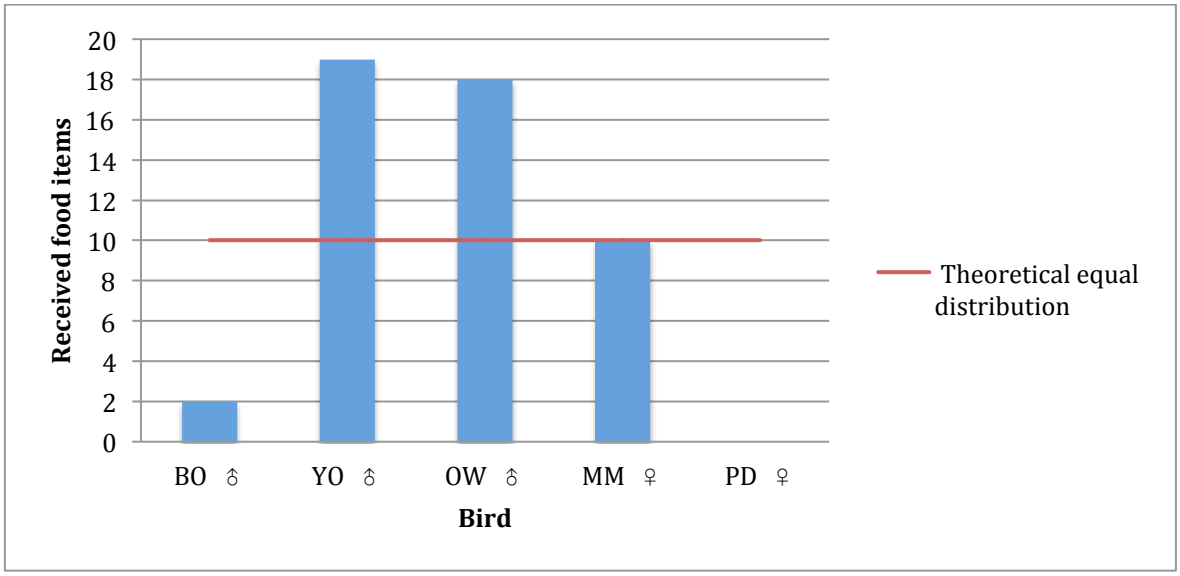

Figure 3: Received food items per bird. Red line shows the theoretical equal distribution of 5 crickets per bird

Apparatus Training (Phase IV)

It took the birds on average a median of 23 sessions (STDV 3.35) to reach the criterion of phase III (apparatus training): Boots: 24, Yoda: 22, Obi-Wan Kenobi: 22, Mon Mothma: 30 and Padme 23 sessions.

Prosocial Test (Phase V)

Successful food provisioning happened in 89.6% of all test trials, counting all sessions of the prosocial test (phase V). Considering only the last two sessions birds provided food in 98% of the trials successfully. When taking together all sessions, there was a non-significant trend that birds landed on the serving perch more often in test sessions than in empty control sessions ($Z = -1.753$, $p = .080$). However, there was no significant difference when considering only the last two test and empty control sessions ($Z = -1.461$, $p = .144$).

Looking at the performance of the individual birds over all sessions, two of them landed on the serving perch significantly more often during the test than during empty control sessions (Obi-Wan Kenobi and Mon Mothma), while two, Boots and Yoda showed no significant difference between test and empty control sessions. Padme showed a non-significant trend (see *Tab. 3*). When taking into account only the last two sessions Obi-Wan Kenobi, Yoda and Mon Mothma landed significantly more often during test sessions than during empty control sessions, Boots and Padme did not (*Tab. 4*).

Table 3: Number of successfully provided food items over all sessions. Total number of landings on the serving perch (all sessions) during the prosocial test and empty control per bird. Fischer's exact test: test vs. empty control sessions calculated over all sessions.

Birds	Successfully provided foods	Prosocial Test	Control Empty	Fischer's Exact Test	
				p	df
BO	0	2	3	1.0000	1
YO	1	24	18	.3979	1
OW	64	99	8	< .0001	1
MM	46	103	18	< .0001	1
PD	1	17	7	.0515	1
Total	112	145	54		

Table 4: Number of successfully provided food items over the last two sessions (session 4 and 5). Total number of landings on the serving perch (last two sessions) during the prosocial test and empty control per bird. Fischer's exact test: test vs. empty control sessions calculated over the last two sessions.

Birds	Successfully provided foods	Prosocial Test	Control Empty	Fischer's Exact Test	
				p	df
BO	0	0	1	1.0000	1
YO	1	9	0	.0026	1
OW	21	32	6	< .0001	1
MM	27	46	3	< .0001	1
PD	0	3	3	1.0000	1
Total	49	90	13		

The three individuals that landed on the serving perch more often during the prosocial test than during the empty control trials were responsible for 99.1% of the successful food provisioning counting all sessions and for 100% counting the last two sessions.
There was a strong bias in who provided and who received food considering all sessions and only the last two. Mainly two birds (i.e. Obi-Wan Kenobi, Mon Mothma) landed on the serving perch and thus provided food for the others. During the last two sessions 98 % of all successfully provided food items were done by Obi-Wan Kenobi (43%) and Mon Mothma (55%). Yoda (19%) and especially Boots (78%) received most of the provided crickets. Padme did not provide nor receive a single cricket (*Fig. 4).* A very similar result was found when looking at all sessions.

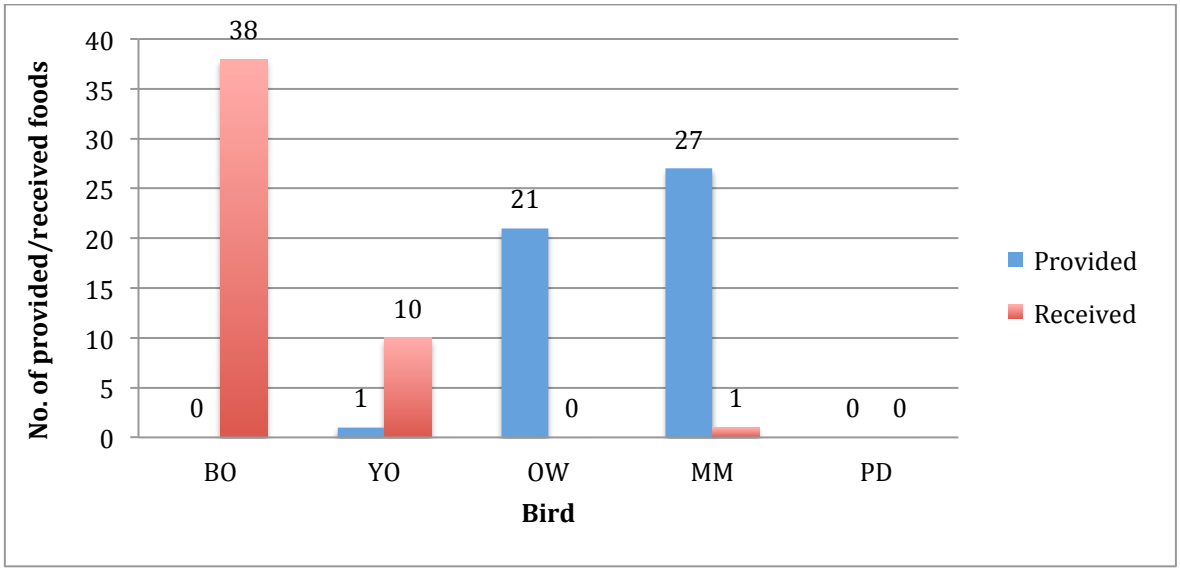

Figure 4: Number of successfully provided and received food items per bird. Numbers are pooled for the last two sessions (session 4 and 5).

Blocked Control (Phase VI)

Taking all sessions together, there was no significant difference between the birds' total number of landings on the serving perch during prosocial test than during the blocked control (Z = -1.461, p = .144). There was also no significant difference when considering only the last two sessions (Z = -1.604, p = .109).

When looking at the birds individually over all sessions, all but one bird landed on the serving perch significantly more often in the test sessions of the prosocial test than in the blocked control. (*see table 5*). Considering the last two sessions, only three birds landed significantly more often during the prosocial test than during the blocked control (Yoda, Obi-Wan Kenobi, Mon Mothma). (*Tab.: 6*).

Table 5: Number of landings on serving perch over all sessions during the prosocial test and blocked control per bird. Fischer's exact test: test vs. blocked control sessions calculated over all sessions.

Birds	Prosocial Test	Blocked Control	Fischer's Exact Test	
			p	df
BO	2	0	.4980	1
YO	24	1	< .0001	1
OW	99	44	< .0001	1
MM	103	25	< .0001	1
PD	17	6	.0268	1
Total	145	76		

Table 6: Number of landings on serving perch over the last two sessions (session 4 and 5) during the prosocial test and blocked control per bird. Fischer's exact test: test vs. blocked control sessions calculated over the last two sessions.

Birds	Prosocial Test	Blocked Control	Fischer's Exact Test	
			p	df
BO	0	0	1.0000	1
YO	9	0	.0026	1
OW	32	8	< .0001	1
MM	46	3	< .0001	1
PD	3	3	1.0000	1
Total	90	14		

I also examined how landing on the serving perch changed across the five test sessions. Again, I calculated per trial whether landings occurred or not. Landing on the serving perch occurred in 100% of the trials during the prosocial test from the first session on. The percentage of successfully provided food items increased from 76% in the first session to

up to 100% in later sessions. During the empty control the percentage of trials, in which a bird landed on the serving perch decreased from 48% in the first to 8% in the last session. Likewise during the blocked control the percentage decreased from 64% to 20% (*Fig. 6*).

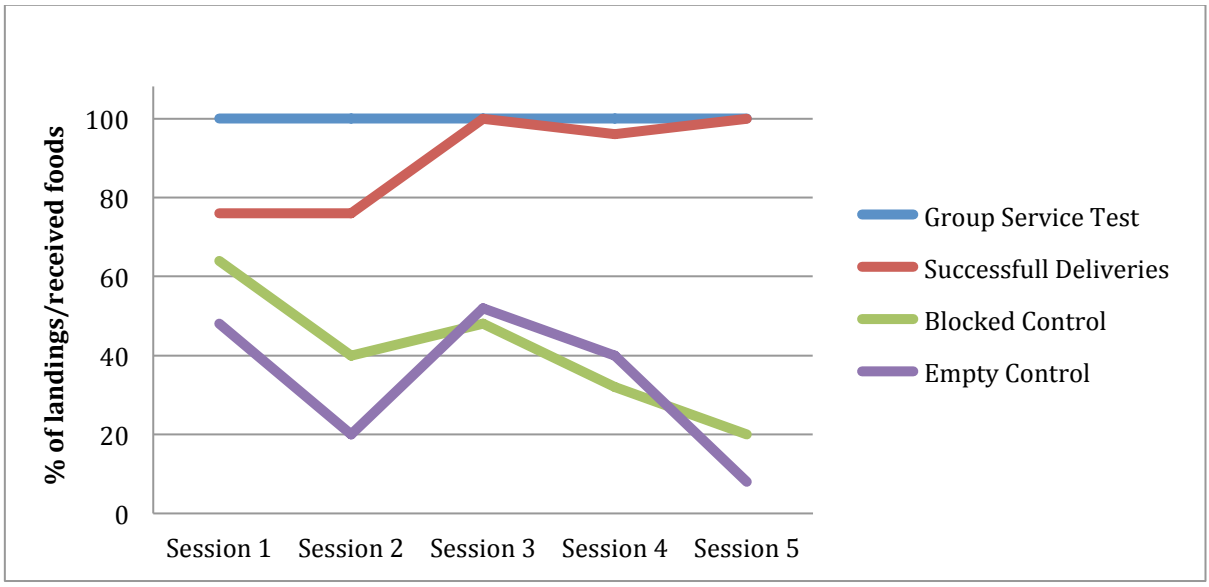

Figure 5: Percentage of landings on serving perch during the prosocial test, empty and blocked control over five sessions. Percentage of successfully provided food items per trial over all sessions.

Behavioral coding of each individual revealed only one displacement in position 1 during the prosocial test. Boots displaced Mon Mothma, nevertheless Mon Mothma still obtained the food item. No displacements were observed in any other condition. I observed nine reaching behaviors all during blocked control and none in other conditions. However at the moment of reaching there was never a bird in position 0. I could never observe any pattern of birds landing first in position 1 followed by a second bird providing food in any condition.

Discussion

Azure-winged magpies scored high in the social tolerance assessment. This verifies my first hypothesis, that social tolerance should be high in this cooperatively breeding species, as it was observed in wild living azure-winged magpies in central Japan (Komeda et al. 1987). During the last two sessions of the prosocial test 98% of all placed food items were successfully provided to group members. Although landings on the serving perch of all individuals taken together as a group did not differ significantly between the prosocial test sessions and both empty and blocked control sessions, three individual birds landed significantly more often during the prosocial test than during both the empty and the blocked control. This result can be strengthened by the fact that azure-winged magpies were found to land at a sustaining rate during the prosocial test, even though no food could be obtained by the donor. Landing during both control conditions on the other hand, when no food could be provided to group members, decreased over the five sessions. Given that the results at group level were not significant but landings during the prosocial test sustained and during both control conditions decreased, my second hypothesis could partly be verified.

As observed in wild living azure-winged magpies (Komeda et al.1987), the azure-winged magpies in my experiment had a high social tolerance score (Pilou's J': 0.72). This number is comparable with cooperatively breeding primates i.e. the common marmosets (Pilou's J': 0.74), as opposed to non-cooperatively breeding species like the Japanese macaques with a J' of only 0.32 (Burkart & van Schaik 2013). Two azure-winged magpies, Yoda and Obi-Wan Kenobi, who took most food items, were also the first to fulfill the criterion during the previous training phase (apparatus training). Padme who was already slow to approach the apparatus during early training phases (habituation to the apparatus, habituation to the procedure) was not able to receive any crickets on either day.
When looking at the results of the prosocial test, I only discuss the results of the last two sessions. By then every individual was considered to have learned that by landing on the serving perch food was only available to the group but not to oneself (see also Burkart & van Schaik 2013, Burkart et al 2014). As hypothesized, azure-winged magpies provided a high percentage of food items to group members successfully, similar to cooperatively breeding primate species (Burkart et al. 2014). Two birds, Boots and Padme, did not land significantly more often during test sessions than during empty control sessions. However, these two birds hardly landed at all during any condition. This did not influence the results of successfully provided food items since both did not participate in food provisioning.
The question whether the landings on the serving perch during the prosocial test occurred for prosocial reasons was examined in two separate control conditions: the empty control

and the blocked control. If birds only land on the apparatus due to exploration or play behavior, than landings should occur at the same frequency during the empty control, when no food was placed in position 1. However if landings decrease during the empty control than one possible explanation could be prosociality. Nevertheless there is still the possibility that birds landed due to a lack of inhibition control (Burkart & van Schaik 2013) since the birds were trained to be rewarded when food was placed on the board during previous training phases. The second control, when access to food in position 1 was blocked by a fine net controlled for this possibility. This enabled me to test whether the birds that landed on the serving perch during the prosocial test acted prosocially.
However, the not significant difference when comparing landings of all individuals at the group level could indicate the birds' lack of understanding of the consequences when landing on the apparatus. Despite numerous opportunities to learn they might still expect to receive the placed food item. Another explanation could be the possible chance of retrieving the cricket once brought into the aviary. If food was successfully provided, the serving bird had still the possibility to take it back from the bird, which first received it. On the other hand the not significant difference can also be ascribed to the small sample size of only five birds. Therefore looking at individual level gives a clearer result.
Three birds (Yoda, Mon Mothma, and Obi-Wan Kenobi) did act prosocially, as they landed significantly more often on the serving perch during the prosocial test than during both control conditions. Results from ongoing observations indicate that Yoda is high-ranking, while Mon Mothma has been observed to be the lowest-ranking bird and Obi-Wan Kenobi is in the middle of the group hierarchy (unpublished data). Given the fact that those three birds are not all high ranking individuals is not in line with the literature. As mostly reported the majority of transfers occur from the dominant towards the subdominant individuals (Cronin et al. 2012). Neither could these results support the observation in the wild that mainly male birds assist others during breeding (Valencia et al. 2003). The two main receiving birds were the oldest males of the group. While one of them, Yoda, was also one of the prosocial birds, Boots only received food items. Padme, who was neither providing nor receiving food, is in the middle of the group hierarchy (unpublished data). She was the last bird to reach criterion during most training phases. I therefore cannot exclude that Padme would have landed on the serving perch if the other birds would not have been quicker in each trial.
Over all conditions every but one motivation trials were taken by the three main providing birds, Yoda, Obi-Wan Kenobi and Mon Mothma. This indicates that birds were always interested in the reward and the decrease in later phase cannot be ascribed to a loss of motivation.

Particularly interesting is the development of landings on the serving perch over the five sessions. The tested azure-winged magpies showed a sustained rate of landings during the prosocial test. This means that individuals did not loose interest in participating, even though they learned that they could never reach the food themselves – this can be considered as true prosociality (Burkart & van Schaik 2013). The number of landings during both the empty and the blocked control decreased over time. This fact indicates that birds were no longer interested in the apparatus when they could not provide any food to others. The rate of successfully provided food items increased, most likely because birds got better coordinated where and when to approach position 1.

I observed only one displacement in position 1 by another individual than the serving bird. Displacements by the serving animal never occurred. An agonistic occasion could have happened when a serving individual, who previously provided food to the group, gets frustrated when others obtain the reward, which could be found in a providing macaque showing aggression towards the recipient during or immediately after pulling (Burkart & van Schaik 2013). The fact that this behavior occurred only once further supports the results that azure-winged magpies are very tolerant. Receiving birds did not perform any begging or signaling behavior, which could have resulted in food provisioning by another individual. The only reaching behavior observed happened when no other bird was near position 0 nor was it followed by another bird landing in position 0. There was never any pattern observed of one bird landing first in position 1 followed by a second bird landing in position 0 to provide food to the first one, as it could be argued to enhance food provisioning as well. Signaling towards the actor was found to enhance prosocial behavior in jackdaws (Schwab et al. 2012). In contrast, food provisioning in my study can be considered as proactive prosociality rather than reactive prosociality (see Burkart & van Schaik 2013), since food provisioning occurred independently from reaching for the food.

Burkart and van Schaik (2013) identified several possible underlying mechanisms other than prosocial behavior when individuals provide food to group members during the prosocial test. One of which, lack of understanding of the mechanism, is unlikely because all birds passed the training criterion in each of the phases and showed sustained rather than declining provisioning rates during the prosocial test while rates declined during both control phases. Other potentially influencing factors, such as reputation seeking or expectation of reciprocity are cognitively more demanding traits (Stevens et al. 2005) and are not known to exist in azure-winged magpies.

The major advantage of the group service paradigm, namely being able to test subjects within their group, happens to be also its main limitation. In this setup, lower ranking or slower individuals do not get the chance to provide or to receive food. Thus the group service paradigm could neither provide individual data from all group members nor from

dyad specific constellations (Burkart & van Schaik 2013), which have often been proposed to influence the prosocial behavior of species (de Waal 2008, Stevens 2010).
This experiment could show that some azure-winged magpies have the potential to behave prosocially without being solicited. Thereby, they are the first corvids species in which proactive prosociality could be documented in an experimental set up. To test the cooperative breeding hypothesis however many different species with varying breeding systems need to be compared. Contrary to the current results of azure-winged magpies, ravens tested in dyads were shown to be indifferent to other regarding preferences (di Lascio et al. 2012, Massen et al. 2015). However jackdaws were found to be prosocially if solicited by the recipient showing interest in the reward. Those results may originate from their different socio-ecological background: jackdaws breed in colonies, which means that they have to be socially tolerant towards group members, whereas ravens are strongly territorial once they are adult and pair-bonded (Massen et al. 2015). This needs further investigation on whether prosociality increases along with extending degree of cooperative breeding or whether other socio-ecological traits, as intraspecific tolerance and pair bonding further enhance this kind of intensive cooperation.
The results of this study strengthen the argument that corvids are an interesting non-primate taxon for investigating the prosocial concern and show that apart from the existence of prosocial tendencies in non-human primates and in humans, they may also exists in some birds.

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Abstract

Prosociality, a behavior that benefits others at no or low cost to the actor, is usually linked to altruism, which is defined as being costly to the donor. Prosociality has for a long time believed to be human specific, but was recently found in other non-human primates. However, contradicting results in many primate species led to a variety of hypothesis about the origins of prosociality. In this thesis, I focus on the cooperative breeding hypothesis, which states that prosociality is dependent on allomaternal care. A comparative study of several primate species supported this hypothesis, showing that those species with allomaternal care were also the most prosocial. However, it remains unclear whether these results can be applied to other taxa, since it was only tested in primates. Corvids species form strong social bonds and are cooperative breeders to varying degrees, which makes them an interesting non-primate taxon for further investigation of the cooperative breeding hypothesis. The aim of this thesis was to investigate the prosocial behavior of the azure-winged magpie (*Cyanopica cyana*), a colonial and cooperatively breeding corvid with a complex helper system. I used the group service paradigm, where any bird can provide food to the group by using an apparatus. As expected according to the cooperative breeding hypothesis, the azure-winged magpies provided 98% of all food items to the group. Three of the five tested birds used the apparatus significantly more often during test sessions, where they could deliver food to the group members, than during an empty control, where no food was placed on the apparatus, and during a blocked control, where access to food for group members was blocked. On group level, the difference was not significant. This experiment shows prosocial behavior on the individual level in a cooperatively breeding species from a non-primate taxon. Furthermore, the results are the first indication of unsolicited prosociality in corvids.

Zusammenfassung

Prosozialität ist ein Verhalten, das zu Gunsten anderer ausgeübt wird. Der einzige Unterschied zu Altruismus mit dem es oft assoziiert wird, ist, dass prosoziales Verhalten mit keinem oder nur geringem Aufwand für das handelnde Individuum verbunden ist. Lange Zeit wurde prosoziales Verhalten ausschließlich Menschen zugeordnet, doch Studien der letzten Jahre beweisen, dass sich auch Primaten unter bestimmten Umständen prosozial verhalten. Seither wurden viele Hypothesen zum Ursprung dieser besonderen Art der Kooperation aufgestellt. Ein Konzept, auf das ich näher in meiner Arbeit eingehe, besagt, dass sich prosoziales Verhalten besonders stark bei jenen Arten entwickelt hat, die sich kooperativ um ihren Nachwuchs kümmern. Diese Hypothese, die “Cooperative Breeding Hypothesis”, wurde bisher vor allem von einer großen Studie mit Primaten und Menschen belegt. Ob die Resultate auch auf andere Tiergruppen zutreffen, ist unklar, da nur Primaten getestet wurden. Auch unter den Rabenvögeln gibt es kooperative Brüter und viele Arten leben in engen sozialen Gemeinschaften. Neben diesen Eigenschaften machen ihre kognitiven Fähigkeiten sie zu interessanten Kandidaten für die „Cooperative Breeding Hypothesis“. Das Ziel meiner Arbeit ist es daher, die Diskussion über den Ursprung prosozialen Verhaltens auf die Gruppe der Vögel auszuweiten und die „Cooperative Breeding Hypothesis“ an Blauelstern (*Cyanopica cyana*) zu testen. Blauelstern leben in großen sozialen Gruppen und werden während der Brutsaison von Helfer-Vögeln unterstützt.

Das prosoziale Verhalten der Blauelstern untersuchte ich in einem „Group-Service Paradigm“. Hier kann ein Vogel durch Aktivieren eines Apparats der ganzen Gruppe ein Futterstück in Reichweite bringen, ohne selbst eines zu bekommen. Jedes andere Tier aus der Gruppe hat die Möglichkeit, sich dieses Futterstück zu holen. Passend zur „Cooperative Breeding Hypothesis“ verhielten sich drei von fünf getesteten Blauelstern prosozial gegenüber ihrer Gruppe. Sie nützten den Apparat signifikant öfter während des prosozialen Tests als während beider Kontrollen, wenn entweder kein Futter auf den Apparat gelegt wurde, oder der Zugang zum Futter blockiert war. Diese Studie ist der erste Hinweis auf unaufgefordertes prosoziales Verhalten bei Rabenvögeln.

Figure Index

References

Baglione, V., Canestrari, D., Marcos, M., & Ekman, J. (2003). Kin Selection in Cooperative Alliances of Carrion Crows. *Science*, *300*, 1947–1949.

Bugnyar, T., Kijne, M., & Kotrschal, K. (2001). Food calling in ravens : are yells referential signals ? *Animal Behaviour*, *61*, 949–958. http://doi.org/10.1006/anbe.2000.1668

Burkart, J. M., Hrdy, S. B., & Van Schaik, C. P. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, *18*(5), 175–186. http://doi.org/10.1002/evan.20222

Burkart, J. M., Fehr, E., Efferson, C., & Schaik, C. P. Van. (2007). Other-regarding preferences in a non-human primate : Common marmosets provision food altruistically. *PNAS*, *104*(50), 19762–19766.

Burkart, J. M., & van Schaik, C. (2013). Group service in macaques (Macaca fuscata), capuchins (Cebus apella) and marmosets (Callithrix jacchus): a comparative approach to identifying proactive prosocial motivations. *Journal of Comparative Psychology*, *127*(2), 212–25. http://doi.org/10.1037/a0026392

Burkart, J. M., & van Schaik, C. P. (2009). Cognitive consequences of cooperative breeding in primates? *Animal Cognition*, *13*(1), 1–19. http://doi.org/10.1007/s10071-009-0263-7

Burkart, M. J., Allon, O., Amici, F., Finkenwirth, C., Heschl, A., Huber, J., … Schaik, C. P. Van. (2014). The evolutionary origin of human hyper-cooperation. *Nature Communication*, *5*, 1–9. http://doi.org/10.1038/ncomms5747

Chang, S. W. C. (2011). Vicarious reinforcement in rhesus macaques (Macaca mulatta). *Frontiers in Neuroscience*, *5*(March), 1–10. http://doi.org/10.3389/fnins.2011.00027

Clayton, N. S., & Emery, N. J. (2007). The social life of corvids. *Current Biology*, *17*(16), 652–656.

Cronin, K. A. (2012). Prosocial behaviour in animals : the in fl uence of social relationships , communication and rewards. *Animal Behaviour*, *84*(5), 1085–1093. http://doi.org/10.1016/j.anbehav.2012.08.009

Cronin, K. A., Schroeder, K. K. E., Rothwell, E. S., Silk, J. B., & Snowdon, C. T. (2009). Cooperatively Breeding Cottontop Tamarins (Saguinus oedipus) Do Not Donate Rewards to Their Long-Term Mates. *Journal of Comparative Psychology*, *123*(3), 231–241. http://doi.org/10.1037/a0015094

Cronin, K. a, Schroeder, K. K. E., & Snowdon, C. T. (2010). Prosocial behaviour emerges independent of reciprocity in cottontop tamarins. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1701), 3845–51. http://doi.org/10.1098/rspb.2010.0879

Di Lascio, F., Nyffeler, F., Bshary, R., & Bugnyar, T. (2012). Ravens (Corvus corax) are indifferent to the gains of conspecific recipients or human partners in experimental tasks. *Animal Cognition*, *16*(1), 35–43. http://doi.org/10.1007/s10071-012-0548-0

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), 172–5. http://doi.org/10.1098/rsbl.2008.0644

Emery, N. J., & Clayton, N. S. (2004). The mentality of crows. Convergent evolution of intelligence in corvids and apes.pdf.

Hare, B., & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology*, *20*(5), 230–231. http://doi.org/10.1016/j.cub.2009.12.038

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis : evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), 573–585. http://doi.org/10.1016/j.anbehav.2011.12.007

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. M. (2011). Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(33), 13847–13851. http://doi.org/10.1073/pnas.1111088108

Hosono, T. (1989). Characteristic Features of Group Living Life of the Azure-winged Magpie Cyanopica cyana.

Hrdy, S. B. (2009). Mothers and Others: The Evolutionary Origins of Mutual Understanding. Cambridge,MA:Harvard University Press.

Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *273*(January), 1013–1021. http://doi.org/10.1098/rspb.2005.3417

Komeda, S., Yamagishi, S., & Fujioka, M. (1987). COOPERATIVE BREEDING IN AZURE-WINGED MAGPIES , CYANOPICA CYANA , LIVING IN A REGION OF HEAVY SNOWFALL '. *The Condor*, *89*(4), 835–841.

Lakchminarayanan, V. R., & Santos, L. R. (2008). Capuchin monkeys are sensitive to others' welfare. *Current Biology*, *18*, 999–1000.

Liebal, K., Vais, A., Haun, D., & Tomasello, M. (2014). Does sympathy motivate prosocial behaviour in great apes? *PLoS ONE*, *9*(1). http://doi.org/10.1371/journal.pone.0084299

Massen, J. J. M., Lambert, M., Schiestl, M., & Bugnyar, T. (2015). Subadult ravens generally don ' t transfer valuable tokens to conspecifics when there is nothing to gain for themselves, *6*(June), 1–10. http://doi.org/10.3389/fpsyg.2015.00885

Massen, J. J. M., Luyten, I. J. A. F., Spruijt, B. M., & Sterck, E. H. M. (2011). Benefiting friends or dominants: Prosocial choices mainly depend on rank position in long-tailed macaques (Macaca fascicularis). *Primates*, *52*(3), 237–247. http://doi.org/10.1007/s10329-011-0244-8

Massen, J. J. M., van den Berg, L. M., Spruijt, B. M., & Sterck, E. H. M. (2010). Generous leaders and selfish underdogs: Pro-sociality in despotic macaques. *PLoS ONE*, *5*(3), 1–5. http://doi.org/10.1371/journal.pone.0009734

Melis, A. P., Warneken, F., Schneider, A., Jensen, K., Call, J., & Tomasello, M. (2010). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society B*, *278*(October 2010), 1405–1413. http://doi.org/10.1098/rspb.2010.1735

Mulder, C. P. H., Bazeley-White, E., Dimitrakopoulos, P. G., Hector, A., Scherer-Lorenzen, M., & Schmid, B. (2004). Species evenness and productivity in experimental plant communities. *Oikos*, *107*(1), 50–63. http://doi.org/10.1111/j.0030-1299.2004.13110.x

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. http://doi.org/10.1037/a0017253

Scheid, C., Schmidt, J., & Noe, R. (2008). Distinct patterns of food offering and co-feeding in rooks. *Animal Behaviour, ELSEVIER*, *76*, 1701–1707. http://doi.org/10.1016/j.anbehav.2008.07.023

Schwab, C., Swoboda, R., Kotrschal, K., & Bugnyar, T. (2012). Recipients Affect Prosocial and Altruistic Choices in Jackdaws , Corvus monedula. *Plos One*, *7*(4), 1–8. http://doi.org/10.1371/journal.pone.0034922

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., … Schapiro, S. J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature Letters*, *437*, 1357–1359. http://doi.org/10.1038/nature04243

Silk, J. B., & House, B. R. (2011). Evolutionary foundations of human prosocial sentiments. *Proceedings of the National Academy of Sciences of the United States of America*, *108 Suppl* , 10910–10917. http://doi.org/10.1073/pnas.1100305108

Stevens, J. V. R. (2010). Donor payo V s and other-regarding preferences in cotton-top tamarins (Saguinus oedipus). *Animal Cognition*, *13*, 663–670. http://doi.org/10.1007/s10071-010-0309-x

Stevens, J. R., Cushman, F. a., & Hauser, M. D. (2005). Evolving the Psychological Mechanisms for Cooperation. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 499–518. http://doi.org/10.1146/annurev.ecolsys.36.113004.083814

Thornton, A., & Mcauliffe, K. (2015). Cognitive consequences of cooperative breeding ? A critical appraisal, *295*, 12–22. http://doi.org/10.1111/jzo.12198

Valencia, J., Cruz, C. De, & Gonza, B. (2003). Flexible Helping Behaviour in the Azure-Winged Magpie. *Ecology*, *109*, 545–558.

Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., … Povinelli, D. J. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour*, *75*(5), 1757–1770. http://doi.org/10.1016/j.anbehav.2007.09.036

Waal, F. B. M. De. (2008). Putting the Altruism Back into Altruism : The Evolution of Empathy. http://doi.org/10.1146/annurev.psych.59.103006.093625

Warneken, F., Hare, B., Melis, A. P., Hanus, D., & Tomasello, M. (2007). Spontaneous Altruism by Chimpanzees and Young Children. *Plos Biology*, *5*(7), 1414–1420. http://doi.org/10.1371/journal.pbio.0050184

Westergaard, G. C., Avery, T., & Sue, E. (2007). Token mediated tool exchange between tufted capuchin monkeys (Cebus apella), 407–414. http://doi.org/10.1007/s10071-007-0072-9

Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees ' fl exible targeted helping based on an understanding of conspeci fi cs ' goals. *Proceedings of the National Academy of Sciences*. http://doi.org/10.1073/pnas.1108517109/-/DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1108517109

Yamamoto, S., & Tanaka, M. (2009),a. How did altruism and reciprocity evolve in humans?: Perspectives from experiments on chimpanzees (*Pan troglodytes*). *Interaction Studies*, *10*(2), 150–182. http://doi.org/10.1075/is.10.2.04yam

Yamamoto, S., & Tanaka, M. (2009),b. Do chimpanzees (Pan troglodytes) spontaneously take turns in a reciprocal cooperation task? *Journal of Comparative Psychology*, *123*(3), 242–249. http://doi.org/10.1037/a0015838