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„Social tolerance and prosocial tendencies in rooks (*Corvus frugilegus*)"

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Social tolerance and prosocial tendencies in rooks (*Corvus frugilegus*)

Abstract

Other-regarding preferences constitute an essential characteristic of human cooperation and have recently also been found to be present in some primate and corvid species. But conducted studies reveal ambiguous results, which led to intense scientific discussions and the formulation of various hypotheses about the impact of socio-ecological differences and other proximate mechanisms on the evolution of enhanced prosocial tendencies in humans and non-human species. The present study examined the level of intraspecific social tolerance and the existence of prosocial tendencies in rooks (*Corvus frugilegus*), a communally breeding corvid species, by applying the group service paradigm. Potential underlying motivations, like an influence of social relationships as well as dominance hierarchies on prosocial behaviour have further been analysed. Results of this study demonstrate, that rooks show very high levels of social tolerance. But results of the prosocial test do not allow to draw conclusions of an existence of proactive prosociality on species level since only three individuals participated in the test. However, some instances of prosocial behaviour were observed in test sessions of the group service paradigm. Five out of 8 successfully delivered food pieces during the last two test sessions of the prosocial test were delivered proactively, without any individual waiting in the receiver's position or showing any begging behaviour or signs of need and importantly, without the presence of any aggressive behaviours. It remains unclear, if more individuals would have reached the criterion during habituation and training phases, whether they would have provided more food and hence would have shown more prosocial behaviour in this experimental context. Individual's inexperience to experimental testing and amputated wings (a consequences of injuries) are being discussed to be an important influencing factors on individuals' performance during the experiment and thus need to be taken into consideration. The findings of the present study highlight that rooks are a promising candidate to show proactive prosocial behaviour, but more individuals need to be tested to be able to draw clearer conclusions on the presence of other-regarding preferences in rooks.

Keywords
prosociality, social tolerance, group service paradigm, rooks, *corvus frugilegus*, relationship quality, dominance hierarchy

Introduction

The evolution of altruism and prosociality has been an intensely discussed topic in science in recent years since this trait constitutes a fundamental feature of human cooperation, social organization and cognition (Burkart et al. 2014; Tomasello et al. 2005). Prosocial behaviour is also discussed to have played a crucial role in the evolution of human's complex technology and culture (Fehr & Fischbacher 2003).

Prosocial behaviour is functionally defined as "behaviour that benefits others at no or low cost to the actor" (Silk & House 2011) and is closely linked to altruism. According to Marshall-Pescini et al. (2016), cooperation implies a synchronized action of at least two individuals, whereas in altruism and prosociality only the actor performs a behaviour that results in a benefit for other individuals. Altruism and prosociality are typically distinguished by a minor, but important difference: while altruism implies an immediate cost to the actor, prosociality does not necessarily do. It is further important to distinguish between proactive and reactive prosocial behaviour. Proactive prosociality presents a spontaneous motivation, reflecting a concern for the welfare of others without being solicited (Burkart & van Schaik 2013). In contrast, in reactive prosociality the actor is motivated to assist, e.g. in response to signs of need or by direct solicitation by another group member.

Scientific studies regarding prosocial behaviour have mainly focused on the motivational mechanisms underlying other-regarding preferences in humans and other primates while only little is known about non-primate species. Especially studies on other animal orders are still very scarce.

The first experimental evidence on other-regarding preferences (Silk et al. 2005) in non-human animals was described by Burkart and colleagues (2007) in cooperatively breeding common marmosets (*Callithrix jacchus*), members of the callitrichid family. However, looking on primates in general, studies on prosocial concern yield ambiguous results. Chimpanzees (*Pan troglodytes*) for instance, known to exhibit a variety of cooperative behaviours in the wild like cooperative hunting, coalition formation and food sharing (Silk et al. 2005), did not show prosocial preferences in a variety of controlled laboratory experiments (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008). Even at no cost to themselves, chimpanzees behaved indifferent to payoffs for their conspecifics and consequently failed to donate food to familiar group members (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008). Contrary, in another study where chimpanzees could choose between a "selfish" and a "prosocial" token, subjects chose the prosocial option significantly more often (Horner et al. 2011). Prosocial food deliveries in this context were particularly more pronounced when partners tried to reach for the reward. Similarly to investigations on chimpanzees, studies on prosocial tendencies in cotton-top tamarins (*Saguinus oedipus*) show mixed results as well (Cronin et al. 2010; Cronin et al. 2009). In one study, cotton-top tamarins did not demonstrate other-regarding preferences, even when tested with their pair-bonded mates (Cronin et al. 2009). In another study, prosocial

tendencies emerged, but only after individuals had ample opportunities to experience the outcome of their actions (Cronin et al. 2010). Also in brown capuchin monkeys (*Cebus apella*: Lakshminarayanan & Santos 2008; Takimoto et al. 2010; Burkart & van Schaik 2013; Waal et al. 2008) and long-tailed macaques (*Macaca fascicularis*: Massen et al. 2010; Burkart & van Schaik 2013) results of different studies do not lead to a clear and explicit picture. Burkart and van Schaik (2013) found that in both capuchin monkeys and macaques the frequency of prosocial food deliveries was very low and decreased over time. Contrary, Lakshminarayanan and Santos (2008) found capuchin monkeys to provide food at higher rates and remarkably, results revealed that subjects chose the prosocial option more often if their partner could receive food of higher quality compared to their own. Takimoto and colleagues (2010) found that capuchin monkeys acted prosocially only towards subordniate recipients, but not towards dominant partners. In another study, capuchin monkeys provided food prosocially only to familiar partners and if the food reward was of equal value (de Waal et al. 2008). Similarly, macaques showed more prosocial tendencies towards kin than towards non-kin individuals, but dominant subjects also provided food to non-kin partners (Massen et al. 2010).

These above-mentioned differences in the presence of other-regarding preferences within and between species led to the formulation of various hypotheses, trying to explain the emergence of prosocial behaviour and aiming to interpret those seemingly equivocal results in different primate species.

One hypothesis claims that prosocial behaviour is cognitively demanding and consequently dependent on advanced cognitive abilities (Silk et al. 2005). One example of these cognitive abilities is for instance inhibitory control, since in many tasks on prosociality the actor has to forego its own desire for a certain reward, mostly a piece of favoured food (Burkart et al. 2014). Behavioural flexibility and the existence of fission-fusion dynamics in species' social organization have been shown to be positively associated to inhibitory control (Amici et al. 2008) and thus might also play an important role in the drive of other-regarding preferences.

A second hypothesis argues that prosocial behaviour may be facilitated by intraspecific social tolerance (Hare et al. 2012). Social tolerance, which is "a low probability of attack when two individuals are in close proximity in a particular context" (Burkart & van Schaik 2013) is very likely a necessary feature since prosocial actions usually require individuals to tolerate each other in close proximity.

A third hypothesis states that other-regarding actions may occur most likely between and may be most prevalent among individuals with strong social bonds (Burkart et al. 2009; Burkart et al. 2014; Silk et al. 2005; Preston & de Waal 2002). Strong social bonds are typically characterized by frequent proximity and affiliation as well as low incidences of aggressive behaviours (Silk et al. 2006).

A fourth hypothesis was formulated by Burkart and colleagues (2014). The authors found in their comparative study on 15 primate species the extent of allomaternal care as being the best predictor of the distribution of prosocial behaviour among primates, which led the

authors to support the cooperative breeding hypothesis, originally formulated by Hrdy (2005). Cooperative breeding, "a breeding system in which group members other than the genetic parents (alloparents), help one or both parents rear their offspring" (Hrdy 2005), is argued to have played a crucial role in the survival of human children during the Pleistocene (Hrdy 2005) and is being hypothesized to have led to human's extensive cooperation (Burkart et al. 2014). According to the cooperative breeding hypothesis, cooperatively breeding primates, like e.g. common marmosets and cotton-top tamarins, should outperform other primate species, including great apes, in experimental tasks on proactive prosociality.

Still, most data of studies discussing the above-mentioned hypotheses and trying to explain the evolutionary origins of other-regarding preferences derive from research on humans and non-human primates. Recently, there has been an intent to test for prosocial tendencies and other-regarding preferences in birds, focusing primarily on corvids. This line of research is particularly interesting because regarding their cognitive abilities corvids are comparable to primates (Güntürkün & Bugnyar 2016; Emery & Clayton 2004; Emery 2006). Corvids are also known to exhibit a range of cooperative behaviours like food sharing (Scheid et al. 2008), recruiting conspecifics in the context of foraging (Bugnyar et al. 2001), providing agonistic support during conflicts (Fraser & Bugnyar 2012) and exhibiting postconflict consolation (Fraser & Bugnyar 2010). Furthermore, corvids show similar or even greater forebrain neuron counts to those of many primate species with larger brain sizes (Olkowicz et al. 2016), additionally indicating corvids high potentials for socio-cognitive abilities.

In one of the first studies on prosociality in corvids, azure-winged magpies (*Cyanopica cyana*) delivered food items to their group members at high rates without being solicited (Horn et al. 2016). Previously, it has also been shown by Schwab et al. (2012) that jackdaws (*Corvus monedula*) show other-regarding preferences, but only if the recipient's behaviour indicated interest in the reward. The reward, a piece of food, had to be pulled into reach by an actor and thus was not accessible to the recipient without the actor's prosocial action. In comparison, no prosocial tendencies have been found in non-breeding ravens (*Corvus corax*) (Massen et al. 2015; Di Lascio et al. 2013; Lambert et al. 2017). These divergent results between closely related corvid species may also highlight the crucial role of socio-ecological differences, like e.g. differences in their social system, especially their breeding system. Azure-winged magpies are cooperative breeders, where several individuals, even non-relatives, contribute to the care of offspring. During the breeding season they form small, loose colonies, usually with a single nest located on each tree. Jackdaws in contrast breed in larger colonies usually with several nests located on one tree, resulting in a higher inter-individual spatial proximity. Ravens are territorial breeders, where the breeding pair monopolizes its own territory. Breeding cooperatively or in close proximity to other conspecifics, as it is the case in colonial breeders, requires higher levels of intraspecific social tolerance compared to territorial breeders. These socio-ecological differences might have led to the evolution of enhanced prosocial tendencies, as proposed by the cooperative

breeding hypothesis (Burkart & van Schaik 2013).
Rooks (*Corvus frugilegus*), the study species of the present investigation, are members of the corvid family (*Corvidae*) and thus closely related to ravens, crows, jackdaws, jays and magpies. Rooks are generally known to form complex social relationships and long-term alliances with other individuals (Emery et al. 2007). Usually, rooks form life-long monogamous pair bonds (Emery et al. 2007), but they are also described to switch partners and to establish valuable pair bonds with different individuals during their life (Boucherie et al. 2018). Members of a partnership frequently engage in behaviours requiring high levels of social tolerance, including affiliative behaviours, food sharing, supporting each other in agonistic encounters and showing post-conflict affiliation (Seed et al. 2007; Seed et al. 2008). Rooks are also reported to frequently share food with conspecifics, independently of kinship (Emery et al. 2007). Rooks are communal breeders and nest in large colonies of tens to hundreds of birds. They also roost and forage in large flocks, usually in close proximity to numerous other individuals. In the wild, rooks have been observed to jointly participate in cooperative behaviours like communally defending rookeries against unaffiliated individuals (Coombs 1961). In a study conducted by Seed and colleagues (2008) this species has further been shown to be capable of solving a cooperative string-pulling task without any training and that the performance in the task was depending on tolerance levels within tested dyads with better results in dyads with high inter-individuals tolerance. Another study applying the loose string paradigm in rooks is discussing the influence of individuals' boldness on the dyadic performance in the cooperative task (Scheid & Noë 2010) with bolder individuals being more disposed to participate in the experiment and shyer subjects being more influenced by their partner's behaviour.
All these above-mentioned behaviours require high amounts of intraspecific social tolerance, making rooks an ideal species to examine the occurrence of prosocial tendencies in these communally breeding birds.

Using a comparative approach by testing closely related species that differ in their socio-ecological adaptations and distantly related species with convergent socio-ecological specifications and social systems, might be the best way to enhance our understanding of important socio-ecological factors that have played a crucial role in the evolution of other-regarding preferences. Unfortunately, currently existing data on prosociality are difficult to compare since a variety of experimental paradigms with differences in experimental set-ups were used. This topic of potentially influencing contextual features on prosocial experiments, that might contribute to an intra- and interspecific variation of results, should be taken into consideration and are of crucial importance for the comparison of data, but unfortunately these limitations are often overlooked (Cronin 2012; Marshall-Pescini et al. 2016). Additionally to the variety of paradigms used to assess prosociality, features like the social relationship and the dominance asymmetry between donor and recipient and the behaviour of the recipient, in cases the recipient shows interest in the reward or is directly requesting assistance of the donor, were shown to play an important role in the

appearance of prosocial behaviour in experimental settings (Cronin 2012). Further contextual features regarding task design, like food visibility and the trade-off between a potential overtraining of subjects against ensuring the subject's understanding of the task as well as the actor's understanding of the consequences of its own actions for the recipient are being discussed to play a crucial role in the emergence of prosocial behaviour in laboratory experiments (Marshall-Pescini et al. 2016; Cronin 2012).

The most commonly used experimental paradigm to assess other-regarding preferences is the prosocial choice task. In this paradigm, a subject is given the opportunity to choose between a prosocial option (typically referred as 1/1 option), which would reward the subject and a partner, and a selfish option (1/0 option), where the reward is delivered to the subject only. Test sessions are usually compared to control sessions with the same procedure, but without any partner being present. So far, studies in general but also on corvids have applied different variations of the prosocial choice task with different methodologies. One study on ravens has used a bar-pulling apparatus, where different shelves could be pulled into reach by an actor, either presenting a reward in the partner's compartment or in an empty compartment (Lambert et al. 2017). Similarly, other studies on ravens (Di Lascio et al. 2013) and jackdaws (Schwab et al. 2012) were using boxes where lids could be opened by an actor, providing a prosocial, a selfish and an altruistic option. In the altruistic option, only the actor's partner would receive a reward (0/1 option).

Another methodological approach of the prosocial choice task is the token exchange paradigm, where a subject has the opportunity to choose between a "selfish" and a "prosocial" token, which should be returned to an experimenter in exchange for a reward. This paradigm has not been used to test prosocial preferences in corvids so far. Massen and colleagues (2015) used a token exchange approach in a helping task, where ravens could provide a partner with a token that could afterwards be exchanged by the partner for a reward.

The experimental approach chosen for the present study, the group service paradigm, was originally designed by Burkart and van Schaik (2013) and allows to measure both social tolerance and prosociality in a group setting. Although this paradigm has originally been developed for primates, it has recently been adapted to test prosocial tendencies in corvids (Horn et al. 2016). In this paradigm, one individual has the possibility to provide food to its group members, without being able to get the food by itself. Testing individuals within their social group represents a more naturalistic setting, which allows social animals to interact freely and repeatedly. Additional advantages of the group service paradigm are, (1) that subjects can be tested in their home aviary, (2) that it is not necessary to separate certain individuals from their social group for testing and (3) that this experimental paradigm uses a cognitively non-demanding experimental setup, as discussed by Burkart and van Schaik (2013). Further, a predefined methodological procedure of the group service paradigm, where individuals have to reach a specific criterion in habituation and training phases in order to pass on to the subsequent phase of the experiment, allows for a comparison of data. Additionally, control conditions are implemented to check for potentially influencing

factors, like a lack of inhibitory control to operate the apparatus in the presence of food or test the subject's understanding of the consequences of its actions. Additional behavioural observations during test conditions allow for a discussion of a possible occurrence of local or stimulus enhancement and weather food deliveries are facilitated by solicitation of other group members. Considering these facts, the group service paradigm represents an ideal paradigm to test a broad variety of species, which would further allow for comparisons and to draw conclusions within and between different species.

In this study, I investigated the inter-individual social tolerance of 12 captive rooks and tested whether they act prosocially towards their conspecifics in an experimental task by applying the group service paradigm.
I expected rooks to show high levels of intraspecific social tolerance in this task in the context of food distribution among the group, since this feature, as well as food sharing, have been described in a variety of studies (Emery et al. 2007; Seed et al. 2008; Scheid et al. 2008). Further, I predicted that the level of social tolerance in rooks should be similar to the level found in azure-winged magpies, since both species breed in colonies, requiring high levels of intraspecific social tolerance. If the characteristics of the breeding system, as discussed by Burkart and colleagues (2013; 2014), in line with the cooperative breeding hypothesis, have an effect on the occurrence of prosocial behaviour, I expected communally breeding rooks to show prosocial tendencies and to provide food to their group members without obtaining anything by themselves. Burkart and colleagues (2014) reported both a positive effect of pair bonds and social tolerance on prosocial behaviour in their comparative study on different primate species. Thus, in line with previous findings (Burkart et al. 2014; Stevens 2010; de Waal et al. 2008), but contrary to other studies which reported no effect of the relationships of tested dyads on other-regarding preferences (Massen et al. 2011; Horner et al. 2011), I expected more prosocial behaviour among individuals with strong social bonds, compared to individuals with weak social bonds since in the group service paradigm, birds can freely choose with whom to cooperate and are not put into artificially assigned dyads. Therefore, I also expected relationship quality of cooperating dyads to have an effect on prosocial preferences in rooks.

Material and methods

Subjects, study site and housing conditions

Data were collected on twelve captive rooks (10 adult (5M/5F), 2 subadult (1M/1F)) housed at the Eulen- und Greifvogelstation Haringsee, Lower Austria. The Eulen- und Greifvogelstation Haringsee is a rehabilitation centre for injured and orphaned wild animals with a focus on birds, especially on owls and birds of prey. All subjects of the present study

were born in the wild and brought to the station because of injuries. Due to lasting injuries, mainly because of broken or amputated wings, they could not be released anymore and thus stayed at the station. Individual rooks were brought to the Eulen- und Greifvogelstation Haringsee at different points in time, therefore kin relations are very unlikely. For this study, we banded all individuals with differently coloured leg rings for individual identification and took blood samples for the determination of bird's sex. Blood samples were analysed at the
Konrad Lorenz Institute of Ethology in Vienna.
All 12 birds were housed in a single outdoor aviary (3.3m × 7.4m × 3.1m). The aviary contained large wooden branches, one roofed platform (3.3m × 1.1m) and one water pool, where birds had ad libitum access to water and a possibility for bathing. Daily feedings consisted of a mixture of cereals, dried mealworms, minced meat mixed with calcium carbonate and small pieces of scrambled eggs. Additionally, birds were fed with nuts and chicks several times a week.

Behavioural observations: Social relationships and dominance hierarchy

Behavioural data, including social and agonistic interactions of all individuals of the group, had been collected and analysed to get information about the group structure and consequently aimed to draw conclusions on a possible influence of social relationships and dominance hierarchies on the bird's performance in test sessions of the group service paradigm.

Data collection

To assess the social structure of the group, behavioural observations were conducted 4 times a month (generally once a week) from the end of May 2016 until beginning of February 2017. Data were collected in random order between 8 am and 5 pm, consisting of 5-minute focal sampling per individual (Altmann 1974). All focal observations were recorded on video. For all focal observations, I stood at the same spot outside the aviary, approximately, due to space constraints, only one meter away from the wire mesh. To minimize a possible influence on the birds' behaviour, I always waited for 10 minutes before starting to record the first focal video.
For the analysis of agonistic behavioural data, data were divided into three blocks: from end of May until beginning of August (block 1); from end of August until beginning of November (block 2); from end of November until beginning of February (block 3). Each block contained 10 hours of behavioural observations, resulting in a total of 30 hours of video material, corresponding to 150 minutes of video material per bird. A division into different blocks was made to get a broader picture of possible changes in the dominance hierarchy and to be able to obtain clear results about the status of the dominance hierarchy at the time of the food distribution assessment as well as the prosocial test of the group service paradigm. For the food distribution assessment, which was conducted mid of November (between block 2 and 3), agonistic data of block 1 and 2 were analysed.

Comparably, for a discussion of the bird's performance in the prosocial test, which was conducted beginning of march (after block 3), all agonistic data (including block 1, 2 and 3) were analysed.

Ethogram and analysed variables

To assess social bonds, affiliative behaviours (contact sit, allo-preening and allo-feeding) and spatial proximities (perch and ground proximity) as well as co-feeding behaviour (as an indication for inter-individual social tolerance) were recorded and analysed.

For the analysis of dominance hierarchies, agonistic behaviours (displacement, peck and chase) were recorded.

All behaviours were coded using the Solomon Coder beta 17.03.22 (Péter 2017). Table 1 shows a complete list of recorded and analysed behaviours including their definitions.

Tab. 1: Ethogram of analysed variables.

Behaviour	**Definition**
	Affiliative behaviours
Contact sit	Two birds sit next to each other in reaching distance (< 10cm apart on the perch)
Initiate Contact sit	Focal individual initiates contact sit
Terminate Contact sit	Focal individual terminates contact sit
Allo-preening	Focal individual is running its beak through the feathers of another individual
Allo-feeding	Focal individual actively puts a food item into the beak of the other individual
Bill twining	Focal individual gently touches the beak of another individual
	Social tolerance at feeding
Co-feeding	Focal individual feeds together with one or more birds at the same food source (e.g. food bowl)
	Agonistic behaviours
Displacement	Focal individual approaches and another bird retreats within two seconds
Peck	Focal individual pecks another bird or pecks in the direction of another bird, the other bird does not retreat
Chase	Focal individual pursues another individual in flight (e.g. after a fight)

	Spatial proximities
Perch proximity	Focal individual sits together with one or more birds 10-50cm apart on the perch
Ground proximity	Focal individual sits together with one or more birds 0-1m apart on the ground

Group Service Paradigm

Apparatus and set-up

I used the same apparatus as Horn and colleagues (2016), but adjusted for the size and weight of my species. The apparatus consisted of a wooden board with a see-saw mechanism that was attached to the wire-mesh on the outside of the aviary. Two sticks reached into the aviary at one side of the board, forming the *serving perch*. Additionally, a second perch, the *receiving perch*, which was not connected to the see-saw mechanism, was fixed at the inside of the aviary near the other end of the wooden board (Fig. 1a and b). Two u-shaped metal channels on top of the wooden board, served to deliver food during training and test sessions (Fig. 1a). On these metal channels, food could slide down towards the wire-mesh and consequently was at disposal for the birds. A clear plastic cover around the apparatus and especially the serving perch prevented birds of reaching food while sitting on the wire-mesh (Fig. 1a and b).

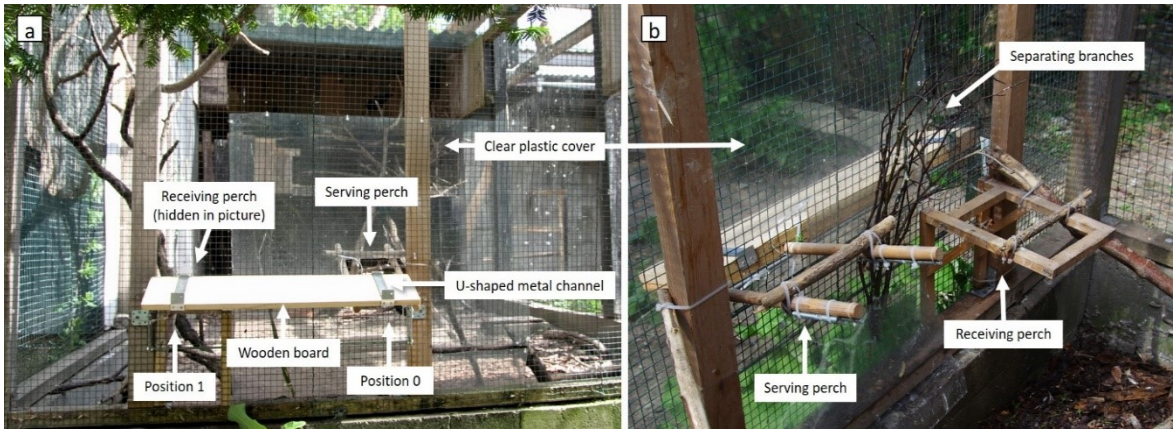

Fig. 1: (a) Apparatus seen from the outside of the aviary. (b) Apparatus seen from the inside of the aviary.

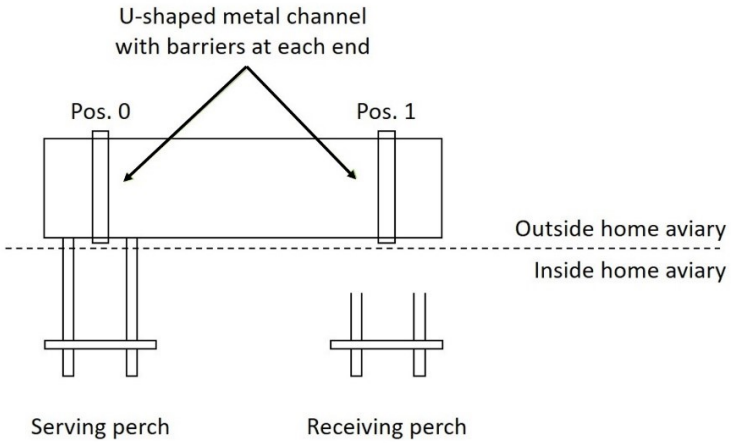

Fig. 2: Schematic depiction of the apparatus from bird´s eye view (adapted from Horn et al. 2016).

The apparatus' see-saw mechanism was balanced in such a way that in its original position the serving perch was pointing upwards and if one bird landed on the serving perch, the perch was slowly tilting downwards with the bird´s weight (Fig. 3). Consequently, if one bird was landing on the serving perch and food was presented on the u-shaped metal channels outside the aviary (either at position 0 or position 1; Fig. 1a, Fig. 2), food was sliding towards the wire-mesh and thus was accessible for the birds. As soon as the bird left the serving perch, the apparatus was moving back to its original position and food was sliding back out of the birds' reach. Importantly, if food was presented at position 1, it could not be reached from the serving perch (position 0) because it was too far to be reached. Additionally, several branches in between the serving and the receiving perch (Fig. 1b) were aimed to prevent the birds of quickly changing from one perch to the other.

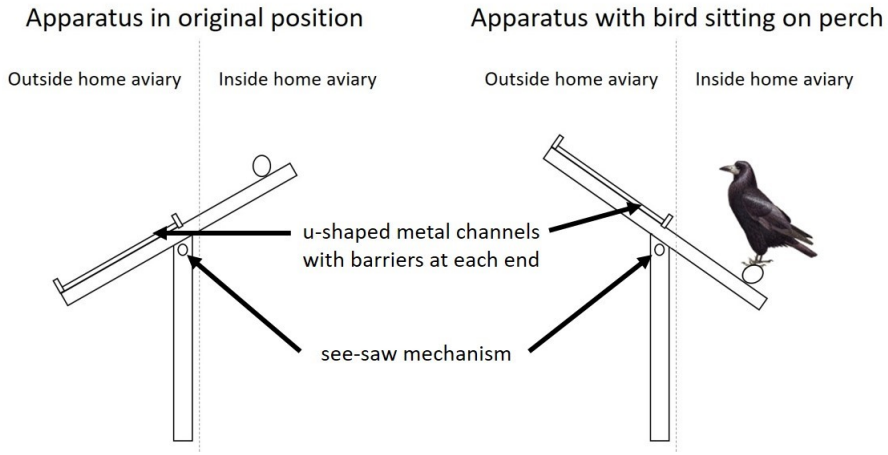

Fig. 3: Schematic depiction of the apparatus' see-saw mechanism (adapted from Horn et al. 2016); rook: https://www.birdguides.com

Further, a construction of branches in front of the apparatus made it possible for all birds, also more handicapped individuals, to access the apparatus at both position 0 and position 1 (Fig. 4) more easily.

Fig. 4: The apparatus seen from inside the aviary with branches in front of the serving and receiving perch providing all handicapped individuals access to the apparatus.

Procedure

Training and testing took place from May 2016 until March 2017. I adopted the procedure of Horn et al. (2016) to prevailing conditions. The experimental design of Horn et al. (2016), who were working with azure-winged magpies and of this study are both close replicates of the procedure of Burkart and van Schaik (2013), who were testing macaques, capuchins and marmosets. In comparison to Burkart and van Schaik, Horn and colleagues as well as the present study were confronted with the need of making two slight modifications based on different species' needs: (1) At the very beginning, due to the corvids' considerable neophobia related to newly introduced objects, an additional habituation phase (Phase 0) was introduced. (2) In the present study the number of trials was reduced from 70 to 60 trials per session (according to the number of subjects; 5 x N birds) in habituation and training phases, as well as in the food distribution assessment (phase II) and to 30 trials per session in the group service and blocked control test phases (phase IV and V) to avoid a satiation of the subjects (Horn et al. 2016).

Regarding these changes, the experimental setup consisted of six successive phases. Three phases were composed of habituation to the apparatus and the experimenter as well as a stepwise training of the function of the apparatus. The remaining three phases constituted test phases. For quantitative and qualitative analysis, all habituation, training and test sessions were video recorded.

Phase 0 - Habituation to the apparatus

For this first phase, which was aimed to habituate the birds to the apparatus, the see-saw mechanism was blocked with the serving perch pointing downwards. A food bowl was

installed at the inside of the home aviary at position 0 in front of the serving perch (Fig. 5). In every habituation session, the food bowl was filled with mealworms and small pieces of cheese and peanuts. Habituation sessions lasted half an hour each. In principle, birds had to reach the criterion of sitting on the serving perch and feeding from the bowl at least five times. In total I conducted 60 habituation sessions. Although not all birds had reached the criterion, I decided to move to phase I after habituation session number 60, based on a lacking interest in the apparatus of the remaining non-habituated birds.

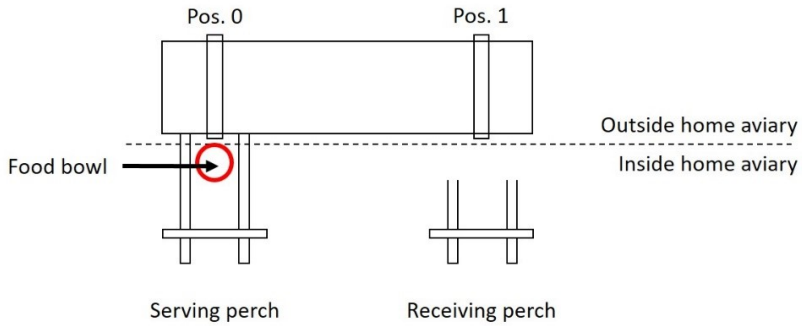

Fig. 5: Schematic depiction of the apparatus in phase 0 (adapted from Horn et al. 2016).

Phase I - Habituation to the procedure

Phase I was aimed to habituate all individuals to the presence of the experimenter. During this phase the see-saw mechanism was still blocked with the serving perch in a downwards position and food (mealworms or small pieces of cheese or peanuts) was placed on the board close to the wire mesh by the experimenter either at position 0 or position 1 (Fig. 6) on alternating days. For each trial I approached the apparatus, called the bird´s attention and placed one piece of food on the board and moved slowly back again (approximately 7 meters away of the aviary). One trial ended after a bird took the piece of food or after the time limit of two minutes was reached. One session consisted of 60 trials each. If none of the birds landed on the perch during three successive trials, the session was terminated. Birds had to reach the criterion of taking at least ten pieces of food in a minimum of five sessions. In total I conducted 52 habituation sessions. After habituation sessions number 52, I decided to move to the successive test phase (phase II) because none of the remaining non-habituated birds had tried to approach the apparatus since training session number 13.

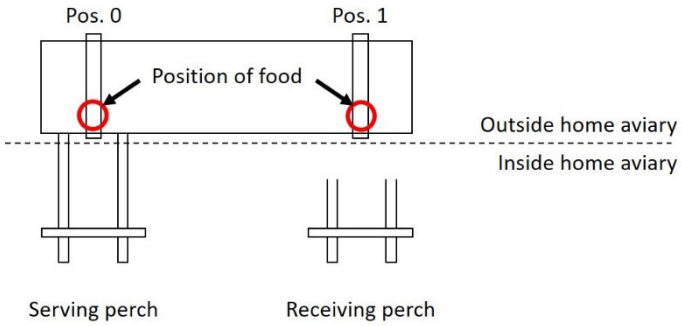

Fig. 6: Schematic depiction of the apparatus in phase 1 (adapted from Horn et al. 2016).

Phase II - Food distribution assessment (Test phase)

For the first test phase, the see-saw mechanism was still blocked in a downwards position. Two test sessions were conducted on consecutive days, consisting of 60 trials each. As before, I approached the apparatus every trial, called the bird´s attention and placed one piece of food (a small piece of cheese) on the board. Afterwards I moved slowly back again. In this phase food was always baited at position 1 (Fig. 7). Like in phase I, I always placed another piece of food onto the test apparatus after the food had been taken by one of the birds or after the time limit of two minutes was reached. For every session the number of food pieces obtained by each bird was recorded.

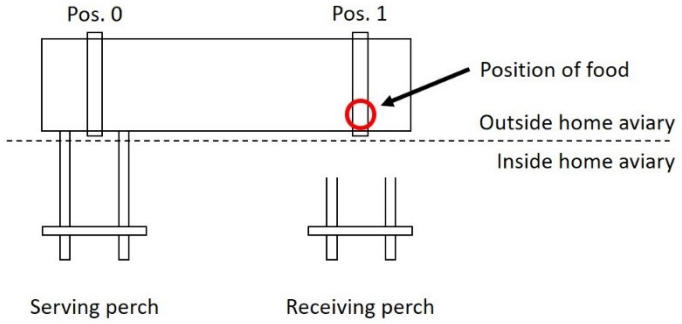

Fig. 7: Schematic depiction of the apparatus in the food distribution assessment (phase 2) (adapted from Horn et al. 2016).

Phase III - Apparatus training

In this training phase, birds learnt to move pieces of food towards the wire mesh by landing on the serving perch. Food (mealworms or small pieces of chees or peanuts) was always presented at position 0. To facilitate the learning process, food was placed near the wire mesh and the see-saw mechanism was only loosened slightly in the beginning of this phase (the see-saw's mechanism was constructed to be independently adjustable in its up- and downwards movement). After all birds, which successfully reached the criterion in the

previous training phase (phase I), obtained at least one piece of food, the see-saw mechanism was loosened step by step and food was little by little placed further away from the wire mesh. In between, the see-saw mechanism was slightly tightened again to make it easier for birds which showed neophobic behaviours based on an increased movement of the serving perch. In the final training step, the see-saw mechanism was released completely and pieces of food were placed at the upper end of the u-shaped metal channels on the board (Fig. 8). As previously, in every trial I approached the apparatus, called the bird´s attention and placed one piece of food on the board at position 0 and moved slowly back again. Training session consisted of 60 trials each. The next trial started after one bird had taken the piece of food or if the time limit of two minutes was reached. Birds had to reach the criterion of taking at least ten pieces of food in a minimum of five training sessions with the see-saw mechanism released completely.

After training session number 65, training was discontinued because the remaining non-habituated birds which had shown interest in the apparatus and the food reward still had notably problems with the freely moving see-saw (and especially with an increased inclination of the serving perch in an upwards position). This decision was taken because from training session number 35 until session number 65 the bird's behaviour towards the movement of the perch did not have changed.

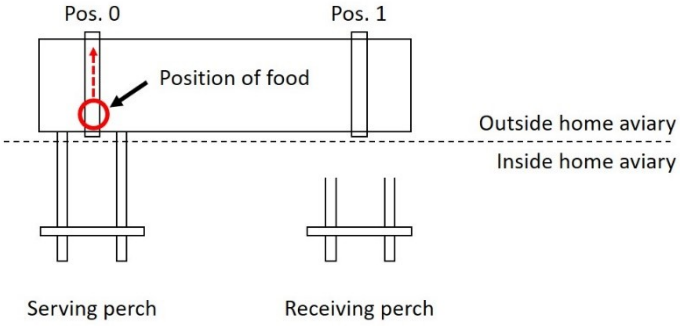

Fig. 8: Schematic depiction of the apparatus in phase 3 (adapted from Horn et al. 2016).

Phase IV – Group service (Test phase)

The Group service test consisted of five test sessions and five empty control sessions, conducted on alternating days. In all sessions the see-saw mechanism was fully released and food (a piece of cheese) was always baited at position 1 in regular test trials, thus the bird operating the apparatus by landing on the serving perch could only deliver food to other individuals of the group, but not to itself (Fig. 9). Test and control sessions consisted of 30 trials (based on the number of birds that had reached criterion in the previous habituation and training phase) and one motivation trial at the beginning of each session and after every fifth regular test trial. During motivation trials food was baited at position 0 and thus could be retrieved by the subject operating the serving perch itself, aiming to keep birds motivated of participating in the experiment.

Group service test trials lasted until one bird manipulated the serving perch and another bird took the food at position 1 or after the time limit of two minutes was reached. In each trial I approached the apparatus, called the birds' attention and placed one piece of food on the board and slowly moved back again.
Control sessions were identical to test sessions, with the only difference that no food was placed on the board, but I pretended to leave a piece of food at position 1. Trials of empty control sessions lasted for two minutes each.
In every trial I recorded which bird(s) landed on the serving perch (position 0) and which bird(s) landed on the receiving perch (position 1). Additionally, I recorded which bird provided the food by manipulating the apparatus' see-saw mechanism and which bird obtained the piece of food and whether a bird was already present at the receiving perch in position 1 prior to the manipulation of the see-saw mechanism.

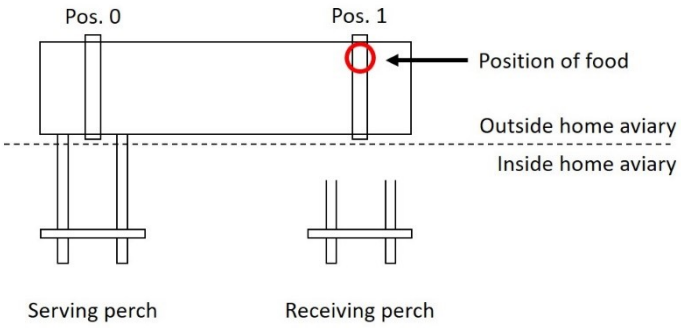

Fig. 9: Schematic depiction of the apparatus in the group service test (phase 4) (adapted from Horn et al. 2016).

Phase V – Blocked control (Test phase)
During this phase, the apparatus' see-saw mechanism was fully released and the access to the board at position 1 was blocked with a fine wire-mesh in front of the opening (Fig. 10), hence no food could be obtained at position 1 while sitting on the receiving perch. This phase aimed to test whether the birds' landings on the perch was just elicited by the presence of food.
The blocked control consisted of five test sessions and five empty control sessions, conducted on alternating days. The procedure of the blocked control was identical to test and control sessions of the group service (phase IV). In case no bird landed on the serving perch during three successive motivation trials, the session was ended and repeated the following day.
In each trial I recorded which bird(s) landed on the serving perch in front of position 0 and which bird(s) landed on the receiving perch in position 1.

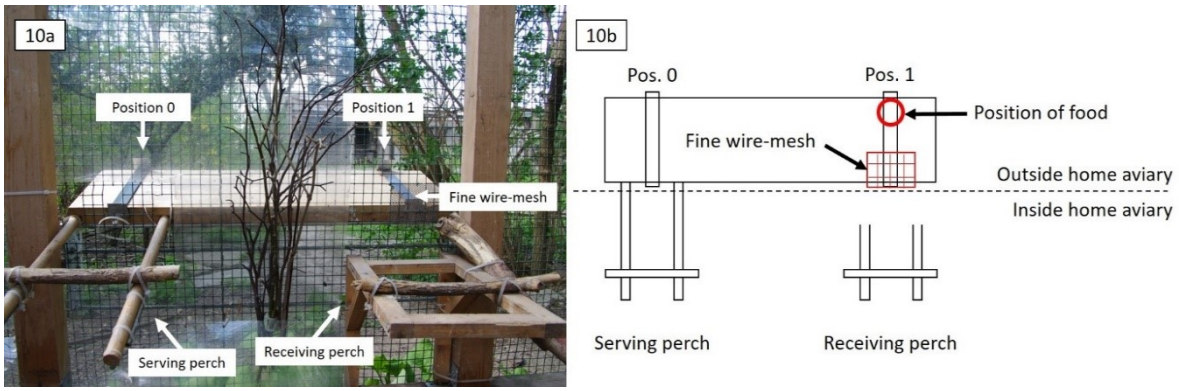

Fig. 10: (a) Apparatus with a fine wire-mesh blocking the access to food at position 1 during phase V (blocked control). (b) Schematic depiction of the apparatus in phase V (adapted from Horn et al. 2016).

Re-testing

I re-tested phase IV in June 2017. Two prosocial test sessions and two empty control sessions were conducted on alternating days. The birds received no training between the original test and the re-test.

Statistical analyses

Behavioural observations

The analysis of affiliative data and spatial proximities served to identify paired individuals and the strength of social bonds between all different dyads of the group. This information was further used to interpret the influence of social bonds on results of the group service paradigm.

To categorize social relationships within the group and to detect differences in pair bond strength, I calculated a dyadic sociality index (Silk et al. 2006; Boucherie et al. 2016) using affiliative behaviours (contact sit (CS), allo-preening (AP), allo-feeding (AF) and bill-twining (BT)), co-feeding (CF) and spatial proximities (perch proximity (PP) and ground proximity (GP)).

The durations of affiliative behaviours and spatial proximities were strongly correlated to their frequencies (for all variables (contact sit, allo-preening, allo-feeding, bill-twining, co-feeding, perch proximity and ground proximity): matrix correlation using Spearman's rank correlation: $p<0.001$, rho=0,99; performed in R function cor.test, package stats version 3.2.5; R Core Team 2016). Based on this correlation, I only used frequencies of behavioural variables for the analysis of the sociality index. The dyadic sociality index was calculated as follows:

$$SI_{xy} = \frac{\left(\frac{CS_{xy}}{CS}\right) + \left(\frac{AP_{xy}}{AP}\right) + \left(\frac{AF_{xy}}{AF}\right) + \left(\frac{BT_{xy}}{BT}\right) + \left(\frac{CF_{xy}}{CF}\right) + \left(\frac{PP_{xy}}{PP}\right) + \left(\frac{GP_{xy}}{GP}\right)}{7}$$

The sociality index (SI) for dyad xy was the sum of all affiliative behaviours, where the dyadic frequency of e.g. contact sit of dyad xy (CS_{xy}) was divided by the overall mean

frequency of contact sit (CS). The same operation had to be applied for all other variables as well. The mean frequency of a variable was obtained by dividing its total frequency (summing the frequencies of all individuals of the group) by 66, the number of potential dyads in the group. The denominator was given by the number of behavioural variables that contributed to the calculation of the index, in this case 7.
The dyadic sociality index compared the strength of relationships of all possible dyads in the group. The higher the value of the index, the stronger the social bond between a given dyad. Low values of the sociality index represented dyads with weak social bonds (Silk et al. 2006). According to Boucherie et al. (2016) dyadic sociality indices of primary relationships, which characterize strongly bonded pairs, always represented more than 50% of both partners total individual sociality indices (the sum of sociality indices of dyads, in which the individual was involved). Hence, two birds were considered as paired if their social investment in the relationship was more than 50% of their total investment with all other group members (Boucherie et al. 2018). Secondary relationships were defined as relationships, that represented 5-50% of both partners' individual indices or just one of the partners' individual indices, in the case the other partner represented >50%. Weak relationships represented less than 5% of both or one of the partner's individual sociality indices (Boucherie et al. 2016).
The social network of the group, based on sociality indices of primary, secondary and weak relationships, was built using the software Gephi 0.9.2.

Like affiliative data and spatial proximities, agonistic data, which served to analyse the dominance hierarchy of the group, were further used to interpret the influence of individual's dominance rank on results of the group service paradigm.
To analyse the dominance hierarchy within the group, I constructed a sociometric matrix of dominance interactions by using the frequency of displacements. I decided to use displacements for this analysis only, since chase did not occur at all during focal observations and peck only occurred very scarce. The dominance interaction matrix took the identity of each opponent and the number of wins and losses, observed during focal observations, into account.
Further, I analysed whether the dominance hierarchy was linear and calculated the steepness of the dominance hierarchy within the group. To test whether the dominance hierarchy was linear, the improved Landau's index h' (de Vries 1995), which takes unknown and tied relationships into account, was calculated using the function linear.hierarchy.test in R (Package *DyaDA* version 0.1.1, Leiva et al. 2016) with 10.000 randomizations. The steepness of the dominance hierarchy, which measures absolute differences between adjacently ranked birds in their success of winning dominance encounters (de Vries et al. 2006), was calculated in Socprog 2.8 (for 10 000 permutations) and in R, using the function steeptest in R package *steepness* version 0.2-2 (Leiva & de Vries 2014). If differences between adjacently ranked birds are large, the dominance hierarchy is steep, in contrast if differences are small, the dominance hierarchy is shallow. In a shallow hierarchy the chance of winning dominance encounters between closely ranked birds is not reliable and predictable any more compared to a steep dominance hierarchy. The calculation of the steepness of the hierarchy was based on normalized David's scores. Values of the steepness

measure can vary between 0 and 1, with 1 indicating a perfect linearity with a maximum steepness (de Vries et al. 2006).
Additionally, birds were ordered into a linear or near-linear dominance hierarchy according the values of David's scores as applied by the function steeptest in R package *steepness* version 0.2-2 (Leiva & de Vries 2014).

Group service paradigm

For the analysis of the food distribution assessment (phase II) the evenness of food distribution was calculated, using Pielou's J' as evenness measure (Pielou 1977). The distribution of food within the group is argued to be a proxy of social tolerance. It is reflecting social tolerance within the group, but it is no direct measure for intraspecific social tolerance. Pielou's eveness index J', which was originally developed as a measure of biodiversity, quantifying the relative abundance of species within a community, was calculated as H'/H'_{max}. H' derives from the Shannon diversity index and H'_{max} is the maximum value of H'. Pielou's J' is expressed as a value between 0 and 1, whereas 0 is indicating a maximum unequal distribution and 1 indicating a maximum equal distribution of food pieces within the group. Pielou's J' was calculated in R package vegan version 2.4-3 (Oksanen et al. 2017) by applying the function diversity and further calculating Pielou's J'.
For the analysis of the prosocial test (phase IV) and the blocked control (phase V) only data from the last two test sessions (session 4 and 5 of each condition) were used. Beforehand, birds had the opportunity and time to learn about the consequences of operating the serving perch from session 1 to session 3 of each condition. Data were analysed on an individual level. The number of landings on the serving perch per bird and test condition were summed for session 4 and 5. Fischer's exact test was used to compare whether landings occurred more frequently in prosocial test sessions compared to empty control and blocked control sessions. Fischer's exact test was calculated using the function fisher.test in R package stats version 3.2.5 (R Core Team 2016). P-values were corrected for multiple comparisons using the Holm-Bonferroni correction by applying the function p.adjust("holm") in R package stats version 3.2.5 (R Core Team 2016). Additionally, the percentage of successful food deliveries was calculated in the prosocial test condition.
During all test sessions agonistic interactions (e.g. displacements in position 0 and position 1 or attacking recipients after they obtained food) and signs of need (e.g. reaching attempts in position 1) and solicitation (e.g. begging behaviour) were coded if shown by the birds.
Additionally, the number and direction of food offerings of received food items was coded during habituation and training as well as during test sessions of the group service paradigm.

Results

Behavioural observations: Social relationships and dominance hierarchy

During focal observations of the present study the following frequencies of behavioural variables were recorded: 522 agonistic interactions (467 displacements (including received displacements), 55 pecks (including received pecks) and 0 chases), 334 events of contact sit, 341 allo-preenings (including received allo-preenings), 2 cases of allo-feeding (including received allo-feedings), 26 events of bill twining, 947 perch proximities, 570 ground proximities and 10 events of co-feeding.

Taking all affiliative data and spatial proximities into account (including data of block 1, 2 and 3), 8 out of 12 individuals were involved in a primary relationship, forming 4 pairs (DB-WE, LI-GR, HB-OR and GE-RT; all mixed sex). Further 6 secondary relationships (HB-RO, GG-RO, GG-LI, GG-GR, GG-GB and GW-GB; 5 of mixed sex and 1 secondary relationship formed by 2 males) and 56 weak relationships could be identified during the time of observation. Generally, some dyads had very high values of sociality indices compared to others, indicating that affiliations and spatial proximities varied greatly between different dyads (Fig. 15). Figure 16 visualizes the social network of the group, which was constructed based on values of the sociality index of all 66 dyads.

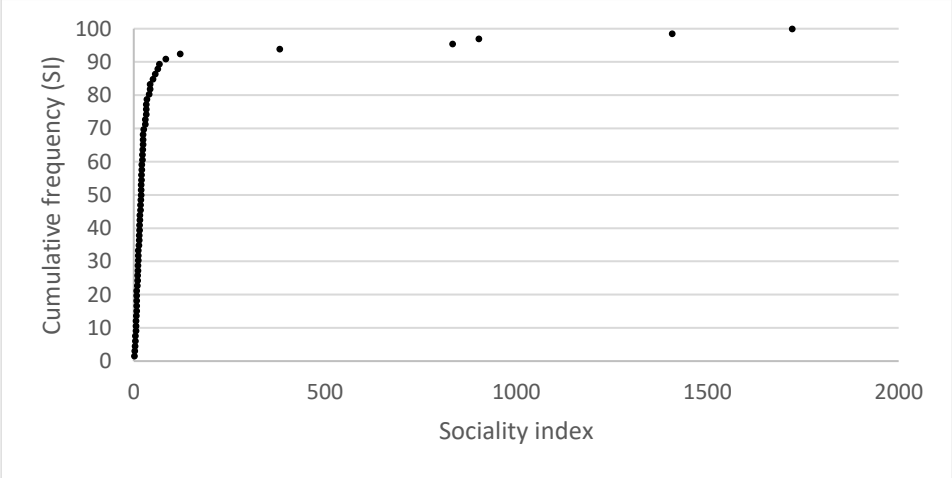

Fig. 15: Cumulative distribution of sociality indices of all possible dyads of the group. The x-axis shows the sociality index * 100 and the y-axis the cumulative frequency of sociality indices * 100.

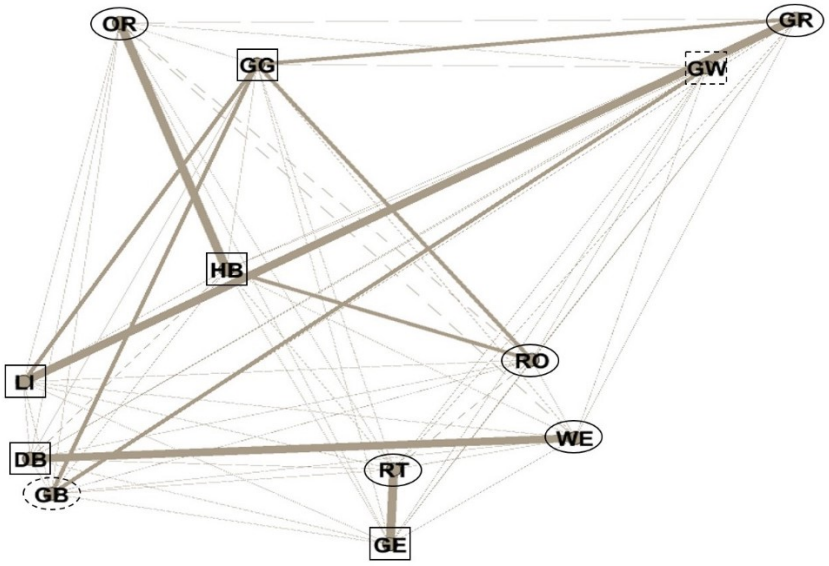

Fig. 16: Social network based on sociality indices of primary, secondary and weak relationships. Individuals are represented by nodes and the thickness of edges indicate the strength of relationships between given dyads (thick lines: primary relationships, intermediate lines: secondary relationships and thin dotted lines: weak relationships). Rectangles indicate males and ovals females. The dashed rectangle and oval represent subadult individuals.

Considering all observational data (including data of block 1, 2 and 3), the dominance hierarchy of the group showed a significant degree of linearity (h' = 0.913, right-tailed $p < 0.001$) and steepness (steepness = 0.768, right-tailed $p < 0.001$). Agonistic interactions of the group revealed one unknown relationship between individual LI (m) and GW (m, subad.) and two tied relationships between the individuals OR (f) and WE (f) as well as GR (f) and WE (Tab. 7).

Tab. 7: Matrix of dyadic displacement frequencies based on all recorded focal observations. Individuals are ordered according their rank based on David´s scores. Individual with highest rank: DB and lowest rank: GW. Light grey fields indicate an unknown relationship and dark grey fields tied relationships.

		Displaced bird											
Displacing bird		DB	HB	LI	GE	GG	RT	OR	WE	RO	GR	GB	GW
	DB	-	6	1	11	14	9	18	1	12	5	22	9
	HB	1	-	2	9	20	8	3	5	28	3	16	6
	LI	4	3	-	3	4	4	2	3	1	1	8	0
	GE	1	1	0	-	12	1	3	4	6	5	4	4
	GG	0	0	1	2	-	4	11	11	6	2	11	3
	RT	0	0	0	0	0	-	7	2	1	7	5	1
	OR	2	0	0	0	1	0	-	1	11	6	10	3
	WE	0	0	0	0	0	0	1	-	3	1	10	4
	RO	0	0	0	0	0	0	3	1	-	3	11	13
	GR	0	0	0	0	0	0	0	1	0	-	11	8
	GB	0	0	0	0	0	0	0	0	0	0	-	6
	GW	0	0	0	0	0	0	0	0	0	0	0	-

The analysis of agonistic interactions until the food distribution assessment of the group service paradigm (including data of block 1 and 2), served to give detailed information about the linearity and steepness of the dominance hierarchy until the time of this first test. Additionally, an analysis of the 3 blocks separately allowed for a more accurate information about the hierarchical rank order at the time of the food distribution assessment and the prosocial test of the group service paradigm.

Results of agonistic data up until the food distribution assessment revealed a significant linearity ($h' = 0.699$, right-tailed $p < 0.001$) and an average, but significant degree of steepness of the dominance hierarchy (steepness = 0.523, right-tailed $p < 0.001$; block 1 + 2). Looking at results of the analysis of each block 1, block 2 and block 3 showed that the rank order of individuals changed during the year (Fig. 17). Similarly, the linearity and steepness of the hierarchy revealed changes during the year (Fig. 17). Generally, all adult male birds, regardless their rank, were dominant over all females and subadult individuals over the 10 months of observation.

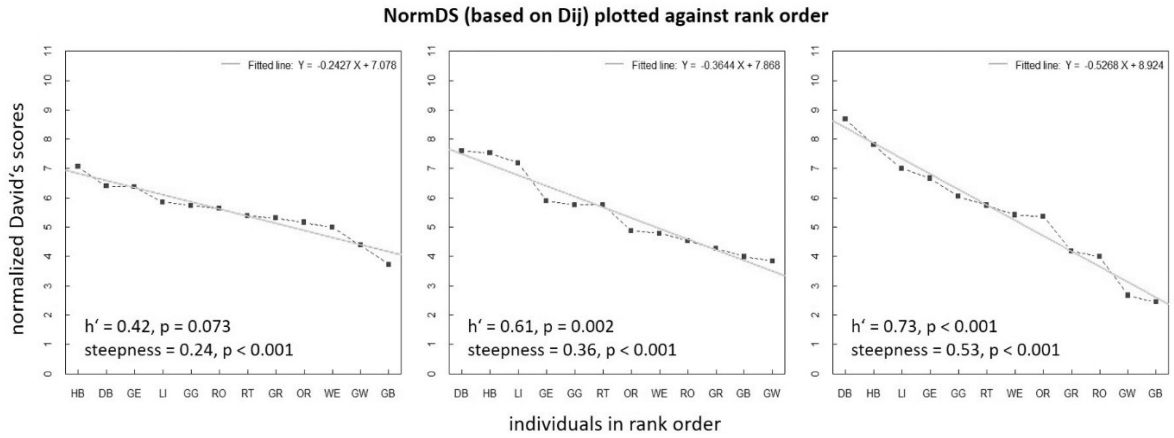

Fig. 17: The linearity and steepness of dominance hierarchy and the rank order of individuals during the year (from left to right: block 1, block 2, block 3). Individual with highest rank on the left side, individual with the lowest rank on the right side. On the bottom left of each graph the linearity and steepness of the hierarchy, including p-values, are depicted.

Group Service Paradigm

Habituation to the apparatus and to the procedure (Phase 0 and I)

Birds received 60 habituation sessions in phase 0. Until then, 9 birds reached the criterion in this phase. One individual (GG) landed on the apparatus 3 times and thus almost reached the criterion of 5 landings on the apparatus in phase 0. Two birds (GE and WE) never came to the apparatus. Birds needed a median of 30 sessions (min. 8, max. 59 sessions) to reach criterion in phase 0 (Tab. 2). After 60 conducted habituation sessions in phase 0 and due to a lack of interest in the apparatus of subject GG, GE and WE, I decided to move to phase I, although not all birds reached the criterion in phase 0.

In phase I, the habituation to the procedure, birds received 52 training sessions. Five birds reached the criterion in this phase (4 females (GR, OR, RO, GB) and 1 male (DB)). One individual, HB, did not fully meet the criterion of taking at least 10 pieces of food in a minimum of 5 sessions in phase I. HB landed on the apparatus only during 2 sessions and received 8 pieces of food. From session 12, HB stopped coming to the apparatus. LI only came once in session number 12 and received one piece of food during phase I. Three birds that came to the apparatus in phase 0 (RT, GW and GG), stopped coming in phase I. Birds needed a median of 10 sessions (min. 5, max. 17) to reach the criterion in phase I (Tab. 2).

Tab. 2: Number of sessions birds needed to reach the criterion in phase 0 (habituation to the apparatus) and phase I (habituation to the procedure). ()* indicating birds that did not fully meet the criterion.

Individual			Phase 0	Phase I
name	sex	age	sessions until criterion	sessions until criterion
DB	M	ad.	8	5
GR	F	ad.	11	10
OR	F	ad.	15	10
RT	F	ad.	29	-
RO	F	ad.	30	7
HB	M	ad.	35	(52)*
LI	M	ad.	39	(52)*
GB	F	subad.	59	17
GW	M	subad.	59	-
GG	M	ad.	(60)*	-
GE	M	ad.	-	-
WE	F	ad.	-	-

Food distribution assessment (Phase II)

For the calculation of evenness of food distribution within the group, which served as a proxy for social tolerance, a distinction between 120 trials (5 x 12 individuals / test session; Fig. 11) and 50 trials (5 x 5 habituated individuals / test session; Fig. 12) was made.

The food distribution was among average when taking 120 trials and all 12 birds into account (Pielou's J' = 0.63).

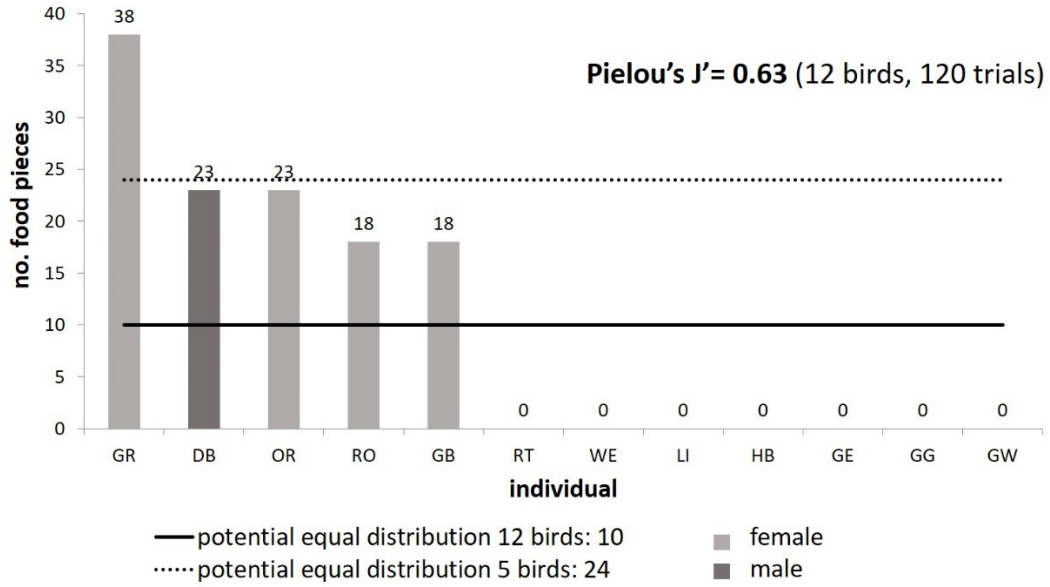

Fig. 11: The number of food pieces obtained per individual during the food distribution assessment (phase II) with 120 test trials. The solid line represents the potential equal distribution among all 12 birds and the dotted line the potential equal distribution of food pieces among the 5 habituated individuals.

None of the birds that had not reached the criterion in the previous habituation phase obtained a single piece of food in the food distribution assessment. Therefore, I decided to redo the calculation of Pielou's J' by the first 25 trials per test session (5 x N habituated individuals / test session) instead of 60 trials per test session. Calculating Pielou's J' according the number of participating individuals in the test reflects a more realistic value of the evenness of food distribution. Applying this calculation, the evenness of food distribution among the habituated individuals was very high (Pielou's J' = 0.96; day 1: Pielou's J' = 0.72, day 2: Pielou's J' = 0.99; Fig. 12).

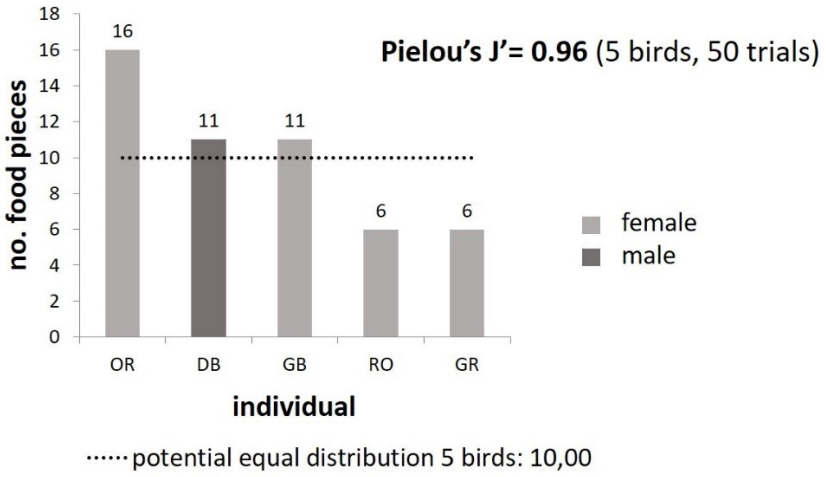

Fig. 12: The number of food pieces obtained per individual during the food distribution assessment (phase II) with 50 test trials. The dotted line represents the potential equal distribution of food pieces among all habituated individuals.

As visible in table 3, always one individual out of a couple participated in the food distribution assessment, except for one pair (GE and RT) where both individuals were not habituated in phase I.

Tab. 3: The number of food pieces obtained per bird during the food distribution assessment (phase II) with 50 test trials. Rectangles indicate habituated birds and brackets paired individuals.

Individual			*Food distribution assessment*
name	sex	age	number of food pieces obtained
DB	M	ad.	11
WE	F	ad.	0
LI	M	ad.	0
GR	F	ad.	6
HB	M	ad.	0
OR	F	ad.	16
GE	M	ad.	0
RT	F	ad.	0
GG	M	ad.	0
RO	F	ad.	6
GW	M	subad.	0
GB	F	subad.	11

habituated birds

- 1 male
- 4 females

paired individuals

Apparatus training (Phase III)

In phase III, the apparatus training, birds received 65 training sessions. Three birds (1 male (DB), 1 female (OR) and 1 subadult female individual (GB)) reached the criterion in this phase. All 3 birds reached the criterion in training session number 65, which was the fifth session with the apparatus's see-saw mechanism loosened completely.

Three additional birds (GR, LI and RO) came to the apparatus during training sessions with the see-saw mechanism just loosened partially.

In training session number 4 the apparatus's see-saw mechanism was loosened carefully a little more. In this session, GR manipulated the serving perch once and after that stopped coming to the apparatus at position 0 for the rest of phase III (although I tightened the see-saw mechanism again to facilitate GR to step onto the serving perch). LI, GR's partner, although not habituated in phase I, started to come to the apparatus after GR stopped coming. LI successfully obtained food from the serving perch during several training sessions (in total during 66 trials), but only if the serving perch was not or just slightly pointing upwards (a freely moving perch in the downwards direction posed no problem).

The third individual which came to the apparatus during training sessions with the see-saw mechanism loosened partially was RO. RO came to the serving perch successfully during several training sessions (in total during 151 trials), but, as well as LI, only if the serving perch was not or just slightly pointing upwards. For the group service test, the serving perch needed to point upwards, because food had to slide back out of the bird's reach if individuals got off the serving perch. Thus, to successfully reach the criterion in training phase III, the serving perch needed to move freely in an upwards and downwards direction.

Group service (Phase IV) and Blocked control (Phase V)

During all group service test sessions birds delivered food successfully to other group members, but only at low rates. Successful deliveries stayed more or less stable throughout the experiment and varied between 3 to 6 (median = 5) pieces of food per test session (Fig. 13b). In the last two test sessions, two individuals (DB and GB) provided food successfully in 13,3% of trials (8 food pieces). GB (subadult female) provided 7 out of 8 food pieces, but did not receive any piece of food at all. DB (adult male) provided 1 piece of food and received 7 pieces or 87.5% of food. OR (adult female) provided no food but received one piece of food (Tab. 4).

The number of trials with landings across all five test sessions decreased slightly over the first three test sessions, decreased more in test sessions 4 and increased again in the last test session. During empty control sessions, the number of trials with landings decreased to zero in session number 3 and stayed very low during the last two test sessions (2 trials with landings in session 4 and 1 trial in session 5). During all five blocked control sessions, the number of trials with ladings stayed very low, but showed a slight increase in session number 5 (Fig. 13b).

Considering the number of trials with landings of the last two test sessions, there were significantly more trials with landings in the prosocial test compared to both empty and blocked control (for both test vs empty control and test vs blocked control: $p < 0.001$, Fisher's exact test, Holm-Bonferroni corrected; Fig. 13a).

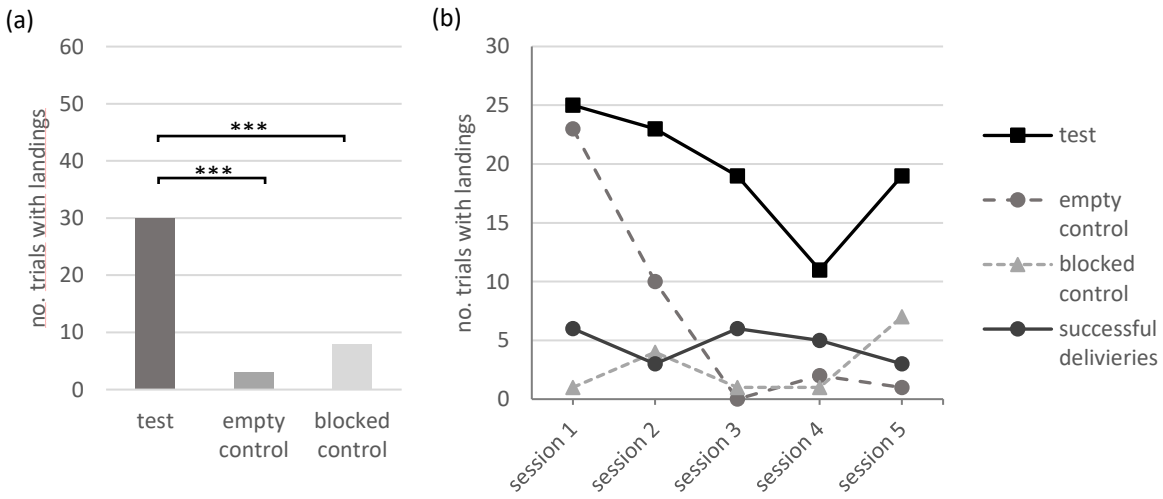

Fig. 13: (a) The number of trials with landings in the last two test, empty and blocked control sessions (*** $p<0.001$, Fisher's exact test, Holm-Bonferroni corrected); (b) the number of trials with landings across all five test sessions, empty and blocked control sessions as well as the number of trials with successful deliveries.

Looking at the results on individual level and only considering the last two test sessions, one individual (DB) landed significantly more often on the serving perch in test vs empty and blocked control sessions. GB showed a positive non-significant trend when comparing both empty and blocked control sessions with prosocial test sessions. OR only landed on

the serving perch during two prosocial test trials and thus showed no significant difference in test vs empty and blocked control sessions (Tab. 4 and 5).

Tab. 4: Subject's individual results in the last two test sessions of phase IV (food provided to and received from others, the number of trials with landings on the serving perch) and Fisher's exact test (test vs empty control, Holm-Bonferroni corrected).

Individual			Food phase IV		Landings phase IV		Fisher's exact test
name	sex	age	received	provided	test	empty control	p-value
DB	M	ad.	7	1	22	0	<0.001
OR	F	ad.	1	0	2	0	0.992
GB	F	subad.	0	7	10	3	0.075

Tab. 5: Subject's individual results in the last two test sessions of phase IV and V (the number of trials with landings on the serving perch) and Fisher's exact test (test vs blocked control, Holm-Bonferroni corrected).

Individual			Landings phase IV	Landings phase V	Fisher's exact test
name	sex	age	test	blocked control	p-value
DB	M	ad.	22	6	<0.001
OR	F	ad.	2	0	0.992
GB	F	subad.	10	2	0.059

In the last two test sessions, food was delivered to a waiting recipient (DB), already sitting on the receiving perch in front of position 1 when the other individual (GB) approached the apparatus's serving perch and delivered the food during three trials. Five out of 8 food pieces (63% of food) were delivered without any individual waiting in position 1 or showing any begging behaviour or signs of need.

Re-testing

Comparing the number of trials with landings during prosocial test sessions of the retest with the last two prosocial test sessions of phase IV, birds landed on the apparatus's serving perch similarly often (a median of 13 trials in the retest vs a median of 15 trials during the last two test sessions of phase IV; Fig 14b). Considering empty control sessions, birds landed a median of 0.5 trials during the retest and a median of 1.5 trials during the last two empty control sessions of phase IV. In the retest, successful food deliveries only occurred once in session 1 (Fig. 14b).

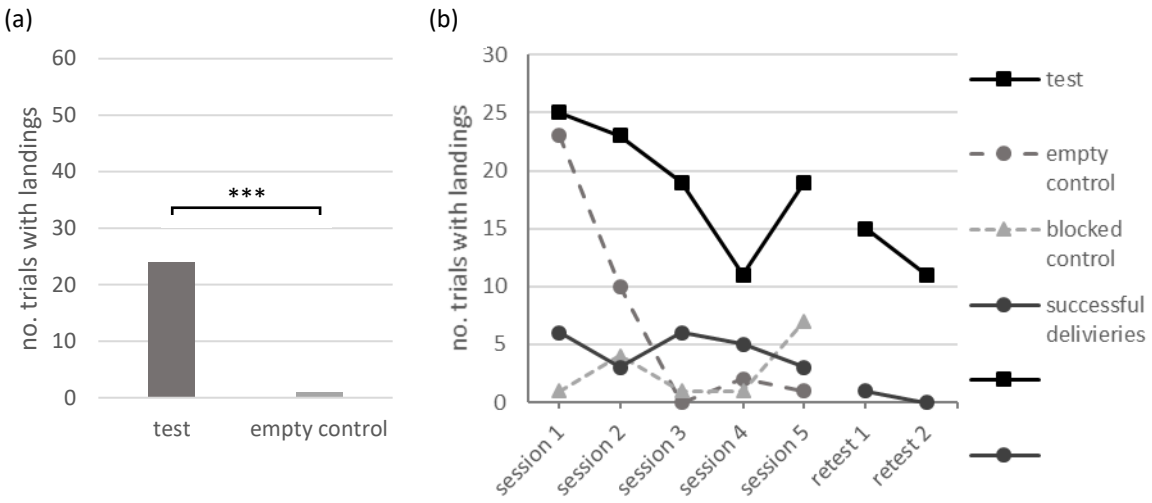

Fig. 14: (a) The number of trials with landings during test and empty control sessions of the retest (*** $p<0.001$, Fisher's exact test); (b) the number of trials with landings across all five test, empty and blocked control sessions of phase IV and V, compared to test and empty control sessions of the retest, as well as the number of trials with successful deliveries.

In the retest, there were significantly more trials with landings in the prosocial test than in the empty control ($p < 0.001$, Fisher's exact test; Fig. 14a).
On the individual level, two birds (OR and GB) landed significantly more often in test sessions, compared to empty control sessions. DB, landed in 5 test and zero empty control trials, although when comparing test vs control showed a non-significant trend (Tab. 6).
One adult female (GR), which reached the criterion in phase 0 and I, but did not reach the criterion in the last training phase (phase III) received food in one trial of the retest (Tab. 6). Beforehand, during prosocial test sessions of phase IV, GR did not receive any piece of food.

Tab. 6: Subject's individual results in the retest (food provided to and received from others, the number of trials with landings on the serving perch) and Fisher's exact test (test vs empty control).

Individual			Food Re-test		Landings Re-test		Fisher's exact test
name	sex	age	received	provided	test	empty control	p-value
DB	M	ad.	0	0	5	0	0.057
OR	F	ad.	0	0	9	0	0.003
GB	F	subad.	0	1	12	1	0.002
GR	F	ad.	1	0	0	0	1.000

Food offerings of retrieved food items during training and test sessions of the group service paradigm were mostly observed from participating individuals towards their bonded partners. During habituation and training phases, food offerings mainly occurred from

participating individuals towards their bonded partners. Most feeding events occurred from DB towards WE (68.8% of all observed feedings). Food offerings occurred additionally from GR towards LI and from HB towards OR as well as from RO towards HB. In general, 83.3% of feedings occurred between individuals with strong social bonds (primary relationships), where two males (DB and HB) and one female (GR) were feeding their partners. The remaining 16.7% of food offerings were observed between two individuals forming a secondary relationship, where the female (RO) was feeding the male bird (HB).
During test sessions of the group service paradigm, one food item was actively offered by one subjects during one trial: after GB had successfully provided DB one piece of food in prosocial test session 3, DB actively approached GB and fed GB with the recently received food item. During test sessions of the group service paradigm birds did never scrounge for retrieved food items.

Discussion

The results of the present study demonstrate, that rooks show very high levels of social tolerance towards group members. The evenness of food distribution, which served as proxy for social tolerance within the group (Burkart & van Schaik 2013; Horn et al. 2016), was very high for the 5 successfully habituated birds in phase I (Pielou's J' = 0.96). This result meets my expectations and is in line with previous findings, where social tolerance had already been experimentally shown in this communally breeding bird species (Seed et al. 2008). Furthermore, the level of social tolerance found in the present study exceeds results of cooperatively breeding azure-winged magpies (group 1: Pielou's J' = 0.74, group 2: Pielou's J' = 0.85; Horn et al. 2016) as well as levels of social tolerance in cooperatively breeding common marmosets (Pielou's J' = 0.74; Burkart & van Schaik 2013). This is surprising, since cooperatively breeding species were expected to show the highest levels of social tolerance (Burkart & van Schaik 2013). In primates, allomaternal care was found to have a strong effect on social tolerance (Burkart et al. 2014; Burkart & van Schaik 2016). Consequently, also in communally breeding species like rooks, very high levels of social tolerance were expected. This expectation was based on previous studies, where several individuals were observed to engage in joint defence of nesting sites in the wild (Coombs 1961) or where partners of a relationship supported each other in agonistic encounters and showed post-conflict affiliation (Seed et al. 2007). Furthermore, rooks live in large groups during the whole year, which also requires a high degree of intraspecific social tolerance.
In addition to the levels of social tolerance found in rooks, no influence of the dominance hierarchy nor the individual's rank order on the number of food pieces obtained during the food distribution assessment could be found. In general, when analysing dyadic dominance indices including data up until the food distribution assessment of the group service paradigm, rook's dominance hierarchy showed relatively low values of linearity (h' = 0.699) as well as steepness (slope = 0.523). All these findings support that rook's social system, although showing high fission-fusion dynamics in their social organisation (Clayton & Emery 2007), is characterized in part by egalitarian dynamics within their colony.

In the group service test, birds showed sustained, but constantly low delivery rates, varying between 3 and 6 successful deliveries across the 5 prosocial test sessions. In the last two test sessions two individuals provided food successfully in 13.3% of trials (8 food pieces), in which DB, the dominant male of the group, received 7 out of 8 pieces (87.5% of food). Conversely, DB only provided 1 piece of food. GB, the subadult and most subordinate female, provided 7 pieces and received none. OR, one female of intermediate rank and the third habituated bird in training phase III, provided no piece of food but received one piece. These results suggest, that food provisionings in this experimental context occur most likely from subordinate towards dominant individuals in rooks. But unfortunately, since only 3 individuals participated in the prosocial test, there cannot be drawn clear conclusions nor results can be tested on significance. Nevertheless is this result in contrast to most findings of other studies, where prosocial behaviour is mainly reported from dominant individuals directed towards subordinate (Cronin 2012; Massen et al. 2010; Takimoto et al. 2010). Dominant individuals were reported to use prosocial actions to emphasize their dominance position. On the other hand, prosocial food provisionings from subordinate individuals directed towards dominants, can also be used by subordinates to obtain benefits from dominants or could occur as a strategy for harassment avoidance in order to protect themselves against future acts of aggression. Another explanation of this behaviour is that it might occur due to social pressure as reported in keas (Tebbich et al. 1996). Acts of social pressure were not observed during test sessions of the present study and thus can be ruled out. Displacements on the apparatus were observed in 4 out of 60 trials during the last 2 prosocial test sessions, mainly directed from DB towards GB, by displacing GB from the receiving perch at position 1 two times and one time from the serving perch at position 0. Once, RO displaced OR from position 1. Acts of aggression towards the recipient in trials of successfully delivered food items did not occur. Generally, the observed trend of food provisionings in the direction of subordinate towards dominant individuals in rooks could not be analysed statistically. To confirm these findings in rooks and to test the influence of dominance hierarchy on prosocial behaviour in different corvid species in general, further studies have to be conducted since there are no data available in corvids yet.

Throughout the last 2 prosocial test sessions, food was delivered to a recipient already waiting in position 1 in 3 out of 8 trials. During these trials, local or stimulus enhancement might had facilitated the donor's motivation to provide food. In jackdaws, prosocial food deliveries were significantly depending on the recipients' showing interest in the reward (Schwab et al. 2012). Actors were more likely to deliver food to a recipient if the recipient approached the apparatus and stayed next to it prior to the actors' arrival. Here, the authors concluded that the actor's choices were most likely facilitated by local or stimulus enhancement mechanisms rather than prosocial preferences per se. Other studies on marmosets (Burkart et al. 2007), cotton-top tamarins (Cronin et al. 2009) and chimpanzees (Vonk et al. 2008) found that the recipient's intent to reach for the reward was not influencing prosocial tendencies. Contrary, Burkart and van Schaik (2013) found that reaching attempts resulted in decreasing bar-pulling rates in common marmosets, whereas begging did not occur at all. In the present study on rooks, there was no evidence for active vocal signalling, like begging calls, nor did individuals display begging related behaviours and signs of need. Hence, the remaining 5 successful food deliveries during the last 2 test

sessions (62.5% of successful deliveries) can be ascribed to proactive prosociality. But unfortunately, based on the low delivery rates, it is difficult to draw significant conclusions. Potentially occurring alternative factors influencing prosocial behaviour, like an expectation of reciprocity or seeking for reputation (Burkart & van Schaik 2013), are enhanced cognitively demanding traits (Stevens et al. 2005) not being described in rooks and thus unlikely to explain prosocial behaviour in this corvid species. Social facilitation as proximate mechanism can additionally be ruled out, since the group composition as well as the identity of cooperating dyads were not manipulated and modified in the group service paradigm (Burkart & van Schaik 2013).

Generally, food deliveries were expected to be much higher in rooks, considering that in primates, prosocial tendencies were found to be positively correlated to social tolerance (Burkart et al. 2014) and rooks showed very high levels of social tolerance in the food distribution assessment of the group service paradigm. Nevertheless, low delivery numbers might be an artefact of the small sample size of just 3 (out of 12) individuals successfully habituated in the last training phase (phase III) and thus participating in test phase IV and V. Additionally, in the prosocial test birds had to coordinate their actions because food was only accessible as long as the providing bird was sitting on the serving perch and being tolerant enough, allowing other birds to retrieve the food. A small sample size of just 3 individuals in this regard might be challenging, making the coordination of actions more difficult compared to a bigger sample size, where more individuals have the possibility to interact.

An alternative or additional explanation influencing prosocial behaviour might be that individuals did not fully understand the requirements of the task and thus the consequences of manipulating the serving perch and providing food exclusively to the group. In this context, birds might had still expected to receive the food themselves since habituation and training phases, where the reward could always be obtained by the birds themselves, lasted for a quite long period of 10 month. To control for the bird's comprehension of the task design, two control conditions, an empty control, where no food was present, and a blocked control, where the access to the reward was blocked but allowed visual and olfactory cues to be still present, were introduced (Burkart & van Schaik 2013). Further, individuals had to pass a specific criterion during each habituation and training phase, additionally ensuring an understanding of task requirements. In this context, I will only regard to results of the last two sessions of test phase IV and V because until then all participating individuals had many opportunities to experience the outcome of their actions and thus were expected to have learnt, that manipulating the serving perch does not create access to food to themselves but to their group members exclusively (Burkart & van Schaik 2013; Horn et al. 2016). Therefore, looking at results on an individual level allowed for a clearer understanding of individual's task comprehension and a potential occurrence of additional proximate mechanisms, like e.g. a lack of inhibitory control.

DB, the dominant male, landed significantly more often during test sessions, compared to both empty and blocked control and therefore it can be argued that this bird understood the consequences of manipulating the serving perch (Burkart & van Schaik 2013). Additionally, DB received 23 out of 35 food pieces (65.7%) during motivation trials of

prosocial test, 31 pieces (88.6%) during empty and 26 pieces (80%) during blocked control, where food could be obtained directly by the individual manipulating the serving perch, further indicating that DB did not lose interest in the apparatus and kept being interested in the offered reward throughout the experiment.
OR showed non-significant results when comparing both test with empty and blocked control, based on the number of landings. But OR's performance showed a positive tendency: during the last 2 prosocial test sessions, OR landed on the apparatus during 2 trials and did not land during both empty and blocked control at all. A general lack of motivation or interest in the apparatus might be a possible explanation for the performance of OR, since OR hardy landed during the first 3 prosocial test sessions neither. Generally, all birds showed a preference for the offered food reward and did not receive any feeding prior to testing. Hence, birds should always had been hungry and interested in the reward.
GB, the subadult female of the group which provided 7 out of 8 successfully delivered food items, showed a positive trend when comparing the number of trials with landings during prosocial test sessions with sessions of empty or blocked control. Thus, on the one hand it is not totally clear whether GB really understood the contingencies of the task, but on the other hand, GB waited during several trials on the provisioning perch for a longer period of time, making food available to its group members at position 1. Upon these trials some resulted in successful deliveries and during others no one approached the apparatus to retrieve the food item.
Overall, the number of landings on the serving perch decreased throughout the 5 test sessions from 25 trials with landings in test session 1 to 11 trials with landings in test session 4 but increased again in the last test session to 19 trials with landings. Comparably, the number of landings during empty control sessions decreased strongly to cero landings in session number 3 and stayed very low during the last 2 control sessions (2 trials and 1 trail with landings respectively). These findings allow to exclude the possibility that the bird's motivation of manipulating the serving perch was based on play behaviour or exploration of the apparatus. If this would had been the bird's motivation, the number of trials with landings during empty control sessions should be comparable to the number found during prosocial test sessions, but this was apparently not the case.
Blocked control sessions of phase V served to analyse a possibly occurring lack of inhibitory control to manipulate the serving perch in the presence of food. This could occur due to eminent visual as well as olfactory cues or alternatively because birds still might had expected to receive the food themselves. Thus, birds still may have not understood task's features. Both individual results as well as the overall number of trials with landings allow to exclude this possibility. The grouped number of trials with landings of all individuals started already very low at only 1 trial in session 1 and continued staying very low in successive sessions, only showing an increase in the last blocked control session (session 5) to 7 out of 30 trials with landings.
Thornton and McAuliffe (2015) criticised, that by conducing blocked control sessions after prosocial test sessions, order effects might come into play, resulting in an decreasing motivation of birds to land on the apparatus and thus to participate in the experiment in general. Therefore Horn and colleagues (2016) introduced an retest to control for possibly

occurring order effects, consisting of 2 prosocial test sessions and 2 empty control sessions. In the present study, test sessions and empty control sessions of the retest were conducted on alternating days, 10 weeks after the last blocked control session of phase V. The number of trials with landings on the serving perch during test sessions of the retest and the last 2 test sessions of phase IV were similarly high in this study, making an occurrence of order effects unlikely. Additionally, a comparison of motivation trials of the last 2 sessions of both phase IV and phase V as well as of the retest was further supporting this finding. Results indicate that birds continued being interested in the apparatus throughout the experiment. Individuals retrieved 100% of food items (14 out of 14) during motivation trials of the last 2 sessions of the prosocial test and empty control of phase IV, 78.6% (11 pieces) of blocked control and 92.9% (13 out of 14 pieces) of the last 2 sessions of the prosocial test and empty control of the retest. Overall, DB, the dominant male, received most food items during motivation trials. Contrary, if birds would had shown a decrease in retrieved food pieces during motivation trials of succeeding phases, a loss of birds' motivation would have been evident.

Contrary to dyadic or triadic prosocial choice tasks, in the group service paradigm birds can freely choose with whom to cooperate and therefore I expected the strength of social bonds to have an influence on the identity of cooperating dyads. I expected more prosocial behaviour among individuals with stronger social bonds, compared to individuals with weaker social bonds. Previously, a positive effect of pair bonds on prosocial behaviour had been found in primates, where 24 groups of 15 primate species were tested with the group service paradigm (Burkart et al. 2014). Unfortunately, it was not possible to test this hypothesis in rooks in this experimental setting because from habituation phase I ongoing, only one individual out of a couple (with one exception, where both individuals, GE and RT, did not participate in phase I at all) come to the apparatus and participated in the experiment. The same pattern was visible in the food distribution assessment. In a study on food retrieving strategies in rooks, paired individuals were found to perform fewer attempts to obtain a food reward compared to unpaired individuals (Jolles et al. 2013). The authors concluded that for paired individuals, making food available might be costly for the short-run since females were scrounging for the food item frequently, but argued that on a long-run, males allowing females to scrounge might strengthen the relationship (Emery et al. 2007). In the present study, females did not scrounge for food. In contrast, received food items were actively offered by subjects. Video-based data as well as anecdotal observations suggest that food offerings of retrieved food items during habituation and training phases from participating individuals towards their bonded partners might be one explanation for their partner's lacking motivation to participate in the experiment. Feeding events were most prevalent from DB feeding WE (68.8% of all observed feedings), but also occurred from GR towards LI, from RO towards HB as well as from HB towards OR. Generally, 83.3% of feedings occurred between individuals with strong social bonds (primary relationships), where two males (DB and HB) and one female (GR) were feeding their partners. The remaining 16.7% were observed between two individuals forming a secondary relationship, where the female (RO) was feeding the male bird (HB). Previously, a study on rooks found a significant effect of gender on food offerings, with only males offering food to females (Scheid et al. 2008). In contrast to findings of Scheid and

colleagues, in the present study an equal number of males and females offered food. Other alternative strategies, like stealing retrieved food items and pilfering cashes were observed during habituation and training as well.
Addressing the topic of relationship quality and prosocial behaviour again, both individuals GB and DB, which were involved in nearly all successful food deliveries, were found to form a weak relationship (> 5% of GB's, but < 5% of DB's individual total sociality indices). This demonstrates, that food deliveries and more generally prosocial behaviour does occur between weakly bonded individuals in rooks as well. Additionally, after DB retrieved one food item successfully during one trial of the prosocial test, one instance of reciprocity was observed when DB approached GB and fed GB, without GB begging for the food. In a study on food and object sharing in juvenile jackdaws, the authors described reciprocity in this closely related corvid species and discussed it as a by-product of proximity (von Bayern et al. 2007). Contrary, Scheid and colleagues (2008) discussed food-offerings in juvenile rooks to act as costly signal, presenting the social quality of donors to their social group. The authors further did not find any evidence for reciprocity of food-offerings, but they found significant statistical support for mutual tolerance at co-feeding to be reciprocated in rooks. It is difficult to conclude which motivations might be behind the observed act of reciprocity in the present study since it was not possible to statistically test the underlying mechanisms.

Concerning the analysis of group structure in general, pooled data of affiliations as well as proximities revealed the existence of primary, secondary as well as week social relationships in the observed group of rooks. Individuals involved in primary relationships were showing the highest frequencies of both affiliative behaviours and spatial proximities. Primary and secondary relationships are being described to form the backbone of rook's social structure (Boucherie et al. 2016).
Pooled data of agonistic interactions of the time of observation revealed a significantly linear dominance hierarchy (h' = 0.913) with a significant moderate steepness (slope = 0.768). Previous studies have found a linear dominance hierarchy in rook's social organization as well (Scheid et al. 2008; Jolles et al. 2013). When analysing dyadic dominance indices including data up until the food distribution assessment of the group service paradigm, rook's dominance hierarchy showed lower values of linearity (h' = 0.699) as well as steepness (slope = 0.523). An additional comparison of individual's David's scores of each block 1, 2 and 3 separately, revealed a considerable variability of individual's rank order over time. In line with already mentioned results of individuals' rank-shiftings, a shallow steepness of dominance hierarchy may emphasize low individual's differences in their chance to win dominance encounters (de Vries et al. 2006). Rook's dominance hierarchy might therefore not be as transitive as first results of pooled data were indicating.

The present study examined the existence of prosocial tendencies in rooks and tried to analyse underlying motivations like a potential influence of social relationships and dominance hierarchies on prosocial behaviour in this communally breeding corvid species. Results of the food distribution assessment of the group service paradigm go beyond expectations but can still be argued to be in line with the cooperative breeding hypothesis.

Although results of the present study do not allow to draw conclusions of an existence of proactive prosociality on species level, some instances of prosocial behaviour were observed in test sessions of the group service paradigm.
It remains unclear if more individuals would had reached the criterion during habituation and training phases, whether they would had provided more food and hence would had shown more prosocial behaviour in this experimental context.
Further, bird's inexperience to experimental testing and their deficient habituation to a proximity of humans prior to the start of this study, revealed as quite challenging and unfortunately might be an important influencing factors on their performance during the experiment. Additionally, the inability to fly of most birds made a manipulation of the apparatus' see-saw mechanism more difficult. Some birds, like for instance GR, were observed to have troubles with the moving see-saw, lacking the ability to equilibrate on the moving serving perch, based on partly amputated wings. All these additional factors unfortunately cannot be ignored and should be taken into consideration when talking about bird's performance in the present study.
In general, the results of the present study highlight that rooks are a promising candidate to show proactive prosocial behaviour, but more individuals need to be tested to be able to draw clearer conclusions on the presence of other-regarding preferences in rooks.
Generally, still more species, closely and distantly related ones, should be tested with the same experimental set-up to broaden our understanding and knowledge about proximate mechanisms underlying prosocial behaviour. The group service paradigm seems to me a promising experimental approach to do so. Upcoming results will benefit to research on other-regarding preferences and may add important puzzle pieces to the larger picture of the evolution of prosocial behaviour and altruism.

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Appendix

R script

```
#####Correlation of behavioural durations and frequencies#####

###Matrix correlation

#load packages
install.packages("devtools")
library(devtools)
install_github("DLEIVA/DyaDA")
library("DyaDA")

##setting working directory
setwd("D:/UNI/Master Verhaltens- Neuro- und
Kognitionsbiologie/MASTERARBEIT/R")

#Load data_durations
data_dur<-read.csv(file.choose(),sep=";")
#name rows
rownames(data_dur)<-data_dur[,1]
data_dur<-data_dur[,-c(1)]
#create matrix
X<-data.matrix(data_dur, rownames.force = NA)
as.data.frame(X, what="both")

#Load data_frequencies
data_freq<-read.csv(file.choose(),sep=";")
#name rows
rownames(data_freq)<-data_freq[,1]
data_freq<-data_freq[,-c(1)]
#create matrix
Y<-data.matrix(data_freq, rownames.force = NA)
as.data.frame(Y, what="both")

#getspearman: Spearman's Correlation between two matrices (#In
DLEIVA/DyaDA: Dyadic Data Analysis)
getspearman(X,Y)

#and additionally: Test for association between paired samples, using
Spearman's rho.
cor.test(X, Y,
         alternative = c("two.sided"),
         method = c("spearman"),
         exact = NULL, conf.level = 0.95, continuity = FALSE)



#####Group service paradigm#####

###Pielou's eveness index J'

#load packages
install.packages("vegan")
library(vegan)

food_distribution<-read.csv(file.choose(),sep=";",head=FALSE)
```

```
###12 birds
H <- diversity(food_distribution)
## Species richness (S) and Pielou's evenness (J):
S <- 12
J <- H/log(S)
J

###5 birds
H <- diversity(food_distribution)
## Species richness (S) and Pielou's evenness (J):
S <- 5
J <- H/log(S)
J



###Fisher's exact test

#group service_ test vs empty and blocked control

##Session 4 and 5

#DB
##PST vs. EC
#read data
DB_PST_EC<-read.csv(file.choose(),sep=";")
#name rows
rownames(DB_PST_EC)<-DB_PST_EC[,1]
DB_PST_EC<-DB_PST_EC[,-c(1)]
##fisher exact test
results_DB_PST_EC<-fisher.test(DB_PST_EC)

##PST vs. BC
DB_PST_BC<-read.csv(file.choose(),sep=";")
#name rows
rownames(DB_PST_BC)<-DB_PST_BC[,1]
DB_PST_BC<-DB_PST_BC[,-c(1)]
##fisher exact test
results_DB_PST_BC<-fisher.test(DB_PST_BC)


#GB
##PST vs. EC
#read data
GB_PST_EC<-read.csv(file.choose(),sep=";")
#name rows
rownames(GB_PST_EC)<-GB_PST_EC[,1]
GB_PST_EC<-GB_PST_EC[,-c(1)]
##fisher exact test
results_GB_PST_EC<-fisher.test(GB_PST_EC)

##PST vs. BC
GB_PST_BC<-read.csv(file.choose(),sep=";")
#name rows
rownames(GB_PST_BC)<-GB_PST_BC[,1]
GB_PST_BC<-GB_PST_BC[,-c(1)]
##fisher exact test
results_GB_PST_BC<-fisher.test(GB_PST_BC)
```

```
#OR
##PST vs. EC
#read data
O_PST_EC<-read.csv(file.choose(),sep=";")
#name rows
rownames(O_PST_EC)<-O_PST_EC[,1]
O_PST_EC<-O_PST_EC[,-c(1)]
##fisher exact test
results_O_PST_EC<-fisher.test(O_PST_EC)

##PST vs. BC
O_PST_BC<-read.csv(file.choose(),sep=";")
#name rows
rownames(O_PST_BC)<-O_PST_BC[,1]
O_PST_BC<-O_PST_BC[,-c(1)]
##fisher exact test
results_O_PST_BC<-fisher.test(O_PST_BC)



###Holm-Bonferroni correction for multiple comparisons
#group service_ test vs empty and blocked control

p<-read.csv(file.choose(),sep=";",head=FALSE)

p.adjust(p,"holm", n = length(p))



###RE-TEST

#DB
#read data
DB_re_test<-read.csv(file.choose(),sep=";")
#name rows
rownames(DB_re_test)<-DB_re_test[,1]
DB_re_test<-DB_re_test[,-c(1)]
##fisher exact test
results_DB_re_test<-fisher.test(DB_re_test)

#GB
#read data
GB_re_test<-read.csv(file.choose(),sep=";")
#name rows
rownames(GB_re_test)<-GB_re_test[,1]
GB_re_test<-GB_re_test[,-c(1)]
##fisher exact test
results_GB_re_test<-fisher.test(GB_re_test)

#OR
#read data
O_re_test<-read.csv(file.choose(),sep=";")
#name rows
rownames(O_re_test)<-O_re_test[,1]
O_re_test<-O_re_test[,-c(1)]
##fisher exact test
results_O_re_test<-fisher.test(O_re_test)
```

```
#####Analysis of dominance hierarchy#####


###Linearity of dominance hierarchy

#load packages
install.packages("devtools")
library(devtools)
install_github("DLEIVA/DyaDA")
library("DyaDA")

#setting workingdirectory
setwd("D:/UNI/Master Verhaltens- Neuro- und
Kognitionsbiologie/MASTERARBEIT")

#load data
displacements<-read.csv(file.choose(),sep=";")

#name rows
rownames(displacements)<-displacements[,1]
displacements<-displacements[,-c(1)]

#create matrix
X<-data.matrix(displacements, rownames.force = NA)

#linear.hierarchy.test: Testing Linearity in dominanace hierarchies (#In
DLEIVA/DyaDA: Dyadic Data Analysis)
linear.hierarchy.test(X,rep=10000)

#additionally: getimplandau: Improved Landau's Linearity Index -h'- (#In
DLEIVA/DyaDA: Dyadic Data Analysis)
getimplandau(X)



###Steepness of dominance hierarchy

#load packages
install.packages("steepness")
library(steepness)

#load data
S<-read.csv(file.choose(),sep=";")

#name rows
rownames(S)<-S[,1]
S<-S[,-c(1)]
s<-data.matrix(S)

#testing steepness in dominance hierarchy
names(S)
individuals <- c("DB", "GR", "OR", "RT", "RO", "LI", "HB", "GE", "WE",
"GG", "GB", "GW")
STP <- steeptest(s, rep=10000, names=individuals, method="Dij",
order=TRUE)
summary(STP)
x11()
plot(STP)
```

Zusammenfassung

In den letzten Jahren beschäftigten sich viele wissenschaftliche Studien mit dem Thema Prosozialität und Altruismus, da diese Eigenschaft ein wesentliches Merkmal der menschlichen Kooperation darstellt. Erst unlängst wurde prosoziales Verhalten auch bei einigen Primaten- und Rabenvogelarten dokumentiert. Durchgeführte Studien beinhalten jedoch teils widersprüchliche Ergebnisse. Dies führte zu intensiven Diskussionen innerhalb der wissenschaftlichen Gemeinschaft und die Formulierung verschiedener Hypothesen über den Einfluss sozio-ökologischer Unterschiede und anderer Mechanismen, welche zur Entwicklung prosozialer Tendenzen beigetragen haben, war die Folge.
Die vorliegende Studie untersuchte die Existenz sowie Ausprägung von sozialer Toleranz und prosozialem Verhalten in Saatkrähen (*Corvus frugilegus*), eine in Kolonien brütende Art der Familie der Rabenvögel (*Corvidae*). In Gefangenschaft gehaltene Tiere wurden mit dem „Group Service Paradigm“ getestet, wobei ein Tier der Gruppe durch Bedienung eines Apparates mit einem Wippmechanismus, anderen Tieren Futter bereitstellen konnte, ohne dieses selber jedoch bekommen zu können. Sobald dieses Tier den Test-Apparat wieder verließ, war auch das Futter wieder außer Reichweite für die gesamte Gruppe. Diese Studie untersuchte und analysierte des Weiteren zugrunde liegende Motivationen von prosozialem Verhalten, wie einen möglichen Einfluss von sozialen Beziehungen sowie Dominanzhierarchien auf prosoziale Präferenzen. Die Ergebnisse dieser Studie zeigen, dass Saatkrähen eine sehr hohe intraspezifische soziale Toleranz aufweisen. Leider lassen die Ergebnisse des prosozialen Tests keine Rückschlüsse auf das Vorhandensein von proaktiver Prosozialität auf Artebene zu, da schlussendlich nur drei Tiere am Test teilnahmen. Während des hier durchgeführten Tests wurde jedoch prosoziales Verhalten bei den Saatkrähen beobachtet. 5 von 8 der während der letzten beiden Testsitzungen erfolgreich zur Verfügung gestellten Futterstücke, wurden proaktiv bereitgestellt, ohne dass zuvor ein weiterer Vogel bereits auf der Empfänger-Position wartete oder um das Futter bettelte. Währenddessen wurden auch keine aggressiven Verhaltensweisen beobachtet. Es bleibt jedoch unklar, wenn mehr Individuen das Kriterium während der Habituations- und Trainingsphasen erreicht hätten, ob ebenfalls mehr Futterstücke während des Tests bereitgestellt worden wären und somit auch mehr prosoziales Verhalten in diesem experimentellen Kontext gezeigt worden wäre. Die Unerfahrenheit der Tiere in Bezug auf experimentelle Tests sowie amputierte Flügeln, als Folge früherer Verletzungen, werden in dieser Arbeit als potentiell wichtige Einflussfaktoren auf die Leistung einzelner Individuen während des Experiments diskutiert und dürfen nicht außer Acht gelassen werden. Die Ergebnisse der vorliegenden Studie verdeutlichen, dass Saatkrähen ein vielversprechender Kandidat sind, proaktives prosoziales Verhalten im experimentellen Kontext zu zeigen. Mehr Individuen müssen jedoch getestet werden, um in der Lage zu sein klarere Aussagen über das Vorhandensein prosozialer Tendenzen in Saatkrähen treffen zu können.