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# MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„Comparing food sharing and social tolerance in  
jackdaws (*Corvus monedula*) under daily life conditions  
and in experimental settings“

verfasst von / submitted by

Christiane Rössler BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of  
Master of Science (MSc)

Wien, 2017 / Vienna 2017

Studienkennzahl lt. Studienblatt /  
degree programme code as it appears on  
the student record sheet:

A 066 878

Studienrichtung lt. Studienblatt /  
degree programme as it appears on  
the student record sheet:

“Masterstudium  
Verhaltens-, Neuro- und Kognitionsbiologie”

Betreut von / Supervisor:

Univ.-Prof. Mag. Dr. Thomas Bugnyar

Mitbetreut von / Co-Supervisor:

Mag. Dr. Lisa Horn



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## **Acknowledgments**

First, I would like to thank the FÖRDERUNGSSTIPENDIUM of the University of Vienna for supporting this work.

I owe special thanks to my supervisors UNIV.-PROF. MAG. DR. THOMAS BUGNYAR and MAG. DR. LISA HORN for their support and encouragement during the data collection for my master's thesis.

I owe a great debt of gratitude to DR. AUGUSTE VON BAYERN. I collected the data for my master's thesis under the leadership and support of Dr. Auguste von Bayern and benefited from her subject-specific assistance. Additionally, for the use of birds and aviaries I thank the Max-Planck Institute for Ornithology, Bavaria, Germany.

Furthermore, I would like to thank DR. JORG MASSEN, who introduced me to Dr. Auguste von Bayern. Thank you to DR. ANDRÁS PÉTER, who built one seesaw and helped me with the R Code for the statistical analysis.

Also, I want to say thank you to DR. PALMYRE BOUCHERIE for the interesting talk about social networks.

I also want to thank ALL COLLEAGUES AND PROFESSORS who facilitated and encouraged me during this master's thesis.

Finally, I want to thank MY WHOLE FAMILY whose mental and financial support made it possible for me to study for this degree and collect the data for my thesis.



## Introduction

Living in social groups requires certain types of socio-cognitive skills due to animals' need to repeatedly interact with another (Humphrey, 1976). Notably, social animals need to tolerate each other's proximity, whereby different social systems (i.e., breeding systems) may show differences in social tolerance (Burkart, Hrdy, & Van Schaik, 2009; Clayton & Emery, 2007). The structure of social groups is influenced not only by the breeding system (Burkart et al., 2009) but also by differences in individual relationships (Fraser & Bugnyar, 2010).

Behaviours that are essential for forming and maintaining relationships include co-feeding, food sharing, and prosocial behaviour. These behaviours require further proximity and tolerance between the animals (Burkart & Van Schaik, 2013; Horn, Scheer, Bugnyar, & Massen, 2016; Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016; De Waal & Brosnan, 2006). Social tolerance describes tolerating other conspecifics in close proximity (e.g., birds sitting closely together, i.e., contact sit) and can also include proximity in a feeding context (e.g., co-feeding or food sharing) (Asakawa-Haas, Schiestl, Bugnyar, & Massen, 2016). Co-feeding occurs when animals sit in reachable distance of each other and eat together and therefore must allow each other to approach. Food sharing is an active form of cooperation because an individual voluntarily gives a piece of food to another animal with its hands or mouth (Marshall-Pescini et al., 2016; De Waal & Brosnan, 2006) and thus incurs a cost at the benefit of the recipient. Some researchers view food sharing as a naturalistic expression of prosocial behaviour (Von Bayern, De Kort, Clayton, & Emery, 2007). Prosocial behaviour is behaviour that has benefits for others and costs for the actor (Silk & House, 2011).

Primates (Burkart & Van Schaik, 2013) but also corvids are an example of animals with different breeding systems and thus likely have differences in social tolerance (e.g., Emery, Seed, Von Bayern, & Clayton, 2007; Horn et al., 2016; Sima, Pika, & Bugnyar, 2016). For instance, ravens (*Corvus corax*) are territorial breeders that do not tolerate conspecifics in their territory (Braun & Bugnyar, 2012). Rooks (*Corvus frugilegus*) are a colonially breeding species, with pairs nesting close to each other (Scheid et al., 2008). Azure-winged magpies (*Cyanopica cyanus*) are colonial cooperative breeders, in which individuals may help with the rearing of others' young in case they failed breeding themselves (Horn et al., 2016). However, in all corvid species the main social unit is the pair bond (Braun & Bugnyar, 2012; Emery et al., 2007). Not only as juveniles and subadults but also as adults, individuals may form additional affiliative relationships (Boucherie, Mariette, Bret, & Dufour, 2016a; Emery et al., 2007) with other individuals and exhibit food-sharing and co-feeding behaviours with their partner and friends (Emery et al., 2007). This is also true for territorial species like ravens, at least during the non-breeding phase (Braun & Bugnyar, 2012).

Social tolerance can be examined in daily life conditions or in experimental setups. For the natural contexts, studies can include feeding observations (Sima et al., 2016) or analysing relationships and social interactions via observations (Boucherie et al., 2016a). Usually, the behaviours in such monopolising settings are analysed, and it is studied whether animals accept others in their proximity during a feeding context without displacing their conspecifics (Boucherie et al., 2016a; Sima et al., 2016). For the experimental setting, the evenness of food distribution in the group (Burkart & Van Schaik, 2013; Horn et al., 2016) can be used to describe whether the food is equally distributed. Therefore, the value Pielou's  $J'$  is used to measure the evenness (Mulder, Bazeley-White, Dimitrakopoulos Hector, Scherer-Lorenzen, Schmid, 2004; Pielou, 1966).

Social tolerance may also influence the outcome of cooperation tasks, where conditions determine whether both partners, none, or just one partner are rewarded (Di Lascio, Nyffeler, Bshary, & Bugnyar, 2013; Melis, Hare, & Tomasello, 2006; Massen, Ritter, & Bugnyar, 2015; Scheid & Noë, 2010). An example of a mutual rewarding cooperation task is the string-pull paradigm, where two individuals must pull simultaneously on strings that pull a board with food pieces to the wire mesh. In this setting, the donor also has the choice to exchange food pieces or to refuse the task. Better cooperation was seen in primates when they tolerated each other (Melis et al., 2006) and in ravens with the opposite sex (Massen et al., 2015) as well as between friends (Asakawa-Haas et al., 2016).

An example of an other-rewarding cooperation task is the food-sharing paradigm. Here one subject, the donor, is placed on one side of a cage, while another individual, the recipient, is placed in the adjacent compartment. As soon as the donor opens a box by pulling a string and thereby removing the plastic lid, the other recipient has access to the part of the box on its side. The donor has to make a choice between 2 boxes: one contains a reward in both sections thus rewarding both birds, and the other only contains a reward on the donor's side. While the choice makes no difference to the donor, the recipient is either rewarded at no cost to the donor or it does not receive anything. The decision of which box to open can also be influenced by the behaviour of the recipient. For instance, by positioning itself in front of one box, the recipient can signal its preference for that box. Donors have a higher tendency to follow the recipient and open the respective box when the recipient is from the opposite sex (Di Lascio et al., 2013; Schwab, Schwoboda, Kotrschal, & Bugnyar, 2012).

In all of these experiments, cooperation was only seen when the cooperation partners tolerated each other (e.g., Burkart et al., 2013; Horn et al. 2016; Massen et al. 2015). Social tolerance is particularly important for cooperation tasks that need proximity (e.g., birds sitting closely together) (Asakawa-Haas et al., 2016; Burkart & van Schaik, 2013; Di Lascio et al., 2013; Massen et al., 2015). Furthermore, there are different approaches to analyse social tolerance, as it can be analysed in an experimental settings (Burkart & Van Schaik, 2013;

Horn et al., 2016) or under daily life conditions (Boucherie et al., 2016 a; Sima et al., 2016). However, to my knowledge, the above-mentioned experiments and observations were mainly focused either on experimental setups or under daily life conditions and seldom compared the two (but see Melis et al., 2006; Massen, Ritter, & Bugnyar, 2015; Sima et al., 2016).

### Aims & objectives

The goal of this study is to examine social tolerance in a group of captive jackdaws (*Corvus monedula*; Figure 1) using both, an experimental setting and daily life observations in the birds' natural environment.



**Figure 1: Jackdaws (*Corvus monedula*):** A couple (Apache ♀ (left) and Cherokee ♂ (right)) sitting next to each other.

For the experimental setting, I chose a group service paradigm recently established by (Burkart & Van Schaik, 2013) to test for prosocial behaviour in primates. This paradigm has already been successfully adapted to birds by Horn et al. (2016) and consists of six total phases, whereby the third phase explicitly tests for evenness in food distribution, i.e., one of the measures of tolerance. The advantage of using the group service paradigm is that the individuals can choose their cooperation partner(s). Thus each animal of the group has access to the apparatus, allowing every bird to participate during the task because none of the animals have to be separated from the group members (Burkart & Van Schaik, 2013; Horn et al., 2016).

For the daily life context, I conducted focal observations i) on affiliative and agonistic interactions and ii) on food-sharing. Specifically, I wanted to know i) whether social tolerance is affected by social bonds and the hierarchy rank of individuals and ii) whether food-sharing is affected by the relationships between the individuals.

Jackdaws are an ideal candidate species for answering these questions, as they establish long-term pair bonds and show parental care (De Kort, Emery, & Clayton, 2006; Henderson, Hart, & Burke, 2000). Notably, jackdaws are facultative colonial breeders, i.e., if breeding sites are scarce, they nest in close proximity to one another (Kubitza, Bugnyar, & Schwab, 2015), and they also show high tolerance for conspecifics near breeding as well as feeding sites (De Kort et al., 2006) like rooks (Scheid, Schmidt, & Noë, 2008; Scheid & Noë, 2010). Jackdaws also synchronise their breeding within the group but seldom show extra-pair copulation (De Kort et al., 2006; Henderson et al., 2000).

As social animals, jackdaws must remember the ranks of conspecifics to avoid fights and a linear hierarchy may help them minimise conflicts (Wechsler, 1988). Previous observations suggest that jackdaws' rank position remains stable throughout most of the year, but especially during the breeding season changes in rank can be seen. In general, males seem to be more dominant than females (Tamm, 1977). Additionally, females are mostly paired with a higher ranked male. If females are paired with a lower ranked bird it could be that the females show male-typical behaviours and males female-typical behaviours (Lorenz, 1935). If females are paired with a high-ranked male, a female can rise in her rank position if her mate supports her during fights (Lorenz, 1935; Tamm, 1977). Females also support males, especially in spring during the breeding season, but this support decreases during the rest of the year (Lorenz, 1935). High-ranking pairs also exhibit higher reproductive output than lower-rank birds (Tamm, 1977). Furthermore, dominant males actively displace subordinates from their feeding locations (Tamm, 1977). Typically, paired individuals of corvids species (i.e., jackdaws) are more dominant than unpaired individuals (Braun & Bugnyar, 2012; Kubitza et al., 2015).

Juvenile jackdaws indiscriminately show food sharing within the groups, whereas subadults increasingly concentrate food sharing to their partner (De Kort, Emery, & Clayton, 2003; De Kort et al., 2006; Von Bayern et al., 2007). Thus, I expect that adults should only demonstrate food sharing to their specific pair-bonded partner. Due to social tolerance between pair partners (Von Bayern et al., 2007; Kubitza et al., 2015), I expect that birds of both sexes can be donors and can share food pieces.

Additionally, I predict that males receive more food pieces than females, because males are more dominant than females (Lorenz, 1935; Tamm, 1977). Because high-ranked couples also have greater breeding success and a higher chance to care for their chicks, they should be more successful at acquiring food pieces during the food distribution assessment. They should also be more tolerant of their partner and obtain more food pieces than unpaired individuals (Lorenz, 1935; Tamm, 1977).

Furthermore, I argue that the higher the rank, the lower the number of affiliative behaviours within the group, and accordingly the lower the number of interacting partners, the stronger the affiliative behaviour directly to the partner (Tamm, 1977).

From a comparative perspective, I expect that jackdaws show a similar social tolerance with food compared to rooks (Hengl, MSc in prep.) and azure-winged magpies (Horn et al., 2016) and a higher tolerance than crows and adult ravens (Horn et al., in prep.). These differences may be due to differences in the species' breeding system, with colonial breeders (such as jackdaws and rooks) and cooperative breeders (such as azure-winged magpies) requiring higher social tolerance towards conspecifics than territorial breeders (such as ravens and crows) (Braun & Bugnyar, 2012; Kubitza et al., 2015; Horn et al., 2016; Scheid et al., 2008; Von Bolzheim & Bauer, 1993).

## Materials and Methods

### Subjects

I started the data collection of my master's project in the Comparative Cognition Research Group of the Max-Planck-Institute for Ornithology in Seewiesen, Germany on the 8<sup>th</sup> of August in 2016. The possible study population consisted of 21 captive jackdaws (*Corvus monedula*) that were kept separately in two groups at the time (Table 1, Figure 2). Group 1 consisted of 10 individuals (5 females/5 males) and Group 2 consisted of 11 individuals (6 females/5 males).

The group that I eventually tested in the food distribution test consisted of 5 birds of Group 1 (2 females/3 males). On the 23<sup>rd</sup> of November in 2016, the group of five birds was newly composed with another group of 9 individuals of Group 2 (5 females/4 males), which I eventually also tested in the food distribution assessment. That is the reason why I am mostly concentrating on Group 1 and Group 3 (= newly composed group). One couple of Group 1 had to be separated, thus they could not participate in the food distribution test. In total 12 birds (6 females/ 6 males) could participate in the food distribution assessment. One bird (Mokka) in Group 3 was killed by a weasel during the study period (Table 2). All birds in Group 3 were adults older than 5 years. All birds were marked individually with coloured leg rings.

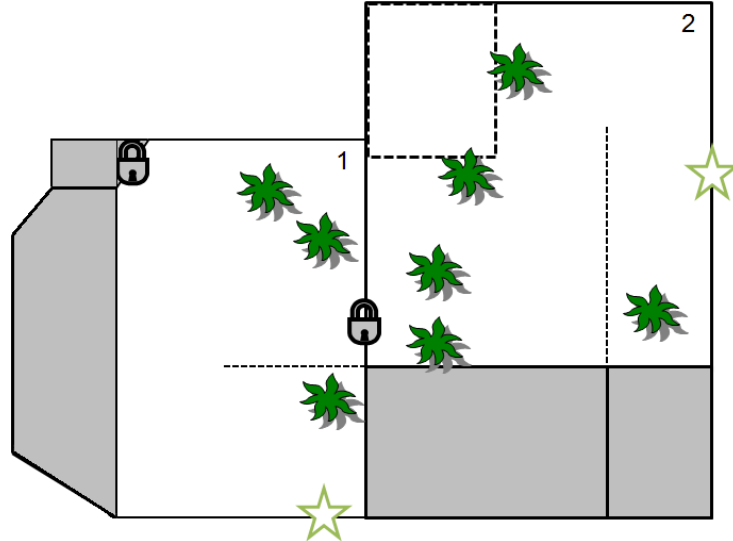
**Table 1: Possible study population at the start of my MSc project:** Names, abbreviations, sex, year of birth, and partner are depicted for each group. "-" no partner.

Group	Name	Abbreviation	Sex	Year	Subadult/Adult	Partner
Aviary 1	Blackfoot	Bl	male	2011	adult	-
	Cherokee	Ce	male	2011	adult	Ap
	Chapa	Ch	male	2011	adult	-
	Mohawk	Mk	male	2011	adult	Pr
	Tschock	Tk	male	2004	adult	Ja
	Apache	Ap	female	2011	adult	Ce
	Jackomo	Ja	female	2003	adult	Tk
	Pronto	Pr	female	2007	adult	Bu/Mk
	Bunny	Bu	male	2014	subadult	Pr
	Monkey	My	female	2014	subadult	-
Aviary 2	Chimney	Ch	male	2011	adult	Ud
	Mokka	Ma	male	unknown	adult	Mo
	Moony	My	male	unknown	adult	Cy
	Pirate	Pi	male	unknown	adult	Do
	Tassilo	Ts	male	unknown	adult	He
	Cyclop	Cy	female	2011	adult	My
	Dohli	Do	female	unknown	adult	Pi
	Hedwig	He	female	unknown	adult	Ts
	Mono	Mo	female	unknown	adult	Ma
	Polli	Po	female	unknown	adult	-
	Udo	Ud	female	2008	adult	Ch

**Table 2: New group composition of Group 3:** Names, abbreviations, sex, year of birth, and partner are depicted for each group. "-" no partner. † Mokka participated in the food distribution assessment but died some days later.

Group 3	Name	Abbreviation	Sex	Year	Subadult/Adult	Partner
Aviary 1 & 2	Blackfoot	Bl	male	2011	adult	-
	Chimney	Ch	male	2011	adult	Ud
	Mohawk	Mk	male	2011	adult	Pr
	Pirate	Pi	male	unknown	adult	Do
	Tassilo	Ts	male	unknown	adult	He
	Cyclop	Cy	female	2011	adult	-
	Dohli	Do	female	unknown	adult	Pi
	Hedwig	He	female	unknown	adult	Ts
	Mono	Mo	female	2003	adult	Ma/-
	Pronto	Pr	female	2007	adult	Bu/Mk
	Udo	Ud	female	2008	adult	Ch
	Mokka†	Ma	male	unknown	adult	Mo

The jackdaws were kept in two aviaries with adjacent experimental compartments. Aviary 1 was 15m x 9m x 2.80m and aviary 2 was 12m x 10m x 2.80m (Figure 2). All compartments had natural soil and vegetation, including bushes and small trees, and were equipped with breeding boxes. There were also mats on the floor with disinfectant properties. The birds had *ad libitum* access to food and water (Von Bayern, 2008).



**Figure 2: Schematic illustration of the aviaries:** Dotted line inside the main cage: nets for separating birds; grey area: non-reachable area and experimental compartments; lock: doors; green plant: main perches and bushes/trees in the aviaries; green star: position of the experimental apparatuses; numbers: depicts the aviaries and the group name.

### Focal observations

To investigate the group structure and relationships within the group, I conducted focal observations twice a week, either in the morning or in the afternoon and either within or outside a feeding context. I stood outside the cage and filmed each bird for five minutes. During each focal day, I pseudo-randomised the sequence of observed focal individuals so that the first and last birds were counterbalanced. In total, I conducted 74 focal observations, including 22 videos per individual of Group 1 (N=10), 22 videos of Group 2 (N=11), and 30 videos per individual of Group 3 (6 videos with Mokka, N=12; 24 videos without Mokka, N=11).

### Food sharing observations in the natural context

To examine food sharing in the natural context, I conducted food-sharing observations. I observed each jackdaw group for 30 minutes twice a week after focal observations, alternating in the morning and in the afternoon, from August 2016 to February 2017. Additionally, I conducted food-sharing observations in two blocks of five consecutive days in February and March (25/2/2017 – 13/3/2017), alternating morning and afternoon sessions. The birds had *ad libitum* access to their normal food and water before and during these observations.

I placed a food bowl with highly desirable food not part of their normal diet, i.e., a mixture of different worms (Zophobas and meal worms) and muesli in the middle of the cage. Two cameras (Panasonic HC V777EG-K and Sony HDRCX220E) filmed the aviary. Additionally, I stood outside the cage and used pen and paper to write down each food-sharing event that occurred outside the camera's view. I performed behavioural sampling (Martin, 1993) and analysed the whole group during the session.

The following variables were recorded for food sharing events:

- 1) "*a donor bird giving a piece of food to another bird (donor-initiated transfer)*" (De Kort et al., 2006)
- 2) the bird that received the food (recipient)
  - a) "*a recipient bird taking a piece of food directly out of another's beak (recipient-initiated transfer)*" (De Kort et al., 2006)
  - b) a recipient bird begging for, but not receiving a piece of food (recipient-initiated without transfer) (De Kort et al., 2006)

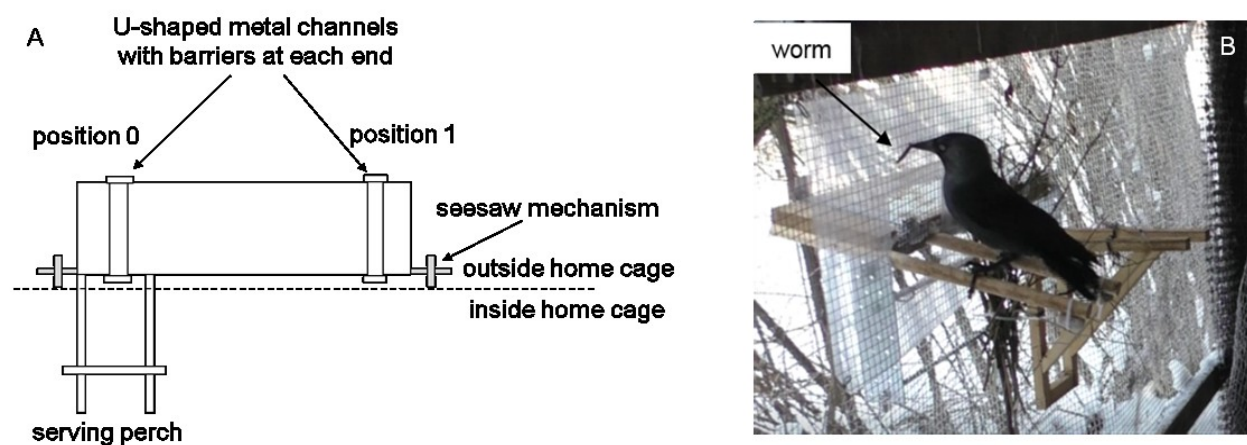
I conducted 13 food-sharing observations with Groups 1 and 17 with Group 2 as well as 30 observations of Group 3.

### Group Service Paradigm (GSP)

I experimentally assessed social tolerance and the evenness of food distribution in the group following the methods of the group service paradigm (Burkart & Van Schaik, 2013; Horn et al., 2016) with the seesaw apparatus in place. The experiment consisted of two habituation phases and one test phase (Horn et al., 2016). First, the birds were habituated to the apparatus and learned the procedure. Afterwards, I conducted the test investigating social tolerance and evenness of food distribution in the group. Originally, I planned to conduct a test for prosocial behaviour as well, but due to the start of the breeding season on 11 April 2017, I could not proceed to the test phase.

### Apparatus for the Group Service Paradigm

I used an apparatus with a seesaw mechanism (Figure 3) like in Horn and colleagues' experiment (Horn et al., 2016). The seesaw had two positions, 0 and 1, and was fixed in a downward position for the first three phases of my MSc project so that a food piece could automatically slide down the wire mesh. The perch in front of position 0 was fixed to the wooden board. If the seesaw was totally released, the bird could move the seesaw to a downward position when landing on this perch. The birds learned this during the training phase. Another perch was installed in front of position 1, out of reach from position 0 and without a connection to the seesaw, so that a bird could take a food piece through the wire mesh.



**Figure 3: Schematic of the apparatus adapted from Horn et al. (2016) and seesaw with bird:** A: *Position 0*: only the bird itself can get a food piece by sitting on the serving perch and thus activating the seesaw mechanism. *Position 1*: as soon as the seesaw is no longer fixed, the bird gets a food piece only with the aid of another bird that is sitting on the other perch and thus activates the tilt mechanism (Horn et al., 2016). The receiving perch is not in the picture; B: After landing on the seesaw a bird (Mohawk ♂) could take the food piece.

### Procedure of the Group Service Paradigm

In general, every bird had access to the seesaw during all phases of the GSP. However, birds were only separated during the habituation phases if an already-habituated individual started monopolising the apparatus, so that all of the birds eventually had access to the apparatus during habituation.

Testing took place from August 2016 until April 2017. The habituation and test phases were carried out in the morning before and after one hour of food deprivation. Tests were performed in the afternoon as well when possible. Due to the fact that the training phase was not essential for the social tolerance test, this phase is not further described. I used pen and paper to record which individuals obtained food, and all sessions were also video recorded (Panasonic HC V777EG-K or Sony HDRCX220E) for later analysis.

#### *I) Habituation Phase - Apparatus*

For two weeks, the seesaw was installed inside the cage and was not baited with food. Afterwards, a food bowl was installed in front of position 0 inside the cage to get the jackdaws habituated to approach the apparatus. The mechanism was partially fixed in a downward position (i.e., the seesaw mechanism only moved a little). I filled the food bowl with muesli and worms, put a camera inside the cage, and left the testing area so that the animals were not disturbed by my presence. Each session lasted thirty minutes. The birds were considered successfully habituated when they fed from the bowl at least five times (Horn et al., 2016). Due to the fact that I tested two groups, I tried to alternate the start time so that the animals had the same duration of food deprivation.

#### *II) Habituation Phase - Procedure*

During this phase, the birds learned the procedure: they had to fly to the seesaw, sit on the perch, take a worm through the wire mesh, vacate the position so that the next worm could be placed, and then return again. As with the first phase, the seesaw was partially fixed so that it could not move and stayed in the same position. For each session, I placed food pieces near the wire mesh, either in position 0 or in position 1 on alternating days, so the birds learned about both positions: the serving perch and the receiving perch. Food pieces were pieces of muesli. I adjusted the number of trials per session to the number of individuals in the group:  $N_{\text{trials}} = N_{\text{individual}} * 5$ . A trial lasted until a bird took the food or until a maximum of two minutes; after that, I caught the birds' attention again and put the next food piece in the same position. If no bird took a food piece after three consecutive trials, the session was ended. The birds were successfully habituated when they took 10 food pieces in a minimum of 5 sessions (Horn et al., 2016). In addition, I attempted to alternate the start time so that the animals of both groups experienced the same duration of food deprivation. After the majority of the birds were habituated (see results), I conducted the food distribution test.

### *III) Food Distribution Assessment*

In this phase, I tested the evenness of the food distribution in the group with a partially fixed seesaw in a downward position. Here, I also used pieces of muesli as food. The procedures were the same as in the second habituation phase, with the difference that food was only provided in position 1. Two sessions were carried out on consecutive days. If a food piece fell out of the cage, the trial was repeated; if food fell inside, I recorded who got the food piece.

I conducted the food distribution test with 5 birds in Group 1 and 12 birds in Group 3.

## Analysis

I used the focal observations to determine the relationships between the animals as well as the social structure in the group. Affiliative behaviour examined includes the duration of contact sit (i.e., a bird was in reaching distance of another bird; Sima, 2012), so seated proximity as well as seldom seen behaviours such as preening and co-feeding (i.e., feeding together) that require contact sit.

Additionally, I calculated the *percentage of affiliative behaviours (% affiliative interactions)* of the whole time the bird was observed during all focal observations. I also recorded the *number of interaction partners* (i.e., number of other birds with which the focal was observed in contact sit; *# interaction partners*). Finally, I was interested in the *strongest bond (str. bond)* between individual birds. The strongest bond is determined by the highest percentage of affiliative behaviours directed towards a specific bird, which most often is (but need not be) the mate (pair-bonded partner).

I used the food-sharing observations to analyse the dominance hierarchy ranks in a natural context. I counted each displacement (i.e., "*a bird approaches and another retreats within two seconds*"; Sima, 2012). I first built a matrix of induced and received displacements. Then, the dominance rank was arranged by who displaced whom and how often displacement took place. A linear rank was built with these data (Table A 1-A 3: Appendix). To control for the significance of the linear rank, I calculated the modified Landau's index  $h'$  with the program RStudio Version 1.0.143 (© 2009-2016 RStudio Inc.) and the R code from Dr. Daizaburo Shizuka from the Shizuka Lab, School of Biology Science University of Nebraska-Lincoln, from the website <http://www.shizukalab.com/toolkits/linearity-tests> (Appendix). I used the improved Landau's index  $h'$  because this value was calculated with two-step randomisations (10,000 randomisations) (Jolles, Ostojić, & Clayton, 2013; De Vries, 1995). The value of 0 indicates a non-linear rank, and 1 indicates a perfect linear rank (Jolles et al., 2013; De Vries, 1995). When the rank was not significantly linearly, I had to calculate the rank via given minus received displacements.

During the food-sharing observations, I also recorded each instance of donor-initiated transfers, recipient-initiated transfers, and begging without transfer (Von Bayern et al., 2007; De Kort et al., 2003; De Kort et al., 2006).

For the focal, dominance, and food-sharing analysis, I used two videos of Group 1, six videos of Group 3 with Mokka, and 20 of Group 3 without Mokka.

To test the evenness of the food distribution in the experimental setting (cf. social tolerance; Burkart et al., 2009; Burkart & Van Schaik, 2013), I recorded the number of food pieces obtained by each individual during the food distribution assessment of the GSP. Pielou's  $J'$  was used as an evenness measurement (Burkart & Van Schaik, 2013; Horn et al., 2016). A

value of 1 indicates a perfectly equal distribution (Mulder et al., 2004; Pielou, 1966). I used Excel<sup>2007</sup> to calculate the Pielou's J' for each group.

Additionally, I analysed whether sex, pair bond, percentage of affiliative behaviours, number of affiliative partners, or dominance rank were connected to the number of food pieces taken in the food distribution assessment.

I used the Solomon Coder (*version beta 15.11.19*; Péter, 2011) to code the videos. For statistical analyses, the data were assessed in IBM SPSS 24.0. All statistical tests were non-parametric.

## Results

### Affiliative behaviours

The birds of Group 1 (N=5; 2 videos) spent between 0% and 9.19% of the total time recorded (mean: 4.31%) exhibiting affiliative behaviours and had between 0 and 3 social partners (median: 1). Between 72.69% and 100% of the affiliative behaviours were directed to the partner with whom the bird had the strongest bond. In Group 3 (N=12; 6 videos), the jackdaws spent between 0% and 81.36% of the total time recorded (mean: 29.65%) exhibiting affiliative behaviours and had between 0 and 2 social partners (median: 1; Table 3). Between 83.12% and 100% of the affiliative behaviour was directed to the partner with whom the bird had the strongest bond.

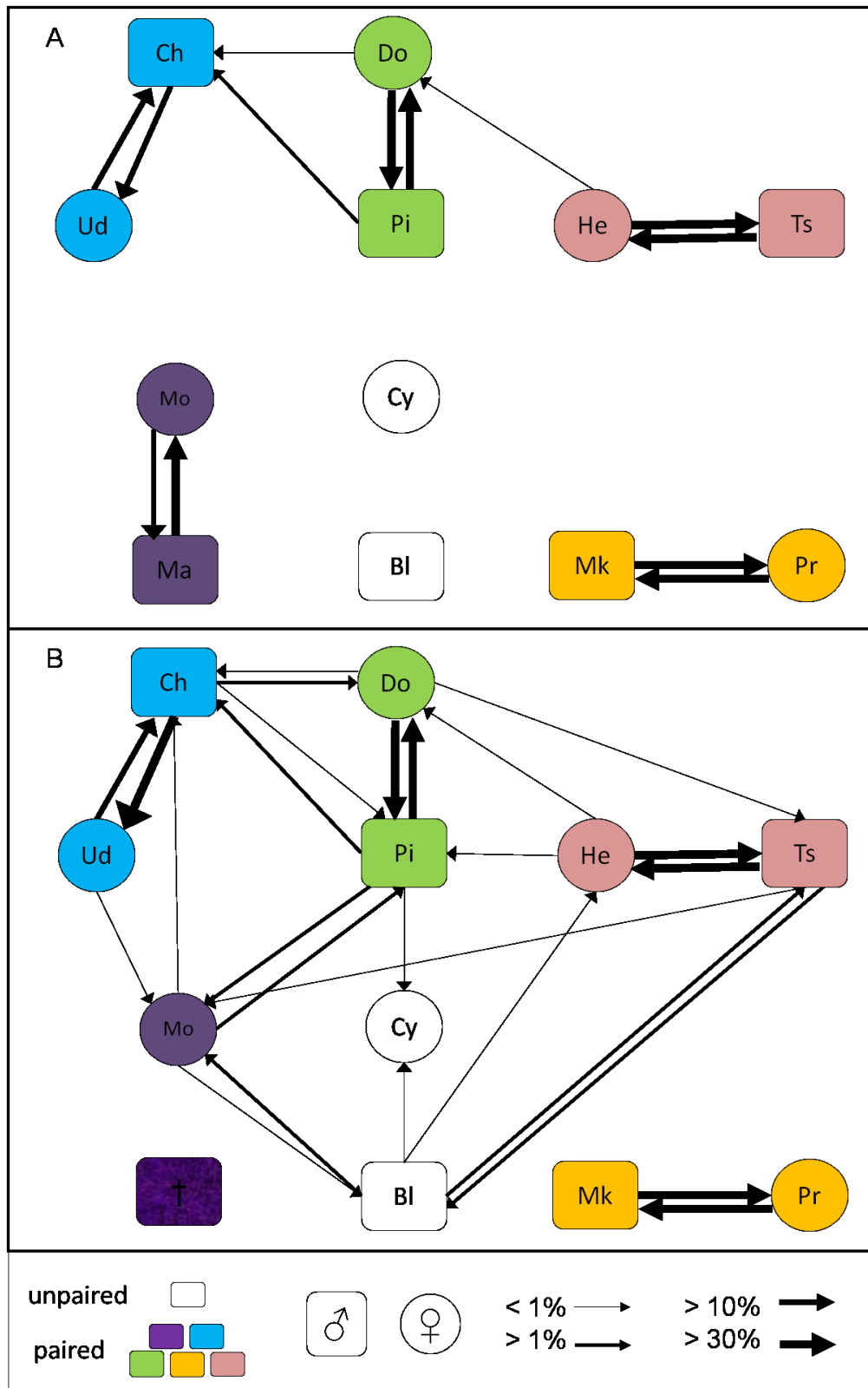
**Table 3: Summary of affiliative behaviour within Group 3 with Mokka:** The percentages of affiliative behaviours (% aff. behav.) of total observation time, the percentage of these affiliative behaviours directed towards the strongest bonded partner (% str. b.), and the number of interaction partners (# of p.). 1=highest rank; 12=lowest rank. Bl: Blackfoot; Ch: Chimney; Cy: Cyclop; Do: Dohli; He: Hedwig; Ma: Mokka; Mk: Mohawk; Mo: Mono; Pi: Pirate; Pr: Pronto; Ts: Tassilo; Ud: Udo.

	Ma	Mk	Ts	Pi	Pr	Do	He	Mo	Ud	Ch	Bl	Cy
% aff. behav.	81.36	66.42	42.37	40.53	34.92	24.72	24.22	16.24	12.81	12.16	0	0
% str. b.	100	100	100	83.12	100	95.60	96.51	100	100	100	0	0
# of p.	1	1	1	2	1	2	2	1	1	1	0	0

After the death of Mokka (N=11; 20 videos), there were changes in the proportions of affiliative behaviours, the percentage of the strongest bond, and the number of affiliative partners. The jackdaws of Group 3 without Mokka spent between 0% and 56.60% of the total time recorded (mean: 26.02%) exhibiting affiliative behaviour and had between 0 and 4 social partners (median: 3; Table 4). Between 60.26% and 100% of the affiliative behaviour was directed to the partner with whom the bird had the strongest bond. A social network of affiliative interactions of Group 3 with and without Mokka is depicted in Figure 4.

**Table 4: Summary of affiliative behaviour within Group 3 without Mokka:** The percentages of affiliative behaviours (% aff. behav.) of total observation time, the percentage of these affiliative behaviours directed towards the strongest bonded partner (% str. b.), and the number of interaction partners (# of p.). Bl: Blackfoot; Ch: Chimney; Cy: Cyclop; Do: Dohli; He: Hedwig; Mk: Mohawk; Mo: Mono; Pi: Pirate; Pr: Pronto; Ts: Tassilo; Ud: Udo.

	Pi	Pr	Do	Mk	Ch	Ts	He	Ud	Bl	Mo	Cy
% time	56,60	45,95	39,48	38,68	28,85	27,70	21,43	17,74	6,08	3,71	0
% str. b.	89,01	100	99	100	90,37	90,29	98,64	94,64	60,26	70,70	0
Nr. of p.	4	1	3	1	3	3	3	2	4	3	0



**Figure 4: Social network of Group 3:** A: Group 3 with Mokka. B: Group 3 without Mokka. The shapes symbolise the sex; the same colour symbolises partners. Unpaired individuals are white. The thickness of the arrow indicates the percentage of the affiliative behaviours between two birds, and the direction of the arrow indicates which bird was the focal individual. Changes are especially seen in the numbers of partners. BI: Blackfoot; Ch: Chimney; Cy: Cyclop; Do: Dohli; He: Hedwig; Ma: Mokka; Mk: Mohawk; Mo: Mono; Pi: Pirate; Pr: Pronto; Ts: Tassilo; Ud: Udo; †: dead bird Mokka.

### **Dominance hierarchies**

Two food-sharing videos of Group 1 were used for the linear matrix (Table 1 A: Appendix). 2.2 displacements were seen per bird per food-sharing video. Cherokee gave 26 displacements and received 0, whereas Blackfoot gave 0 and received 16. In total, 44 displacements were observed. The dominance hierarchy in this group was not linear (modified Landau's  $h'=0.85$ ,  $N=5$ ,  $p=0.1164$ ). Thus, I calculated a matrix based on displacements corrected for received displacements.

Six food-sharing videos were used to analyse interactions for Group 3 with Mokka. Here, on average 5.65 displacements were seen per bird per food-sharing video. Mohawk delivered 58 and received 1 displacement, whereas the second lowest-ranked bird, Blackfoot, received 32 displacements and displaced a bird once. In total, 113 displacements were seen (Table 2 A: Appendix). The dominance hierarchy in this group was significantly linear (modified Landau's  $h'=0.8251748$ ,  $N=12$ ,  $p<0.001$ ).

Without Mokka ( $N=11$ , 20 videos), 35.6 displacements were seen per bird per food-sharing video and 712 displacements were observed (Table 3 A: Appendix). In this case the dominance hierarchy was also significantly linear (modified Landau's  $h'=0.8590909$ ,  $N=11$ ;  $p<0.001$ ).

### Food-sharing observations in the natural context

During the observations, there were 141 donor-initiated transfers, 10 recipient-initiated transfers, and 30 begging-without-transfer events (Table 5). In general, males were donors and females were recipients. Food transfers only occurred between pair-bonded partners.

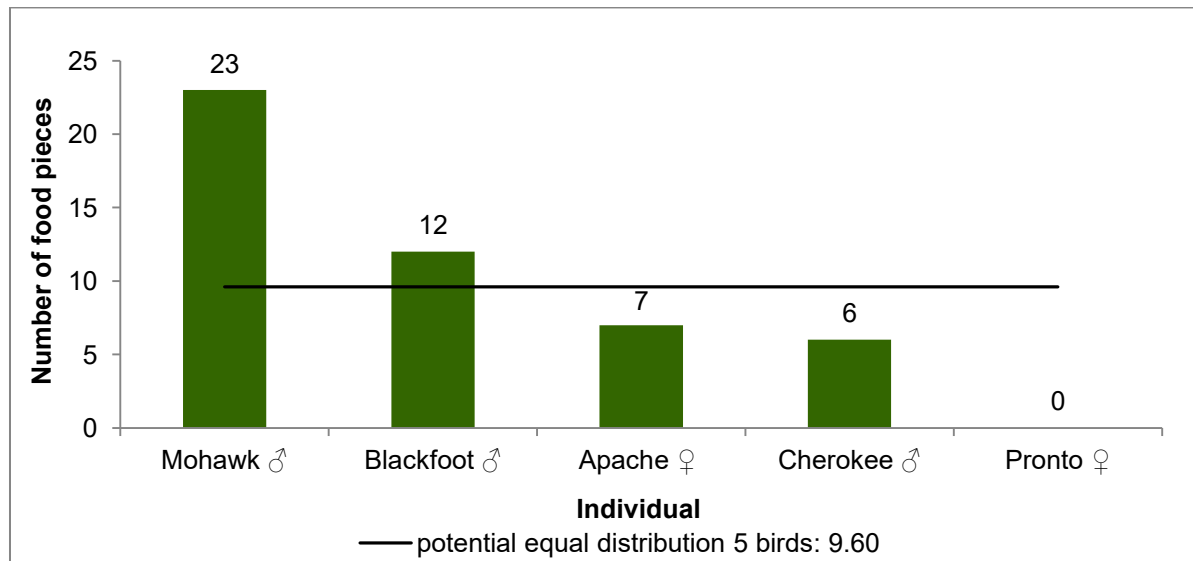
**Table 5: Summary of food-sharing events of Group 3 without Mokka:** The number of food pieces shared are illustrated. Pair-bonded individuals are represented one below the other. The last two birds (Blackfoot and Cyclop) were not paired and thus did not transfer any food pieces. †: dead bird Mokka.

Name	Donor-initiated transfer	Recipient-initiated transfer	Begging without transfer	SUM of transfer types
<b>Mohawk</b> ♂	60	0	0	62
<b>Pronto</b> ♀	0	1	1	
<b>Chimney</b> ♂	35	0	0	50
<b>Udo</b> ♀	0	7	8	
<b>Tassilo</b> ♂	35	0	0	46
<b>Hedwig</b> ♀	0	2	9	
<b>Pirate</b> ♂	7	0	0	17
<b>Dohli</b> ♀	0	0	10	
<b>Cherokee</b> ♂	1	0	0	3
<b>Apache</b> ♀	0	0	2	
<b>Mono</b> ♀	0	0	0	0
<b>Mokka</b> ♂	†	†	†	†
<b>Blackfoot</b> ♂	0	0	0	0
<b>Cyclop</b> ♀	0	0	0	0
<b>SUM</b>	<b>141</b>	<b>10</b>	<b>30</b>	<b>181</b>

### Evenness of food distribution assessment

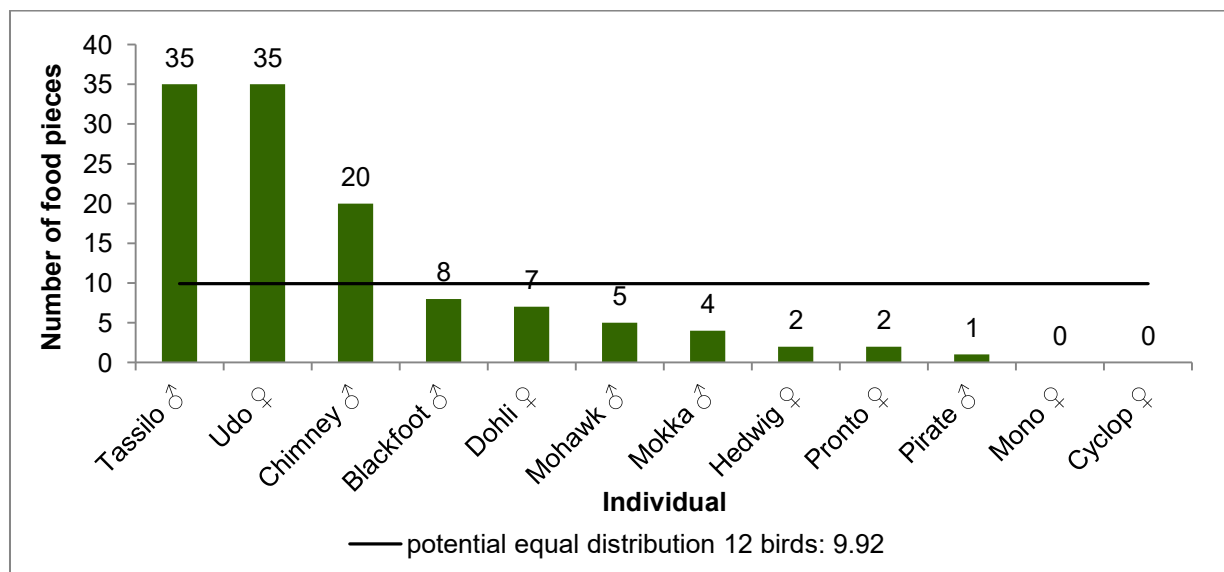
Before conducting the food distribution assessment, the birds had to pass through the habituation phases (Appendix: Tables 4 A - 6 A).

In Group 1, 48 of the 50 food pieces were consumed in the two sessions of the food distribution assessment. Pielou's  $J'$  was  $J'=0.77$  (potential equal distribution=9.60 per bird; Figure 5). The maximum number of food pieces taken was 23 (47.9% of the food pieces) and the minimum 0 (mean: 9.6; median: 7).



**Figure 5: Food distribution assessment for Group 1.**

In Group 3, 119 of the 120 provided food pieces were consumed during the two test sessions. I calculated the Pielou's  $J'$  for all birds to be  $J'=0.72$  (potential equal distribution=9.92 per bird; Figure 6). Two birds took 35 pieces, meaning each of the two ate 29.41% of the food pieces, and two birds took 0 pieces (mean: 9.6; median: 4.5).

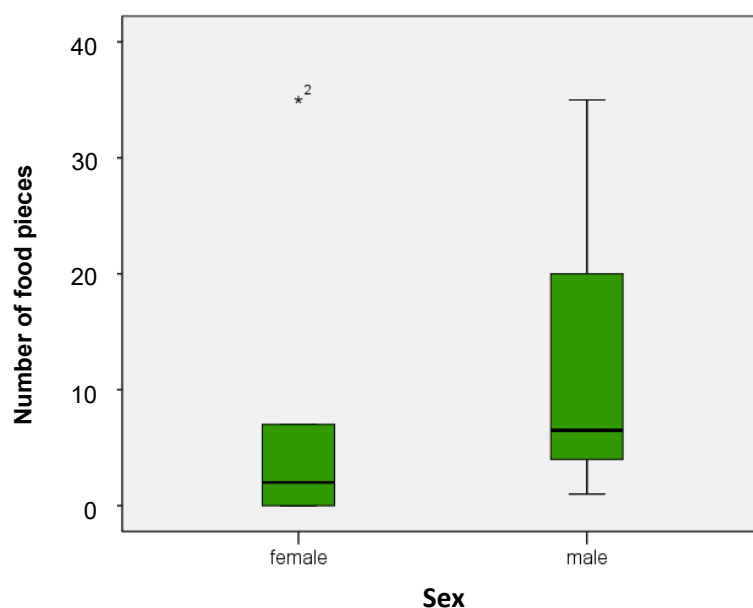


**Figure 6: Food distribution assessment in Group 3 with Mokka:** These are the results for Group 3 with Mokka, shortly after newly composing both groups.

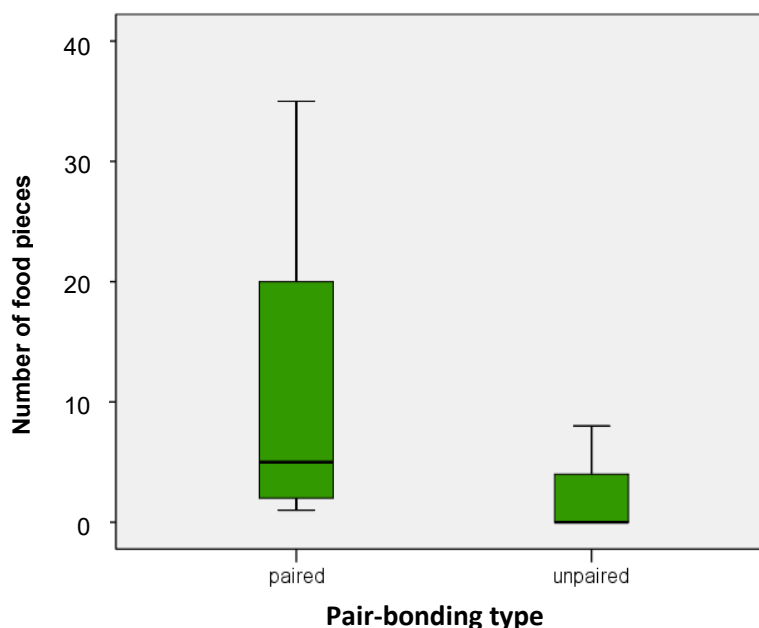
### Factors affecting food distribution and observations

Due to the fact that analysing five individuals (Group 1) is not informative and no correlations or differences were found, I concentrate on the results of Group 3 with Mokka for this analysis.

The number of food pieces taken did not differ significantly between the sexes (Mann Whitney U Test:  $U=25.5$ ,  $N=12$ ,  $p=0.240$ ; Figure 7). Furthermore, no difference was found between the number of food pieces taken and type of affiliative bond (pair-bonding type) (Mann Whitney U Test:  $U=6$ ,  $N=12$ ,  $p=0.209$ ; Figure 8).



**Figure 7: Box-plot of the number of food pieces and sex:** No significant difference was seen (Mann Whitney U Test:  $U=25.5$ ,  $N=12$ ,  $p=0.240$ ).



**Figure 8: Box-plot of the number of food pieces and affiliative bond:** No significant difference was seen (Mann Whitney U Test:  $U=6$ ,  $N=12$ ,  $p=0.209$ ).

There were no correlations found between the number of food pieces obtained in the food distribution assessment and rank (Spearman's  $\rho$ , 2-tailed:  $r_s = -0.028$ ,  $N=12$ ,  $p=0.931$ ), # of interaction partners (Spearman's  $\rho$ , 2-tailed:  $r_s = -0.069$ ,  $N=12$ ,  $p=0.830$ ), or % of affiliative behaviours (Spearman's  $\rho$ , 2-tailed:  $r_s = 0.016$ ,  $N=12$ ,  $p=0.961$ ).

No correlation was found between rank and # of affiliative partners (Spearman's  $\rho$ , 2-tailed:  $r_s = -0.347$ ,  $N=12$ ,  $p=0.230$ ). However, there was a negative correlation found between rank and % of affiliative behaviours (Spearman's  $\rho$ , 2-tailed:  $r_s = -0.949$ ,  $N=12$ ,  $p<0.001$ ).

## Discussion

In this study, I tried to answer the questions i) whether social tolerance is affected by social bonds and the hierarchy rank of individuals and ii) whether food-sharing is affected by the relationships between the individuals. As expected, affiliative behaviours were mostly directed to pair-bonded partners. However, changes in the social networks occurred when the group composition changed, either through a gain of individuals (combination of two groups) or loss of an individual (Mokka) through predation. The dominance hierarchy rank in Group 1 was not significantly linear, but the dominance hierarchy in Group 3 (newly composed group) with and without Mokka was significantly linear. The rank hierarchy itself also differed and the number of displacements increased, especially after the death of Mokka. Furthermore, food sharing in the natural context only occurred between pair-bonded partners and only from males to females. The evenness of the food distribution was rather high in both tested groups. The amount of food pieces taken during the food distribution assessment was not connected to sex, pair-bonding type, rank, number of interactions partners, or percentage of affiliative behaviours. However, the hierarchy rank was negatively correlated with the percentage of affiliative behaviours, meaning that more dominant birds spent more time engaging in affiliative behaviours. This suggests that the social behaviour of jackdaws shown in our study is largely dependent on the social rank.

### Group dynamics

#### Relationships & dominance

Recall that social relationships are an important aspect in socially living animals, which results in affiliative (e.g., allopreening and allofeeding) as well as aggressive behaviour (e.g., displacements) as a predictable outcome (Katzir, 1983; Wechsler, 1988), and therefore different qualities of relationships and thus cooperative interactions can be seen between group members (Fraser & Bugnyar, 2010). In my study, I observed interesting shifts in the social network of the birds, likely because new relationships had to be built after changes in group composition (Fraser & Bugnyar, 2010). Indeed, I found changes in the percentages of affiliative behaviours, number of partners, and interaction intensity. Strong changes in the group dynamics were observed after the death of Mokka. This could be explained by the fact that two females and one male were not paired. It is difficult for single birds to breed or defend their resources, especially the nest (Tamm, 1977). Winning an affiliative partner or potential mate is therefore highly beneficial for an individual's fitness prospects. Hence, it could be expected that the unpaired individuals increased their affiliative behaviours (e.g., Blackfoot and Mono). In addition, paired individuals could increase their affiliative behaviour, perhaps to strengthen their relationship to their mate (e.g., Pirate & Dohli), due to the instability of the social network, or to gain a more valuable partner. The latter could also be a

reason why some individuals increased their aggression towards their partner (Appendix: Table 3 A: e.g., Tassilo & Hedwig), or perhaps it could be to gain a more valuable partner, especially when an individual of a highly ranked pair (Mokka and Mono) becomes single. Therefore, paired individuals can have further relationships between other group members (Boucherie et al., 2016a; Boucherie, Sosa, Pasquaretta, & Dufour, 2016b), thus jackdaws can form relationships of different strengths or categories (Wechsler, 1988). There have been similar observations in rooks, which not only show relationships with their mates but also interactions with other rooks (i.e., friendships). Rooks also form further secondary relationships with friend of their friends. Additionally, several changes in the relationships can be seen over time as well as the fact that two paired individuals seldom seek a new partner (Boucherie et al., 2016a; Boucherie et al., 2016b; Boucherie, 2016).

### **Breeding season**

Besides the above mentioned, the breeding season is typically accompanied by raised levels of aggression and fighting over access to the best resources (e.g., nest boxes) (Henderson et al., 2000; Tamm, 1977; Röell, 1978). Interestingly, in my study changes in the hierarchy were also observed during the rest of the year. This could be explained by the changed composition of the group and the death of Mokka. Usually, jackdaws' linear rank system stays stable over the year, and changes characteristically only occur during the breeding season (Henderson et al., 2000; Tamm, 1977; Röell, 1978). As is characteristic for jackdaws, the hierarchy was also linear in our group. A linear hierarchy is advantageous to avoid needless fights and to create stability within the group (Röell, 1978; Tamm, 1977; Wechsler, 1988). Such linear rank orders are also seen in rooks (Jolles et al., 2013) and ravens (Loretto, Fraser, & Bugnyar, 2012), which indicates that it is a corvid-typical phenomenon (Röell 1978; Jolles et al., 2013; Loretto et al., 2012).

In addition to the changes in the relationships, the new environment might have also been an explanation for the observed new group dynamics and the aggression. The changed group composition also meant that the jackdaws had to deal with a new environment and were focussed on retaining their old resources (e.g., former breeding nests) and obtaining new ones such as new breeding nests (Katzir, 1983). Thus, fights in the groups increased as reflected by the increase in displacements as well as by changes in the hierarchies, especially among the middle-ranked birds, which is an observation found in prior studies as well (Tamm, 1977).

### **Food sharing**

Juvenile jackdaws have been reported to show pronounced food-sharing behaviour within their social group and thus exhibit marked social tolerance (Von Bayern et al., 2007). Previous studies have shown that, during their development, jackdaws first share food indiscriminately and later increasingly focus this behaviour on specific partners with whom

they form a lasting relationship or an actual pair-bond (Von Bayern et al., 2007). The food-sharing behaviours of jackdaws may be initiated by the donor or solicited by the recipient through begging (De Kort et al., 2003; De Kort et al., 2006). In contrast, adult jackdaws only demonstrate food sharing with their mates (Kubitza et al., 2015), which I observed to be true in my study. However, indiscriminate food sharing within the group has been found in other corvid species (Scheid et al., 2008). Interestingly, during my examination only male birds were donors and only female birds were recipients. On the one hand, this behaviour could be explained by a study of Kubitza et al. (2015), where males more often initiated feeding events and females seldom fed their partners. On the other hand, this behaviour could be explained by the instability of the hierarchy due to the changed composition of the group and Mokka's death, resulting in the attempt of the male birds to strengthen their pair bonds (De Kort et al., 2003; De Kort et al., 2006; Von Bayern et al., 2007). Other corvid species such as rooks display this behaviour under similar circumstances (Scheid et al., 2008).

### Social tolerance

The value of Pielou's  $J'$  that placed the jackdaws between 0.72 (N=12) and 0.77 (N=5) demonstrate that they show high social tolerance. This value could be explained by concentrating on the daily life conditions and the fact that jackdaws exhibit food sharing and affiliative behaviours, especially to their partners. Furthermore, it could be that the food sharing behaviour is linked with social tolerance, where animals with food sharing behaviour should have high social tolerance (Dale, Range, Stott, Kotrschal, & Marshall-Pescini, 2017), as confirmed in my study.

The jackdaws' Pielou's  $J'$  values are also similar to those of azure-winged magpies (Pielou's  $J'$ : 0.85 (N=4) and 0.74 (N=5)), and azure-winged magpies also show high social tolerance (Horn et al., 2016). Rooks also have a similar value (Pielou's  $J'$ : 0.84 (N=5)) (Hengl, MSc in prep.). In contrast to jackdaws, ravens (Pielou's  $J'$ : 0.65 (N=9)) and crows (Pielou's  $J'$ : 0.50 (N=9)) show only a tendency for social tolerance (Horn et al., in prep.). To analyse the value of Pielou's  $J'$  in corvids, Horn and colleagues (2016) adapted the group service paradigm of Burkart and Van Schaik (2013) for birds and used a seesaw mechanism. Burkart and Van Schaik (2013) used an adapted string-pull paradigm where one individual (donor) pulls the board near the wire mesh and another one receives a food piece (recipient). Their results suggested that Japanese macaques (*Macaca fuscata*) have a Pielou's  $J'$  of 0.32, capuchin monkeys (*Cebus apella*) have a Pielou's  $J'$  of 0.66, and common marmosets (*Callithrix jacchus*) have a Pielou's  $J'$  of 0.74 (Burkart & Van Schaik, 2013). Therefore, jackdaws' Pielou's  $J'$  value is high and comparable to primates that are cooperative breeders, especially to marmosets (Burkart & Van Schaik, 2013).

These differences and similarities in the Pielou's  $J'$  values might also be explained by the different methods or different social systems of those species. Jackdaws are facultative

colonial breeders and thus in many populations pairs build nests in close proximity to one another (Kubitza et al., 2015). Therefore they should have a lower value than rooks, which are colonial breeders (Scheid & Noë, 2010), but both species may be more tolerant than e.g., territorial breeders, because they live with several individuals in close proximity (Kubitza et al., 2015; Scheid & Noë, 2010). Azure-winged magpies as well as common marmosets are cooperative breeders and thus have a flexible helper system and help both related and unrelated individuals, which indicates a developed social system (Burkart & Van Schaik, 2013; Horn et al., 2016). Ravens show two types of social systems: On the one hand, they have non-breeder groups with high fission-fusion dynamics, and on the other hand, they form territorial pairs (Braun & Bugnyar, 2012; Fraser & Bugnyar, 2010; Sima et al., 2016) much like crows, which are territorial breeders (Von Blotzheim & Bauer, 1993). In addition, capuchin monkeys have intermediate breeding systems, while independent primates such as Japanese macaques do not have to tolerate conspecifics in close proximity and thus have the lowest value of social tolerance (Burkart & Van Schaik, 2013). Furthermore, individuals with high social tolerance also show a higher likelihood of prosocial behaviours as with the common marmoset (Burkart & Van Schaik, 2013) as well as with azure-winged magpies (Horn et al., 2016). Thus, jackdaws should also show prosocial behaviour, and some researchers view food sharing as a naturalistic form of prosocial behaviour (Von Bayern et al., 2007).

### **Social tolerance and affiliative behaviours**

Comparing sex, pair-bond type, and food distribution, males and paired individuals tended to take more food pieces during the food distribution test than females and unpaired individuals. As observed in wild flocks of jackdaws (Röell, 1978; Tamm, 1977), male birds generally dominated females and thus had easier access to the seesaw and therefore to the food. One may speculate that males also look for more food pieces to share with their females. This was observed to be true in this study, especially during the breeding season and observed food sharing events between partners near and on the seesaw (when food was available). This indicates that males first monopolise their food pieces and later share it with their partners, thus tolerating their partners near the feeding sites (Lorenz, 1935; Tamm, 1977).

Neither the proportion of affiliative behaviours, the number of affiliative partners, nor rank had an impact on the number of food pieces taken in the food distribution assessment. Interestingly, a negative correlation was found between rank and percentage of affiliative behaviours in Group 3 with Mokka. Thus, more dominant birds spent more time with affiliative behaviours, which is in contrast to my prediction. Taking a closer look at the ranking, the results can be explained in two ways:

- a) The higher the rank, the easier it may be for the bird to focus on bonding or bond-maintenance behaviour on a specific partner, because the higher-ranked bird can easily displace others and hold onto its resources (Katzir, 1983).
- b) It could also be that due to the group dynamics and changes in the relationships between the individuals, the rank was more important to hold and especially not to lose. As an example, it was observed by Lorenz (1935) that the most dominant couple of a jackdaw's group could be displaced by one male individual that was strong enough. After mating with a subdominant female, both birds rose in rank and were the new most dominant couple in the group (Lorenz, 1935).

### Limitations

However, there are several limitations to this study. Due to the combining of groups, the rate at which birds were habituated to the apparatus as well as to the procedure differed between the groups. Subadults, which are also low-ranked birds, are often more explorative than adults of higher ranks. Higher-ranked birds tend to be more conservative than low-ranking birds (Katzir, 1983), and this might be one reason for the differences in the habituation phase "habituation to the apparatus", where the birds had to approach, access the apparatus, and feed from a food bowl installed near the wire mesh on position 0 (cf. Materials & Methods & Horn et al., 2016). Furthermore, the small sample size and few videos could explain why I did not find any significant differences or correlations between the amount of food pieces taken during the food distribution test and the social bonds, affiliative as well as agonistic behaviours. Another limitation is that I possibly missed some food-sharing events, especially those that were outside the viewing angle of the camera. However, the biggest limitation of this study was likely the approaching breeding season, which caused an increase in both displacements and frequency of food sharing and could have affected the results, as the birds became more concentrated on building and defending their nest (Katzir, 1983; Tamm, 1977) and on strengthening their relationships (De Kort et al., 2003; De Kort et al., 2006; Von Bayern et al., 2007).

### Conclusion

In summary, I have analysed social tolerance in experimental as well as daily life conditions. I have shown through food-sharing and focal observations that jackdaws are socially tolerant, especially towards their specific partners. I have further shown that food distribution in the group tends to correlate with food sharing, at least in male birds, because one may speculate that the male birds have a strong will to acquire food pieces and share them with their females. Thus, social tolerance tends to be important for cooperation tasks, because these tasks and cooperation as well as helping behaviour during such tasks are influenced by friendships, partnerships, sex, and dominance (Asakawa-Haas et al., 2016; Massen et al., 2015). In conclusion, social tolerance is affected by social bonds and the hierarchy rank of

individuals, and food sharing is affected by the relationships between individuals. In addition, food sharing could be a special form of social tolerance that is more than naturalistic (Von Bayern et al., 2007).

For future experiments, correlations between food sharing and the food distribution assessment could be of interest. However, I recommend analysing social tolerance in both experimental and daily life conditions while trying to use the same procedures for both approaches for a better comparison.

## Abstract

In this MSc project, I compared social tolerance, evenness of food distribution, and food sharing in two groups of captive jackdaws (*Corvus monedula*) in daily life conditions and in experimental settings. Jackdaws are facultative colonial breeders, meaning that in many populations pairs nest in close proximity to one another. They show pronounced food sharing within their social group and are thus expected to have high levels of social tolerance. I here investigated if social tolerance is influenced by social bonds and the hierarchy rank of individuals and if food-sharing is influenced by the relationships between the individuals. Therefore, I conducted under daily life conditions both focal observations to analyse social structure as well as social interactions and food-sharing observations to analyse the group's dominance hierarchy and identify food-sharing dyads. To examine social tolerance in the experimental context, I used the first three phases of the "group service paradigm" of Horn et al. (2016) and to assess the evenness of food distribution in the groups. The two groups differed in their pattern of affiliative behaviour and number of affiliative partners, but in both groups most affiliative behaviour was directed to the pair-bonded partner. The dominance hierarchies were significantly linear in only one group. In the natural food-sharing context donors were exclusively male and recipients were female. Food was distributed rather evenly in both groups (Pielou's  $J'$  0.72 and 0.77), only slightly lower than cooperatively breeding species such as azure-winged magpies (*Cyanopica cyanus*). Social tolerance becomes effective when two individuals are in close proximity. It was influenced by the species breeding system, social bonds as well as dominance rank. That could be explained by the jackdaws' breeding systems and their food sharing behaviour, which is further important to strengthen their relationships. In this study, no further influences were found. Social tolerance may influence the likelihood and outcome of cooperative interactions and prosocial behaviour. However, the biggest limitation of this study could have been the upcoming breeding season, that could have had influences on the results, especially on relationships between the animals.

### Zusammenfassung

In dieser Masterarbeit werden die soziale Toleranz, die Futterverteilung in der Gruppe und das Futterteilen in zwei im Käfig gehaltenen Dohlen-Gruppen (*Corvus monedula*) im täglichen Leben und experimentellen Settings verglichen. Dohlen sind fakultativ koloniale Brüter, bei denen viele Populationspaare einander nahe gelegene Nester bauen. Sie zeigen innerhalb ihrer sozialen Gruppe verstärktes Futterteilen, daher erwartet man, dass sie eine hohe soziale Toleranz aufweisen. Ich untersuchte hierbei, ob die soziale Toleranz von den Partnerbindungen und dem Hierarchierang der einzelnen Individuen und ob das Futterteilen von den Beziehungen zwischen den Individuen beeinflusst wird. Deshalb führte ich unter natürlichen Bedingungen sowohl Einzelbeobachtungen, um die soziale Struktur sowie soziale Interaktionen, als auch Beobachtungen von Futterteilungen, um die Dominanzhierarchie in der Gruppe und die Identifizierung von Paaren beim Futterteilen zu analysieren, durch. Um die soziale Toleranz im Experiment zu untersuchen, wurden die ersten drei Phasen des *Group Service Paradigm* nach Horn et al. (2016) durchlaufen, wodurch die Futterverteilung in der Gruppe analysiert werden konnte. Die zwei herangezogenen Gruppen unterschieden sich in Art und Anzahl ihrer affiliativen Verhaltensweisen, wobei sich in beiden Gruppen das affiliative Verhalten vermehrt dem Partner gegenüber äußerte. Die Dominanzhierarchie verlief nur in einer Gruppe signifikant linear. Bei der natürlichen Futterteilung waren nur die Männchen Donatoren und die Weibchen Rezipienten. Innerhalb beider Gruppen wurde das Futter gleichmäßig verteilt (Pielou's J' 0.72 und 0.77), allerdings war der Grad an gleichmäßiger Aufteilung etwas geringer als bei kooperativ züchtenden Spezies wie beispielsweise den Blauelstern (*Cyanopica cyanus*). Soziale Toleranz wird wirksam, wenn sich zwei Individuen in unmittelbarer Nähe zueinander aufhalten. Sie wird summa summarum durch das Brutsystem, die sozialen Bindungen sowie das Dominanzverhalten geprägt. Dies könnte durch das soziale Brutsystem der Dohlen und die Futterteilung erklärt werden, wobei letztere weiters essenziell ist, um Beziehungen zu stärken. Es werden keine weiteren Einflüsse im Rahmen dieser Arbeit festgestellt. Die soziale Toleranz könnte ebenso die Wahrscheinlichkeit und das Ergebnis von kooperativen Interaktionen und prosozialem Verhalten beeinflussen. Die bevorstehende Brutzeit war möglicherweise der größte Einfluss auf diese Studie, da sie die Ergebnisse – vor allem in Hinblick auf Beziehungen zwischen den Tieren – stark beeinflusst haben könnte.

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## Appendix

### Linear dominance matrices

**Table A 1: Linear dominance matrix Group 1:** Calculated rank and linear rank are the same. The highest ranked bird is on the top, the lowest ranked bird on the bottom. # no displacement because it was the same individual.

		Group 1					
given	received						
	Name	Cherokee	Mohawk	Apache	Pronto	Blackfoot	SUM
	Cherokee ♂	#	12	2	5	7	26
	Mohawk ♂	0	#	6	3	6	15
	Apache ♀	0	0	#	0	3	3
	Pronto ♀	0	0	0	#	0	0
	Blackfoot ♂	0	0	0	0	#	0
	SUM	0	12	8	8	16	44

**Table A 2: Linear dominance matrix of Group 3 with Mokka:** The highest ranked bird is on the top, the lowest ranked bird on the bottom. # no displacement because it was the same individual. Bl: Blackfoot; Ch: Chimney; Cy: Cyclop; Do: Dohli; He: Hedwig; Ma: Mokka; Mk: Mohawk Mo: Mono; Pi: Pirate; Pr: Pronto; Ts: Tassilo; Ud: Udo.

		Group 3 with Mokka												
given	received													
	Name	Mk	Ts	Ma	Pr	Pi	He	Mo	Do	Ud	Ch	Bl	Cy	SUM
	Mohawk ♂	#	3	0	0	1	8	1	11	3	11	20	0	58
	Tassilo ♂	1	#	3	2	3	0	2	6	2	2	4	0	25
	Mokka ♂	0	0	#	1	2	2	0	2	2	2	1	1	13
	Pronto ♀	0	0	0	#	0	1	0	1	0	0	1	0	3
	Pirate ♂	0	0	0	0	#	0	0	2	0	0	1	0	3
	Hedwig ♀	0	0	1	0	0	#	1	0	0	0	2	0	4
	Mono ♀	0	0	0	0	0	0	#	0	0	0	0	0	0
	Dohli ♀	0	0	0	0	0	0	0	#	1	0	0	0	1
	Udo ♀	0	0	0	0	0	0	0	0	#	1	0	0	1
	Chimney ♂	0	0	0	0	0	0	0	0	0	#	3	1	4
	Blackfoot ♂	0	0	0	0	0	0	0	0	0	0	#	1	1
	Cyclop ♀	0	0	0	0	0	0	0	0	0	0	0	#	0
	SUM	1	3	4	3	6	11	4	22	8	16	32	3	113

**Table A 3: Linear dominance matrix of Group 3 without Mokka:** The highest ranked bird is on the top, the lowest ranked bird on the bottom. # no displacement because it was the same individual. BI: Blackfoot; Ch: Chimney; Cy: Cyclop; Do: Dohli; He: Hedwig; Mk: Mohawk; Mo: Mono; Pi: Pirate; Pr: Pronto; Ts: Tassilo; Ud: Udo.

Group 3 without Mokka													
	Name	received											SUM
		Mk	Ts	Pr	He	Pi	Do	Ch	Ud	Mo	BI	Cy	
given	Mohawk ♂	#	42	5	36	14	36	90	39	17	75	3	357
	Tassilo ♂	0	#	5	5	14	14	19	6	14	20	7	104
	Pronto ♀	0	2	#	3	1	4	6	1	2	7	0	26
	Hedwig ♀	0	0	0	#	2	3	8	5	29	5	0	52
	Pirate ♂	0	0	0	0	#	3	7	7	8	2	7	34
	Dohli ♀	0	0	0	1	0	#	11	11	6	5	7	41
	Chimney ♂	0	0	1	6	0	2	#	4	5	28	9	55
	Udo ♀	0	0	0	0	0	0	0	#	7	0	3	10
	Mono ♀	0	0	0	0	0	0	1	0	#	7	4	12
	Blackfoot ♂	0	0	5	3	0	1	6	1	3	#	2	21
	Cyclop ♀	0	0	0	0	0	0	0	0	0	0	#	0
	SUM	0	44	16	54	31	63	148	74	91	149	42	712

### Habituation phases to the apparatus and procedure

In Group 1, Cherokee, Apache, and Tschock were the quickest birds to reach criterion in the first phase and Blackfoot the slowest (mean: 36.9; median: 39; Table A 4). In the second phase, most birds met the criterion within a minimum of 5 sessions; only Apache, Blackfoot, and Pronto needed longer (mean: 5.9; median 7; Table A 4).

**Table A 4: Summary of the first and second phase in Group 1:** The table is ordered according to the speed by which the birds met the criterion in the first phase and then in the second phase. An asterisk indicates a bird that did not reach the criterion.

Group 1		
Name	Habituation to apparatus sessions until criterion	Habituation to procedure sessions until criterion
<b>Cherokee</b> ♂	22	5
<b>Apache</b> ♀	22	7
<b>Tschock</b> ♂	22	†
<b>Mohawk</b> ♂	23	5
<b>Monkey</b> ♀	33	5
<b>Jackomo</b> ♀	45	5
<b>Pronto</b> ♀	46	9
<b>Bunny</b> ♂	50	5
<b>Chapa</b> ♂	52	5
<b>Blackfoot</b> ♂	52	7
<b>Polli</b> ♀	*	*
<b>mean</b>	<b>36.9</b>	<b>5.9</b>
<b>median</b>	<b>39</b>	<b>7</b>

In Group 2 (before newly composing the groups), the quickest bird was Mokka and the slowest was Moony in the first phase (mean 46.57; median: 45; Table A 5). Three birds (Chimney, Pirate, and Cyclop) did not meet the criterion in the first phase. I conducted additional sessions in all of the groups in order to habituate all the birds. In total, Group 1 had 60 sessions and Group 2 had 65.

In the second phase, two birds (Dohli and Udo) met the criterion in a minimum of five sessions, and the slowest bird was Mono with 50 sessions (mean 21.43; median: 25; Table A 5). Chimney went onto the seesaw in the second phase and met the criterion in session 27. Only two birds (Pirate and Cyclop) did not meet the criterion in the second phase.

**Table A 5: Summary of the first and second phase in Group 2:** The table is ordered according to the speed by which the birds met the criterion in the first phase and then in the second phase. The birds that did not meet the criterion in the first phase are at the end of the table. An asterisk indicates a bird that did not meet the criterion. Mono met the criterion of the second phase after newly composing the groups.

Group 2		
Name	Habituation to apparatus	Habituation to procedure
	sessions until criterion	sessions until criterion
Mokka ♂	42	27
Mono ♀	43	50
Udo ♀	45	5
Hedwig ♀	45	25
Dohli ♀	46	5
Tassilo ♂	48	11
Moony ♂	57	*
Chimney ♂	*	27
Pirate ♂	*	*
Cyclop ♀	*	*
mean	46.57	21.43
median	45	25

In the newly composed Group 3 (second phase/session 35 of Group 2), Blackfoot, Mohawk, and Pronto had to become habituated to the apparatus of Group 2 installed in Aviary 2 (mean: 27.30 and 27; Table A 6). In total, Group 1 had 20 sessions in the second phase and Group 3 had 51.

**Table A 6: Summary of the second phase in Group 3:** The table is ordered according to the speed by which the birds met the criterion in the second phase. The birds that did not meet the criterion in the second phase are at the end of the table. An asterisk indicates that a bird did not meet the criterion.

Group 3	
Name	Habituation to procedure sessions until criterion
Dohli ♀	5
Udo ♀	5
Tassilo ♂	11
Hedwig	25
Mokka ♂	27
Chimney ♂	27
Mohawk ♂	36
Blackfoot ♂	36
Mono ♀	50
Pronto ♀	51
Pirate ♂	*
Cyclop ♀	*
mean	27.30
median	27

## R Code

The whole following R code is from Dr. Daizaburo Shizuka from the Shizuka Lab, School of Biology Science, University of Nebraska-Lincoln, from the website <http://www.shizukalab.com/toolkits/linearity-tests> [available 21 May 2017]. For the test, I had to add one number in the code "dat=read.csv" (highlighted in yellow).

```
" library(igraph)
dat=read.csv2(file.choose(),header=TRUE,row.names=1,check.names=FALSE) #
read .csv file
m=as.matrix(dat)
g=graph.adjacency(m,mode="directed",weighted=TRUE,diag=FALSE)
E(g)$width=E(g)$weight

totint=m+t(m)

# This set of codes reproduces Appleby's (1983) test of linearity
# First step is to change dyads that have unknown relationship =0.5
mod=m
for (i in 1:nrow(m)){
  for (j in 1:nrow(m)){
    if (m[i,j]>m[j,i]) mod[i,j]=1
    else if (m[i,j]==m[j,i])
      mod[i,j]=mod[j,i]=0.5
    else
      mod[i,j]=0
    if (totint[i,j]==0) mod[i,j]=0.5
  }
}
diag(mod)=0

N=nrow(m)
Si=rowSums(mod)
d=(N*(N-1)*(2*N-1)/12)-(0.5*sum(Si^2))
df=(N*(N-1)*(N-2)/((N-4)^2))
chi=(8/(N-4))*((N*(N-1)*(N-2))/24-(d+0.5))+df
pAppleby=1-pchisq(chi,df=df)
maxd=ifelse(N%%2==1, (N^3-N)/24, (N^3-4*N)/24)
K= 1-d/maxd
K
pAppleby
library(igraph)
dat=read.csv(file.choose(),header=TRUE,row.names=1,check.names=FALSE) #
read adjacency matrix from .csv file
m=as.matrix(dat)
g=graph.adjacency(m,mode="directed",weighted=TRUE,diag=FALSE)
E(g)$width=E(g)$weight
plot.igraph(g,vertex.label=V(g)$name,layout=layout.fruchterman.reingold,
vertex.color="white",edge.color="black",vertex.label.color="black")

totint=m+t(m)
N=nrow(m)
V0=degree(g,mode="out")

rawh=(12/((N^3)-N))*sum((V0-((N-1)/2))^2) #This calculates the original
Landau's h value

## This set is the modified test of linearity a la de Vries (1995). There
are three major steps:
```

#Step 1) randomly fill in the null relationships such that all individuals either wins (=1), loses (=0) to each individual. Known ties are denoted as 0.5 for both individuals. You then calculate the h-value for this tournament -- this is the h0 value. The "modified Landau's h" as denoted by de Vries (1995) is the mean value of these h0 values in 10,000 randomizations.

#Step 2) Create a completely random tournament in which all individuals either win or lose to each individual. Calculate the h-value for this, which is the hr value.

#Step 3) Compare hr and h0: p-value is the number of times hr is bigger or equal to h0 in 10,000 simulations.

```
h0=vector(length=10000)
hr=vector(length=10000)
t=0

for (k in 1:10000){
  newmat=m
  for (i in 1:N){
    for (j in 1:N){
      if (totint[i,j]>0)
        if (m[i,j]>m[j,i]) newmat[i,j]=1
        else if (m[i,j]==m[j,i])
          newmat[i,j]=newmat[j,i]=0.5
        else
          newmat[i,j]=0
      else if (j>i){
        newmat[i,j]=sample(c(0,1),1)
        newmat[j,i]=abs(newmat[i,j]-1)} } }
      diag(newmat)=0
      V=rowSums(newmat)

      h0[k]=(12/((N^3)-N))*sum((V-((N-1)/2))^2)

      nm=matrix(nrow=N,ncol=N)
      for (i in 1:nrow(m)){
        for (j in 1:nrow(m)){
          if (j>i){
            nm[i,j]=sample(c(0,1),1)
            nm[j,i]=abs(nm[i,j]-1)} } }
          diag(nm)=0
          Vr=rowSums(nm)
          hr[k]=(12/((N^3)-N))*sum((Vr-((N-1)/2))^2)

          if (hr[k]>=h0[k]) t=t+1}
hmod=mean(h0)
p=t/10000

cat(" Landau's h= ",rawh,"\n","modified Landau's h= ",hmod,"\n","p-value
from simulations= ",p)
```

```
hist(hr,xlim=c(0,1),xlab="Landau h values from simulation")
abline(v=hmod,lty=3,lwd=1.5) " (Shizuka, n.d:
http://www.shizukalab.com/toolkits/linearity-tests [available 21 May 2017])
```