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Abstract

Food sharing defined as “transfer of a defendable food item” or the “joint use of monopolisable food items” has previously been described for many mammals and birds in context of parental care. However, several studies in birds so far focused on the nestling period. Here, I investigated the food sharing behaviour during both the nestling and post-fledging period in common ravens, who express bi-parental care not only during nestling and fledgling phase, but also several months after fledging. Specifically, I observed parental allo-feeding behaviour in four raven families during the nestling period and food sharing during the post-fledging period in a food monopolisation experiment (together with other related behaviours i.e., agonistic interactions, begging and watching behaviour). During the nestling as well as during the post-fledging period, mothers showed higher rates of allo-feeding. They additionally monopolised most the food sources in the experiment, indicating a dominance reversal between the parents during the breeding season. Fathers, on the other hand, directed most of the agonistic interactions towards the chicks during the post-fledging period. Begging and watching behaviour, mostly directed from chicks to fathers, seemed to serve not only soliciting food or social learning purposes, but might additionally be used as conciliation gesture. In conclusion, this study provides first insights into the parental care and food sharing behaviour during post-fledgling period in the family context in biparental birds.

Keywords

Common Raven, Corvids, Nestling Period, Fledgling Period, Food Monopolisation, Begging, Agonistic Interactions

Zusammenfassung

Das Teilen von Futter im Sinne des „Transfers eines zu verteidigenden Futterstückes“ oder des „gemeinsamen Nutzens eines monopolisierbaren Futterstückes“ wurde bisher für viele Säugetiere und Vögel im Kontext der elterlichen Fürsorge beschrieben. Während viele Studien bei Vögeln auf die Nestlings-Zeit fokussiert waren, habe ich das Futterteilen sowohl in der Nestlings-Zeit als auch in der Phase nach dem Flüggenwerden bei Kolkraben untersucht, welcher sich aufgrund der bi-parentalen Elternfürsorge nicht nur während der Nestlings-Zeit, sondern auch mehrere Monate nach dem Flüggenwerden für diese Studien besonders gut eignet. Während der Nestlings-Zeit habe ich das elterliche Fütterungsverhalten in vier Raben-Familien beobachtet und in einem Futter-Monopolisierungs-Experiment habe ich das Futterteilen in der Zeit nach dem Flüggenwerden beobachtet (in Zusammenhang mit anderen damit verbundenen Verhaltensweisen wie agonistische Interaktionen, Betteln und Beobachten). Während der Nestlings- wie auch der Zeit nach dem Flüggenwerden zeigten fütterten Mütter am häufigsten. Zusätzliche monopolisierten Mütter am häufigsten die Futterquellen, was auf einen Dominanzwechsel zwischen den Eltern während der Brutsaison hindeutet. Väter, auf der anderen Seite, zeigten gegenüber den Jungtieren die meisten agonistischen Verhaltensweisen nach deren Flüggenwerden. Betteln und Beobachten, am häufigsten von Jungtieren an die Väter gerichtet, schienen nicht nur dem Bitten um Futter oder dem sozialen Lernen zu dienen, sondern könnte auch als Versöhnungsgeste genutzt werden. Zusammenfassend bietet diese Studie erste Einblicke in das elterliche Fürsorgeverhalten und Futterteilen im Familienverband nach dem Flüggenwerden der Jungtiere in biparentalen Vögeln.

Schlagwörter

Kolkrabe, Rabenvögel, Nestlings-Zeit, Zeit der flüggen Jungtiere, Futter-Monopolisierung, Bettelverhalten, Agonistische Interaktionen

1. Introduction

1.1 How Can Food Sharing be Defined?

Food sharing can be defined as the “transfer of a defendable food item from one food-motivated individual to another (excluding theft)” (Feistner and McGrew, 1989) or the “joint use of monopolizable food items” (Stevens and Gilby, 2004). Feistner and McGrew (1989) state three crucial characteristics for sharing food: 1) the transfer is voluntary, 2) the food item could be defended and 3) the individual sharing the food has a certain level of motivation regarding the food (Feistner and McGrew, 1989). Two forms of food sharing can be distinguished: food-offering/transfer and co-feeding. Food-offering and food-transferring describes one individual actively offering a food item to another individual with its hands, mouth, or beak. Co-feeding describes individuals feeding together at a food source that could be monopolised by one individual (Scheid et al., 2008).

1.2 Functions and Underlying Mechanisms of Food Sharing

Food sharing is often observed between adults and their young, whereby the reproductive success tends to increase for individuals providing higher amounts of food (Isler and van Schaik, 2012). Food Sharing between related individuals, especially between parents and offspring, can be explained with Hamilton’s Rule, describing the increase of parents’ fitness by investing into current offspring instead of future offspring or own survival (Hamilton, 1964). Parents not only actively transfer food to their offspring, but also tolerate them to co-feed (e.g., New Caledonian crows *Corvus moneduloides*: Holzhaider et al., 2011). Other reasons for food sharing can be the increase of foraging efficiency (Stevens and Gilby, 2004; Heinrich and Marzluff, 1995), predator avoidance (Stevens and Gilby, 2004), or status enhancement (Boesch, 1994; Nolin, 2012; Duque and Stevens, 2016; Zahavi, 1995).

Food sharing between non-kin individuals is harder to explain since several components of the social environment seem to influence with whom to share. Food sharing with absolute strangers (as known for example in humans and some non-human primates: Tan and Hare, 2013; Warneken et al., 2007; Fehr and Fischbacher, 2003; Andreoni and Miller, 1993) can be explained with altruism (Hare and Kwetuenda, 2010; Trivers, 1971). Additionally, reciprocity (Jaeggi and van Schaik, 2011; Feistner and McGrew, 1989; Lehmann and Keller, 2006) or reciprocal altruism (Gurven, 2004; Trivers, 2006), respectively, where food is shared either for later food (for example in vampire bats *Desmodus rotundus*: Carter and Wilkinson, 2013) or other currencies or goods (Hawkes and Bird, 2002; Patton, 2005; Scheid et al., 2008), serve as explanations for food sharing between non-related individuals. More generally, the simplest way to explain and sustain food sharing is the “Tit-for-Tat” strategy, where individuals decide whether to cooperate or not depending on the previous behaviours of the cooperation partner (Axelrod and Hamilton, 1981). Alternatively, in species showing more sophisticated cognitive skills, individuals can engage in a market-like interaction considering the quality and availability of a possible cooperation partner as well as the costs of the cooperation task (Noë and Hammerstein, 1995).

Food sharing in non-kin individuals can also be associated with pair-bonding and the maintenance of relationships, as it was found for example in primates (Nishida and Hosaka, 1996; de Waal, 2000), but also in corvids (Clayton and Emery, 2007; rooks *Corvus frugilegus*: Scheid et al., 2008; jackdaws *Corvus monedula*: e.g., de Kort et al., 2003 or von Bayern et al., 2007; common ravens *Corvus corax*: Sima, 2012). During courtship and/or incubation, male birds feed their females to nourish them and strengthen the pair bonding (i.e., courtship feeding: Lack, 1940), but it can also be used outside of the breeding season to strengthen the relationship (Clayton and Emery, 2007). Outside the pair bond (e.g., in non-breeders)

dominance and sex of the donor can influence with whom to share (Scheid et al., 2008), as well as the effort required to access a food source (Pfuhl et al., 2014). In jackdaws, food sharing can also be interpreted as harassment avoidance, with food-owners tolerating thefts by beggars (e.g., jackdaws: de Kort et al., 2006; Stevens and Stephens, 2002; Blurton Jones, 1987).

1.3 Food Sharing in the Context of Parental Care and Parental Investment

As already mentioned above, food sharing can be observed between parents and offspring as part of parental care. Parental care can be defined as “any form of parental behaviour that increases the fitness of the offspring” (Gonzalez-Voyer and Kolm, 2010). Parental investment refers to “any behaviour of parents that results in an increase of their offspring’s fitness while decreasing the future reproduction of the parents” (Gonzalez-Voyer and Kolm, 2010; Trivers, 1972).

During parental care, parents invest resources they cannot use for their own fitness. Hence, they should only care for their offspring when their won benefits exceed the costs of these caring behaviours. In many species, parents can care alone for the offspring (either mothers or fathers), but in other species both parents share the caring effort. Especially in altricial bird species, where offspring needs a high amount of post-hatching care, it is highly beneficial for both parents to provide care to their chicks (biparental care), as otherwise they might not be able to raise any offspring (Gonzalez-Voyer and Kolm, 2010).

Most bird species (81%) show biparental care, with a male and female caring for their offspring together (Cockburn, 2006; Boucherie et al., 2019). But this does not mean that both parents provide the same type of care. Parents might show different types of investment, e.g., in some species mothers incubate and feed the offspring (“parental effort”), and fathers pay

most of their attention to defending a territory or trying to find extra mates (“mating effort”) (Creelman and Storey, 1991).

Additionally, parents might show different preferences for chicks depending on their sex, age, and size, but also begging rates. Often, chicks with higher begging rates are preferred to be fed by both parents (Teather, 1992; Rosivall et al., 2005). Parental preferences can also depend on the environment: under good environmental conditions, parents feed small chicks with high begging rates, but under bad environmental conditions parents tend to feed big and strong chicks (Caro et al., 2016). In some species, parents showing specific preferences might lead to dividing the broods; this is, a form of “postfledgling care in which each parent has long-term feeding preferences for different young” (Draganoiu et al., 2006). Additionally, in many species fathers seem to prefer specific chicks. For example, in crimson rosella, *Platycercus elegans*, fathers prefer large male chicks, while mothers of this species do not differentiate between sex or age of the chicks (Krebs et al., 1999).

This can create conflicts between parents, on when and for whom to provide how much care (Trivers, 1974). Besides this, conflicts can also arise between parents and offspring regarding the duration and the amount of parental care (Trivers, 1974; Gonzalez-Voyer and Kolm, 2010). During a specific period of parental care, parents are selected to hold back any form of care, whereas offspring are selected to provoke further provisioning by their parents. In general, three phases of parental investment relative to the offspring’s age can be distinguished. During the first phase, parents actively provide care to their offspring without avoidance or aggression towards the offspring. During the second phase, parents and offspring initiate on similar rates, but there might be some avoidance or aggressive behaviour towards the offspring. During the third phase, it is mostly the offspring approaching the

parents for care, but parents avoid their offspring or might show agonistic behaviours towards them (Trivers, 1974).

Between parents and offspring, a communication system thus evolved to allow offspring to signal their need to parents (i.e., they beg to be fed by their parents), and parents to respond appropriately and adjust food provisioning (Trivers, 1974; Clark, 2002). But this system is prone to be utilized by offspring to get more than parents “are selected to give”, and parents need to evolve abilities to discriminate between true need and “lies” (Trivers, 1974). Begging behaviour comprises auditory components, i.e., vocalizing (von Haartman, 1953) and visual components, i.e., directionally stretching the neck, wing flapping (von Haartman, 1953; Betts, 1954; Soler et al., 1999). Apart from signalling their nutritional need, offspring can use begging signals to snatch away food from the parents (Mock and Parker, 1997), or monopolise access to a food source (McRae et al., 1993; Kacelnik et al., 1995); parents on the other hand can use the signals to control the allocation of food resources (Krebs and Magrath, 2000). Using the begging intensity to assess the offspring’s need and feed them efficiently increases the parent’s inclusive fitness (Rodríguez -Gironés et al., 1996).

For all these reasons, begging intensity in many species was shown to vary with clutch size, begging intensity increasing with clutch size (Harper, 1986; Leonard et al., 2000). However, begging frequency can also vary with dominance, with the dominant chicks frequently stopping begging (Johnstone, 2004). Additionally, age and size can lead to increased begging frequencies in young and small chicks to better compete with older and bigger siblings (Ryden and Bengtsson, 1980).

1.4 Why Investigate Food Sharing Behaviour in Common Ravens?

Corvids in general are known for their high cognitive abilities comparable to those found in apes and monkeys (Emery, 2006). Apes and corvids seem to use the same “cognitive tool kit” (i.e., flexibility, imagination, causal reasoning, and prospection), which evolved due to corvids and apes facing similar socioecological problems (e.g., locating perishable food sources in time and space) (Emery and Clayton, 2004). Because of their cognitive skills, one could expect them to sustain food sharing and adjust their provisioning patterns showing more sophisticated mechanisms (comment by Boucherie, 2021). However, as discussed earlier, some forms of food sharing do not necessarily demand high cognitive abilities (Schino and Aureli, 2009; Jaeggi and Gurven, 2013) but are rather enhanced by specific social factors and social systems, as food sharing has previously been investigated in cooperative breeding and group living mammals (Feistner and McGrew, 1989).

Common ravens are suitable to investigate food sharing mainly because of two characteristics in their social systems. On the one hand, they show extensive parental care, where both parents take care of their offspring, not only during nestling and fledgling period, but also for several months after fledging (Gothe, 1961; von Boltzheim, 1993). On the other hand, they are known for their versatile and complex social systems, where individuals live in open but structured social groups with high fission-fusion dynamics, family units, or in monogamous breeding pairs defending a territory (Boucherie et al., 2019; Emery et al., 2007; Braun and Bugnyar 2012; Heinrich and Marzluff, 1995). In the context of food sharing, they are known to form alliances with other individuals to search for food independently. Residents, i.e., a territorial pair, defend food sources in their territory against wanderers, i.e., (sub-adult and adult) ravens without partners. These wanderers cannot access defended food sources unless they recruit other individuals to overpower the resident’s defence (Heinrich

and Marzluff 1991; Heinrich and Marzluff 1995; Heinrich, 2011; Bugnyar et al., 2001). The resulting food sharing leads to higher food income for each individual as well as reduction of patchiness of food sources (Heinrich and Marzluff, 1995).

1.5 Methodology of Experiments Investigating Food Sharing Behaviour in Corvids

Although food sharing in most bird species was investigated focusing on the nestling period, hardly anything seems to be known about parental allo-feeding at the nest in common ravens (Kendeigh, 1952). Most existing studies on food sharing and allo-feeding in corvids consisted of observations and experiments on sub-adults that already left the family (e.g., Kijne and Kotrschal, 2002; de Kort et al., 2006; von Bayern et al., 2007; Pfuhl et al., 2014; Scheid et al., 2008), hand-raised individuals (e.g., de Kort et al., 2006; von Bayern et al., 2007; Scheid et al., 2008), or even captured birds from the wild (e.g., Duque and Stevens, 2016). Sometimes studies were conducted on groups of wild birds (e.g., Kijne and Kotrschal, 2002; Bugnyar and Kotrschal, 2002) but most studies were conducted on birds in captivity (e.g., de Kort et al., 2006; von Bayern et al., 2007). In some studies, individuals were only tested in dyads (e.g., Pfuhl et al., 2014; Duque and Stevens, 2016), and in one study there was even only one same-sex dyad tested (de Kort et al., 2003). Food sharing experiments investigated the influence of dominance hierarchies (e.g., Duque and Stevens, 2016; Scheid et al., 2008), affiliative relationships (e.g., de Kort et al., 2006; von Bayern et al., 2007; Scheid et al., 2008), reciprocity (e.g., Duque and Stevens, 2016; Scheid et al., 2008), or sex of the birds (e.g., Delestrade, 1999). Only few experiments tested food sharing in corvids between individuals at a monopolisable food source under group conditions (e.g., Sima, 2012) or within the family setting (e.g., Holzhaider et al., 2011).

1.6 Aims, Questions and Predictions

To investigate food sharing behaviour in the context of parental care in the common raven *Corvus corax*, I analysed food related behaviour during the family phase. In the first part of the study, I focus on the feeding interactions i) between the parents and ii) from the parents to their chicks in an observational setting during the nestling period. In the second part of the study, I focus on the feeding interactions i) between the parents, ii) between parents and chicks, and iii) between chicks in an experimental setting during the fledgling phase.

Question 1: Nestling Period: Who is Doing Most of the Feeding?

During the nestling period, I expect higher feeding frequencies between parents and chicks than between the parents. For the latter, I expect fathers to provide more food to mothers, than the contrary. Between parents and chicks, I expect the mothers to do most of the feeding.

Question 2: Fledgling Period – Who Monopolises the Food?

During the fledgling period, I expect fathers to monopolise single food sources. Mothers, but also chicks, should be able to access food as soon as there are two food sources available that cannot be monopolised by the fathers at the same time.

Question 3: Fledgling Period – Food Sharing Between Parents

Between parents, I expect a higher frequency of food-sharing when only a single food source is available, with higher food transfer frequencies from fathers to mothers than the contrary. Next to this, I expect higher frequencies of agonistic interactions at a single food source compared to two food sources, and these interactions should mainly be directed from fathers to mothers.

Question 4: Fledgling Period – Food Sharing Between Parents and Chicks

I expect high frequencies of food-sharing between parents and chicks when there is only one food source compared to two food sources. Next to this, I expect high frequencies of agonistic interactions at a single food source compared to two food sources, which should mainly be directed from parents to chicks. Food sharing frequencies should decrease, and agonistic interactions frequencies should increase with the age of the chicks. Begging behaviour, which should mainly be directed from chicks to parents, should decrease with the age of the chicks.

Question 5: Fledgling Period – Food Sharing Between Chicks

Between chicks, I expect a decrease of food sharing and possibly increase of agonistic interactions frequencies with increasing age. But as there is hardly any literature regarding food related behaviour between fledglings, I will not/cannot make any further/specific hypotheses about their behaviours at the food source(s).

2. Materials and Methods

2.1 Subjects and Housing

The families used for observations and experiments were housed in three research stations: at Haidlhof Research Station in Lower Austria (two families in 2019; four families in 2020), at Grünau Research Station in Upper Austria (four families in 2019; three families in 2020) and in the Zoo Schönbrunn in Vienna (one family in 2019 and 2020). All pairs were allowed to breed but sizes of the families were experimentally manipulated so families would be small (families with two chicks) or big (families with four chicks) in a counter-balanced design across two years. Each family lived in its own aviary equipped with several kinds of objects for enrichment purposes and small trees. They were provided with ad libitum water and being opportunistic scavengers with a diverse diet (Marzluff, 2009) they were fed twice a day with a mixture of meat, corn, fruits, and vegetables.

In general, ravens become sexually mature with three to four years of age and the first pair bonding phase starts in their second winter (von Boltzheim, 1993). They start building their nest in January/February and brood three to six eggs for 20-25 days from February until hatching in March/April (von Boltzheim, 1993; Gutjahr, 2018; Tiergarten Schönbrunn, 2021). Chicks fledge in April/May 40-42 days after hatching (von Boltzheim, 1993; Gutjahr, 2018).

2.2 Ethical Note

This study was conducted according to Austrian law and local government guidelines, following the statutes of the University of Vienna concerning animal research. The experiment and observation were non-invasive and conducted in the own aviaries of the birds. The ravens could start and stop to participate on a voluntary basis. After the study, the ravens remained in their aviaries at the respective Research Station.

2.3 Nestling Period: Data Collection and Coding

Observations of the feeding behaviour of the parents during the nestling period were conducted only in 2020 and only on the families housed in Haidlhof Research Station (four families with two chicks each). Two families had two female chicks each and the other two families had one male and one female chick each (see Table S1 in the Supplementary Materials for details). Observations started on the 6th of April and ended on the 10th of May 2020. Cameras were installed in the brood boxes to allow for observations without disturbing the families. Every second day the first ten minutes of every hour from 7am to 6pm were analysed to investigate the parents' feeding behaviour at the nest. Data was collected *ad libitum*, specifically frequencies and durations of all behaviours at the nest were coded, as well as who initiated and received social behaviours. For analyses I focused on allo-feeding behaviour only, whereby "Feed" was defined as an individual bringing food to the nest and feeding another individual (either chick or mate), and "Transfer food" was defined as an individual bringing food to the nest and giving it to the mate, who is feeding it to the chicks (see Table S2 in the Supplementary Materials for a complete ethogram). I was able to differentiate between the parents (beringed) and between parents and chicks, but not between chicks.

2.4 Food Experiment

2.4.1 Data Collection

The food experiment was conducted in summer 2019 and 2020 on all families: at Haidlhof Research Station, Grünau Research Station, and the Zoo Schönbrunn in Vienna. In 2019 I used two of the seven tested families (one with three chicks (two males and one female) and one with two chicks (one male and one female)) for analysis, and in 2020 I used one of the eight tested families (with two chicks (one male and one female)) for analysis (see Table S1 in the Supplementary Materials for details). I was personally responsible for conducting the food

experiment with the four families at Haidlhof and the family in Schönbrunn in 2020. All experiments from 2019 and the experiments in Grünau 2020 were conducted by other students.

The food experiment started once the chicks had fledged. The experiment was replicated over time to investigate the developmental effects of the chick's and parent's food sharing behaviour. It was conducted every third week, for four days in the morning and afternoon between May and June. Each family was thus tested 24 times in the food experiment. Due to the Corona pandemic in 2020, the families in Schönbrunn and Grünau were only tested for two weeks instead of three weeks.

2.4.2 Test Phase

The test phase lasted 15 minutes, in which the families were tested in one of three different conditions (see below). The video recording for the test phase started before either the keeper or the experimenter provided the food in the aviary, to make sure to record the food provision as this event served as starting point for the later coding. The food source(s) and individuals interacting with the food were recorded and the experimenter gave comments on who was at the food, who was manipulating/sharing the food, the distance between the individuals and the food and the distance between individuals. In the beginning of each recording (baseline and test) the experimenter commented on day, time, family, and phase and condition of the experiment.

2.4.3 Test Conditions

The experiment consisted of three conditions: OnePiece condition, TwoPieces condition, and Scramble condition (control condition). For the OnePiece condition, one big piece of food was placed in the aviary. For the TwoPieces condition, two a bit smaller pieces

of food were placed at two different places in the aviary. For the Scramble condition several small food items equalling the number of individuals of the tested family were placed as heap in the aviary. The quantity of food remained the same in all conditions (i.e., every individual received 125g of meat (families with two chicks) or 100g of meat (families with three chicks), respectively), only the distribution changed. In Grünau beef heart, in Haidlhof turkey hen-neck or gooseneck, and in Schönbrunn beef was used. The food was provided on specific spots in the aviaries. To make sure that one individual was unable to monopolize both food sources in the TwoPieces-condition, the food sources in this condition were fixated at opposite positions in the aviary. Using plastic ties and chains the food was attached to either the fence (Spot A and B) or to a stone slab (Spot C) (Figure 1).

Families were tested twice in One-Piece-condition, twice in Two-Pieces-condition and four times in Scramble-condition per week of the experiment. Conditions will be scheduled in a way so that every family is tested in each condition in the morning as well as in the afternoon. Consequently, the families will be tested twice in the morning and twice in the afternoon in the Scramble-condition, and once in the morning and once in the afternoon in each of the other conditions.

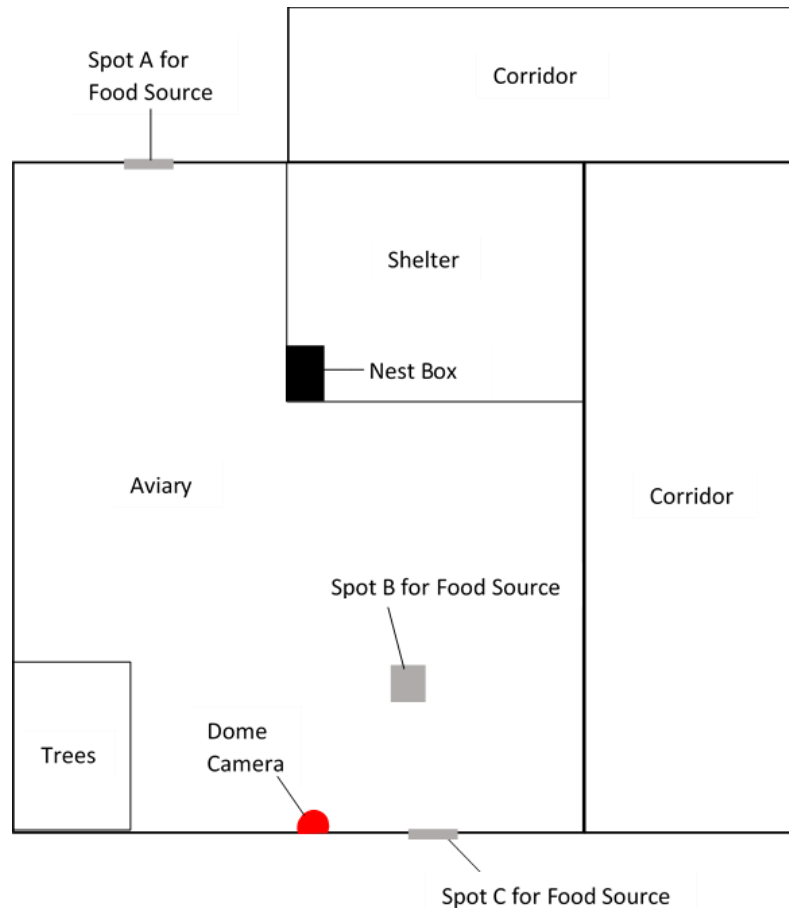


Figure 1: Sketch of the aviary where the families in Haidlhof Research Station are housed. Spot A for the food source is used when Dome camera is available (experiments in 2020), as well as when it is not available. Spot B is only used when Dome camera is available (food experiments 2020). Spot C for food source is only used when Dome camera is not available (food experiment 2019).

2.4.4 Video Recording

The experiments were recorded with i) a hand camera (to focus on interactions and comment on the experiment), ii) one (or two) camera(s) to focus on the food source(s), and iii) one camera for global views (Figures 2 and 3). In Haidlhof I was able to use the cameras that have been installed in the aviaries (“Dome cameras”) to get a global view and to focus on the food source(s) (Figure 4).

In Haidlhof Panasonic HC-V808 and Canon cameras were used. For the additional cameras in Haidlhof a tripod Velbon Videomate 438 was used. In Grünau Panasonic HC-V808 and Sony cameras were used and, on some occasions, also a Canon and a GoPro camera. In Schönbrunn two Panasonic V808 cameras and a JVC Everio GZ-HM30BU camera were used. For the additional cameras in Schönbrunn a tripod ALPHA Design ALPHA 1000 and a tripod Velbon Videomate 438 were used.

2.5 Coding Videos from the Food Experiment

To code the experiments, the videos from the multiple cameras were combined in multiple view videos using the video editing software Blackmagic Design DaVinci Resolve 16 (Petty, 2020). Videos were stored on the Loopbio server where videos were analysed with the Loopy software for quantitative video analysis (Hofbauer and Stowers, 2015). Coding was ad libitum, and all family members were coded simultaneously, including their interactions (specifying initiator and receiver of the interaction) and spatial associations between the individuals. I focused on behaviours within food zones 1 and 2 that were related to sharing and manipulating food, but also agonistic interactions. As parents as well as chicks were beringed, I was able to differentiate between all of them. When defining “food sharing” for my investigation, I differentiated between co-manipulating/co-feeding and allofeeding/food transfer. Co-feeding is defined as two or more individuals manipulating the same or different food sources while being in proximity (i.e., maximum 50cm away from each other). Allofeeding and Food Transfer are defined as transferring food to another individual with the beak (see Table 1 for ethogram containing behaviours used for analysis; for complete ethogram see Table S3 in the Supplementary Materials).



Figure 2: Example of the camera-setup for the OnePiece-condition without Dome camera being available: a) is the global view, b) is the focus camera for the food source and c) is the hand camera to focus on specific behaviours and to give comments on the experiment. The same setup can be used for the Scramble condition.



Figure 3: Example of the camera-setup for the TwoPieces condition without Dome camera being available: a) is the hand camera to focus on specific behaviours and to give comments on the experiment, b) is the focus camera for one of the food sources and c) is the focus camera for the other food source.



Figure 4: Example of the camera-setup for the TwoPieces condition with Dome camera being available: a) is the dome camera to focus on the food sources and to provide a global view and b) is the hand camera to focus on specific behaviours and to give comments on the experiment.

Table 1: Ethogram for the food experiments with the common raven *Corvus corax* in 2019 and 2020 (modified after Boucherie, 2020) defining the behaviours used for statistical analysis.

Behaviour	Description
Agonistic Behaviour (Without Food)	
Agonistic (Threat/Peck/Chase/Charge)	<u>Threat</u>: One bird threatens another one, with display “thick head approach” and/or visual threat (the aggressor pecks in the direction of the victim without touching it), with or without vocalizations. <u>Peck</u>: One bird pecks another one with its beak. Pecking implies physical contact. <u>Chase</u>: One bird pursues another one, typically flying <u>Charge</u>: One bird pursues/rushes toward another one flying/running.
Fight	<u>Undirected</u>: Two birds hit each other with their feet/beaks, with one/both birds jumping in the air or with one bird down on the ground and one sitting on the top. <u>Directed</u>: One bird hit another bird with its feet/beak, with one/both birds jumping in the air or with one bird down on the ground and one sitting on the top.
Submissive Display	One bird displays a submissive posture (e.g., step back and lean forward or bend over) after receiving an aggression from another bird (i.e., threat, peck, chase/charge), with or without vocalizations.
Retreat	One bird retreats/moves away after receiving an aggression from another bird (i.e., threat, peck, chase/charge), with or without vocalizations (i.e., more than 1m away).
Agonistic Behaviour (Involving Food)	
Steal food	One bird steals a food item from another bird, and either stays or goes away with it. Contrary to passive and active item transfer, the transfer is this time initiated by the ‘receiver’/bird stealing the item.
Try to steal food	One bird fails to steal the food item of another bird, either because the other bird left with the item, or because it threatened/aggressed the ‘thief’.
Social Behaviour (Involving Food)	
Co-manipulate/co-feeding (same)	Two birds eat the same food item within a reaching distance (i.e., 0-0.5m).
Co-manipulate/co-feeding (distinct)	Two birds eat the different food items within a reaching distance (i.e., 0-0.5m).
Watch individual with food	One bird is in proximity or contact with another one and observes it handling a piece of food without any attempt to get it.
Begging	One bird touches another’s beak and vocalizes with/without wing flapping; or vocalizes with wing flapping in the direction of another bird to request an item. One bird flapping its wings in the direction of another bird without vocalization is also considered as one instance of begging (i.e., of low intensity).
Allofeeding/Transfer food	<u>Allofeeding</u>: One bird actively transfers a food item from its beak to the beak of another bird. Occurs typically after begging (from the receiver). <u>Transfer</u>: During food manipulation, a food item is being transferred from one bird to another, either passively (the two birds are co-manipulating the food that gets transferred to only one of them) or actively (the bird possessing the food gives it to another bird).
Non-Social Behaviour	
Eat/manipulate food	One bird manipulates a food item with the beak or foot. A bird manipulates food also by holding it in its beak.

2.6 Statistical Analysis

2.6.1 Descriptive Statistics: Nestling Period

The data for the nestling period analysis was entirely analysed using Microsoft Excel (Version 2105). I summed the frequencies of the behaviours Transfer food and Feed: the data were pooled around family (factor with four levels, i.e. the four families I used for the analysis), week (factor with five levels: week 1, week 2, week 3, week 4, week5) and dyad.type (factor with four levels: father-chick, mother-chick, father-mother, mother-father). I calculated means and standard deviations from the resulting categories (per dyad type in each family, and per week) and plotted the results with Microsoft Excel using grouped bar plots.

2.6.2 Fledging Period: Food Experiment

2.6.2 Descriptive Analysis Fledgling Period: Eat/manipulate

To analyse the amount of time the individuals spent at the food source(s), I summed the durations of the behaviour Eat/manipulate separately for each type of individual i.e., chicks, fathers, and mothers, either depending on week or on condition of the experiment. I calculated means and standard deviations from the resulting pivot-table-dataset and plotted the results with Microsoft Excel using grouped bar plots.

2.6.3 Preparation of Data from the Experiments for R Statistics

I chose three families with similar group size for the statistical analysis: Joey-Rocky 2019 (three chicks), Nobel-George 2019 (two chicks) and Aramis-Paul 2020 (two chicks). Before starting the statistical analysis, the data from Loopy had to be prepared for the statistical software R (R Core Team; 2020). This was achieved with the software Microsoft Excel. I calculated the summed frequencies of dyadic food sharing, agonistic interactions, begging and watching. To investigate food sharing behaviour, I summed the frequencies of the following behaviours: Allofeeding (Attempt and Success)/Transfer of food and Co-manipulation (distinct and

same)/Co-feeding. To investigate agonistic interactions at the food source(s), I summed the frequencies of the following behaviours: Agonistic (Threat/Peck/Chase/Charge), Fight, Retreat, Submissive Display, Steal Food and Try to Steal Food.

2.6.4 Statistical Analyses with R

I investigated how the age of the chicks (i.e., week of the experiment, factor with three levels: week 1, week 2, week 3), the condition of the experiment (factor with three levels: OnePiece, TwoPieces, Scramble) and the dyad type (factor with seven levels: chick-chick, chick-father, chick-mother, father-chick, mother-chick, father-mother, mother-father) affected the dyadic frequency of food sharing (model 1), agonistic interactions (model 2) and begging and watching (model 3). To do so, I used Generalized Linear Mixed Models (GLMM; Baayen, 2008). On top of the effects listed above, which were used as fixed effects in all three models, I included random intercepts effects of session number (only model 1 and 3, see below) and identity of bird's dyads (all models) due to repeated observations of the same dyads across the experiments (Schielzeth and Forstmeier, 2008). Because the model for the agonistic interaction response would not converge (despite increasing iterations and using a different optimizer), I used a reduced dataset for this model excluding sessionID to reduce the number of zeroes in the dataset, i.e., I re-arranged the data per week.

Before fitting the models, I inspected the data for missing values (no missing values in the data) and distribution using simple plots (with the function `hist`), which looked fine for all responses.

I started with fitting the GLMMs with a Poisson error distribution, usually used for counting data (Mundry, 2020). But as all three models were highly overdispersed (overdispersion-parameter model 1: 1.402; overdispersion-parameter model 2: 4.275; overdispersion-parameter model 3: 11.866; Mundry, 2020), I thus fitted all models with a

Negative Binomial error distribution and log link function (e.g., Lawless, 1987; Engel, 1984) (overdispersion-parameter model 1: 0.850; overdispersion-parameter model 2: 0.918; overdispersion-parameter model 3: 0.694; Mundry, 2020). I also confirm the better fit of the negative binomial model comparing the Akaike information criterion (AIC) of the two distributions (AIC for model 1 with Poisson error distribution: 1864.65; AIC for model 1 with Negative Binomial error distribution: 1739.124; AIC for model 2 with Poisson error distribution: 1512.662; AIC for model 2 with Negative Binomial error distribution: 999.804; AIC for model 3 with Poisson error distribution: 8884.768; AIC for model 3 with Negative Binomial error distribution: 2946.444) (Akaike, 1974). To test the overall effect of the fixed effects and to avoid cryptic multiple testing (Forstmeier and Schielzeth, 2011) I conducted a full-null model comparison with the null model lacking all fixed predictors (i.e., week, condition, and dyad.type) but including the two random effects (i.e., dayd.identity and sessionID for model 1 and 3; and dyad.identity for model 2) using a likelihood ratio test (Dobson, 2002). The model stability of the respective full models was calculated by dropping one statistical point one at a time from the dataset and comparing the estimates derived from these models to those obtained from the full models (Mundry, 2020). Model stability was shown to be fine for all three models (see results section). Next, I checked for collinearity among predictors by determining the Variance Influence Factors (VIF), which can indicate whether a predictor has a (strong) linear relationship with other predictors (Field, 2005). Collinearity was shown to be of no issue for either of the models.

To illustrate the results, I plotted the significant predictor of condition for model 1 and the significant predictor of dyad.type for models 2 and 3 against the respective response using a box plot. A box plot is a simple technique to display the median, the upper and lower quartile (the box) and the minimum and maximum (whiskers) value of a dataset (Potter, 2006). Using

means and standard deviations, I conducted some additional descriptive analysis on the three models focusing on possible interactions between the factors dyad type and either week or condition of the experiment (see Figures S1 – S6 in the Supplementary Material for details).

Models were fitted with the statistical software R (R Core Team, 2020) using the functions `glmer` (for Poisson distributed GLMM) and `glmer.nb` (for the Negative Binomial distributed GLMM) of the package `lme4` (`lme4` 1.1-23; Bates et al, 2015). The VIF was calculated with the function `vif` of the package `car` (`car` 3.0-9; Fox and Weisberg, 2019). The confidence intervals were calculated with the function `boot.glmm.pred` (Mundry, 2020). The results were plotted using the function `ggplot` of the package `ggplot2` (`ggplot2` 3.3.2; Wickham, 2016).

The sample analysed for the food sharing and the begging and watching model comprised a total of 956 observations each and for the agonistic interaction model the sample comprised 396 observations, each for three weeks, three conditions and seven dyad types. The total number of levels for the random effect of `sessionID` was 24 and for `dyad.identity` it was 44 (see Tables S4, S5 and S6 in the Supplementary Materials for details).

3. Results

3.1 Descriptive Analysis of the Nestling Period

The food sharing frequency during the nestling period decreased with week of observation between parents and offspring, but also between parents. Between parents, allo-feeding occurred mostly from fathers to mothers. Fathers stopped transferring food to the mothers in week four, mothers stopped transferring food to the fathers in week three. Mothers fed the chicks more often than fathers did, and although both parents fed the chicks until week five, mothers generally fed at a higher frequency than fathers (Figure 5).

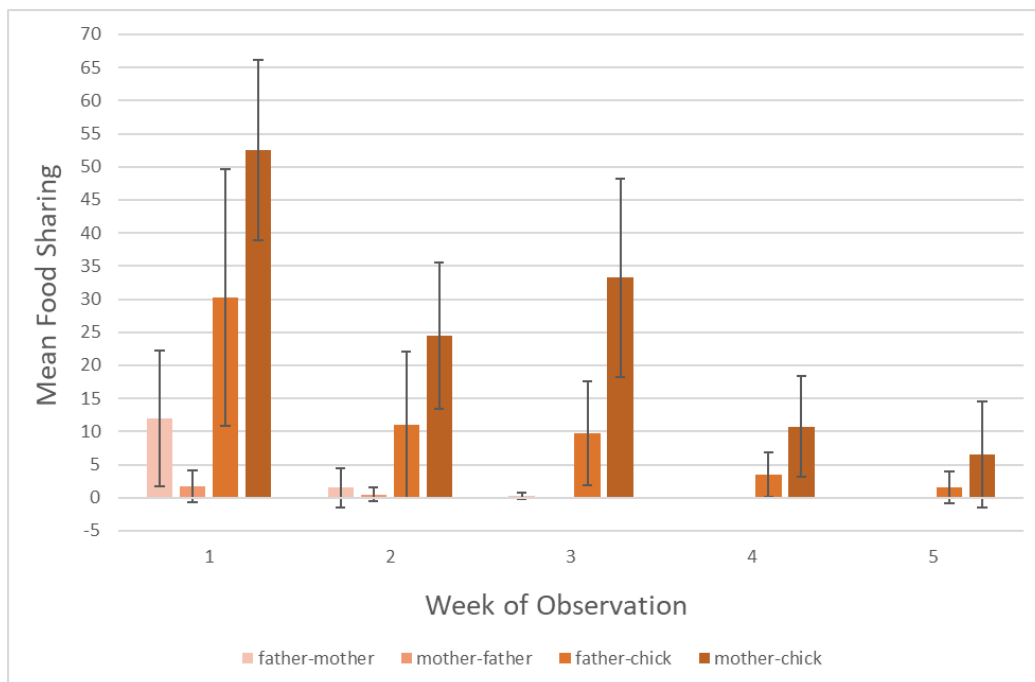


Figure 5: Bar plot illustrating means and standard deviations of the food sharing frequencies during the nestling period for all dyads and all weeks of observation. Sample sizes for the dyads: father-mother = 55, mother-father = 9, father-chick = 224, mother-chick = 510 cases. Sample sizes for the weeks of the observations: week 1 = 386, week 2 = 150, week 3 = 173,

3.2 Food Experiment

3.2.1 Descriptive Analysis of the Eat/manipulate Behaviour

Mean duration of food manipulation was highest for all individuals during the scramble condition compared to all other conditions (OnePiece, TwoPieces). Mothers manipulated more than fathers in the OnePiece and Scramble condition, while they manipulated food for almost the same mean duration in the TwoPieces condition. Chicks hardly manipulated food in the OnePiece condition but did so during Scramble condition (Figure 6a). In all three weeks of the experiment, mothers manipulated food the most, closely followed by fathers, while chicks showed the lowest mean duration of food manipulation. For parents, the mean duration of food manipulation decreased over time and was at its lowest in week three, whereas for chicks the mean duration increased with week and was at its highest in week three (Figure 6b).

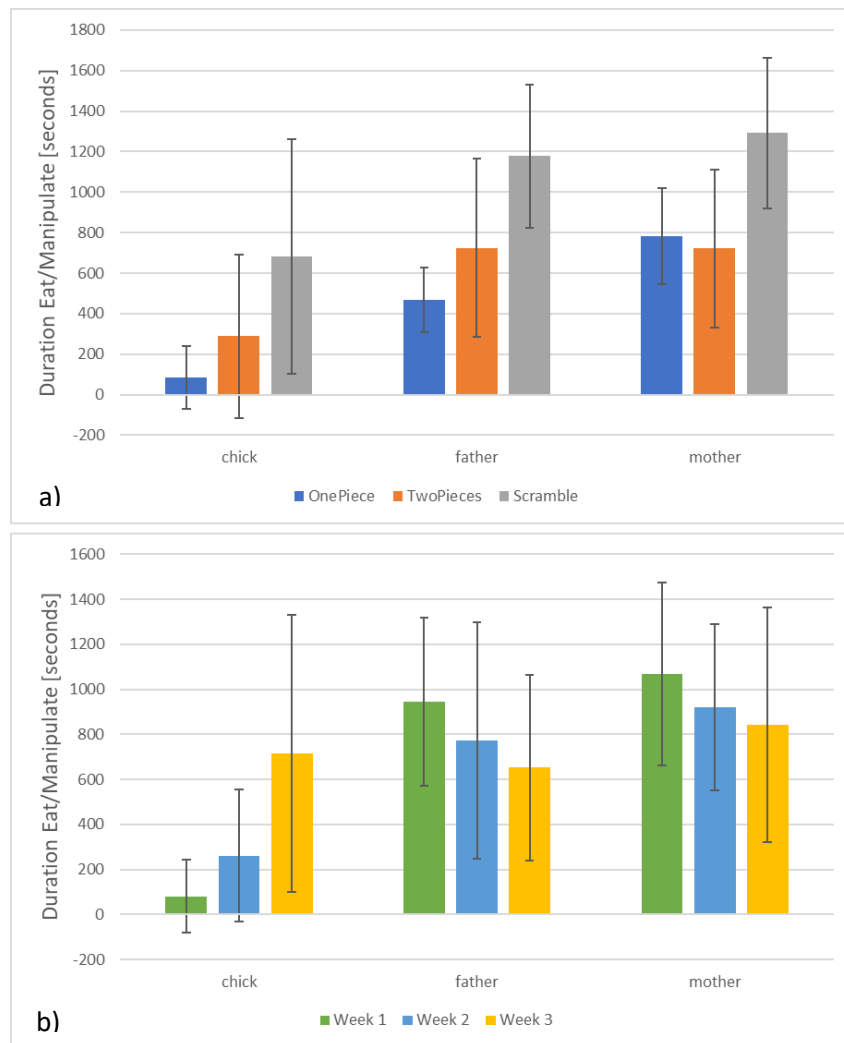


Figure 6: Bar plots illustrating means and standard deviations for the durations of Eat/manipulate behaviour measured in seconds for the three types of individuals for a) all conditions of the experiment and b) all weeks of the experiment. Sample sizes for the types: chick = 22175.6s, father = 21347.04s, mother = 25176.72s. Sample sizes for the conditions of the experiment: OnePiece = 13055.12s, TwoPieces = 19079.04s, Scramble = 36565.2s. Sample sizes for the weeks of the experiment: week 1 = 19804.56s, week 2 = 20414.4s, week 3 = 28480.4s.

3.2.2 Model 1: Food Sharing Frequency

The full model was significantly better than the null model (likelihood ratio test: $\chi^2 = 32.508$, $df = 10$, $P < 0.001$). The only predictor with a significant effect on the food sharing frequency was condition of the experiment. Food sharing frequency significantly decreased during the TwoPieces and Scramble condition compared to the OnePiece condition (Table 2; Figure 7).

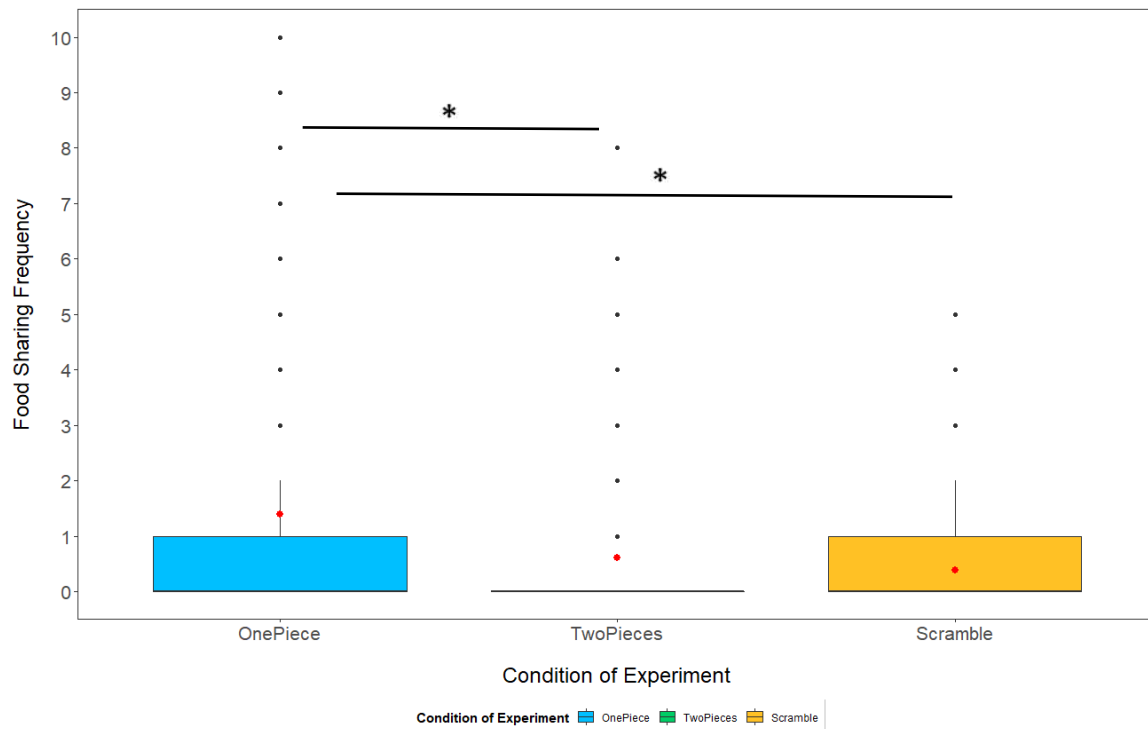


Figure 7: Boxplot of the food sharing model illustrating the food sharing frequencies for the three experimental conditions. The plot focuses on the main data of the food sharing model, i.e., some outliers are not included in the plot (outliers: for OnePiece condition at frequencies 11, 12, 13, 15 and 16; for TwoPieces condition at frequency 14). Means are indicated in red. Boxplots indicate median (thick black line) and first and third quartile. Sample sizes for the conditions of the experiment: OnePiece = 334, TwoPieces = 147, Scramble = 183 cases.

Descriptively, we see that the food sharing frequency during the OnePiece condition was highest between parents and between mothers and chicks (Table 3a; Figure S1 in the

Supplementary Materials), although this was not significant. Furthermore, the food sharing frequency seemed to peak between chicks and between parents and chicks in the second week, with higher frequencies between mothers and chicks than between fathers and chicks; and between parents, food sharing frequencies were highest in the first (father-mother) and second (mother-father) week of the experiment; although again, non-significant (Table 3b; Figure S2 in the Supplementary Materials).

Table 2: Results of the food sharing model (estimates, together with standard errors, confidence intervals, minimum and maximum of model estimates when excluding dyads one at a time, and sample size for each level of a factor).

term	estimate	SE	lower CI	upper CI	P-value	min	max	N
intercept	-1.424	0.472	-2.518	-0.588	¹⁾	-1.686	-1.247	¹⁾
week2	0.493	0.270	-0.058	1.063	0.068	0.257	0.636	333
week3	0.395	0.333	-0.233	1.020	0.236	0.119	0.570	200
conditionScramble	-0.762	0.161	-1.054	-0.425	< 0.001	-0.893	-0.530	183
conditionTwoPieces	-0.871	0.204	-1.256	-0.423	< 0.001	-0.975	-0.694	147
dyad.typechick-father	-0.058	0.620	-1.305	1.251	0.926	-0.379	0.155	69
dyad.typechick-mother	0.493	0.618	-0.745	1.765	0.425	0.152	0.869	158
dyad.typefather-chick	0.101	0.615	-1.146	1.314	0.870	-0.208	0.333	63
dyad.typefather-mother	1.310	0.785	-0.177	2.837	0.095	0.947	1.572	65
dyad.typemother-chick	0.762	0.608	-0.48	2.059	0.21	0.435	1.141	156
dyad.typemother-father	0.967	0.796	-0.643	2.590	0.225	0.161	1.602	85

1): P-value for Intercept not indicated due to limited interpretation; factors are dummy coded

with the Intercept composing the reference levels for the fixed effects of week (week 1, N = 131), condition (OnePiece, N = 334) and dyad.type (chick-chick, N = 68).

Table 3: Means and standard deviations for the food sharing frequency during the food experiment for a) the fixed effects of dyad type and condition, and b) the fixed effects of dyad type and week.

3a			3b		
Dyad Type	Mean	Standard Deviation	Dyad Type	Mean	Standard Deviation
OnePiece condition			Week 1		
chick-chick	0.268	0.884	chick-chick	0.143	0.708
chick-father	1	2.661	chick-father	0.122	0.331
chick-mother	2.184	3.555	chick-mother	0.163	0.59
father-chick	0.5	1.18	father-chick	0.449	0.792
mother-chick	2.211	3.442	mother-chick	0.633	1.112
father-mother	2.375	3.284	father-mother	1.333	2.058
mother-father	3.563	5.278	mother-father	1.238	2.166
TwoPieces condition			Week 2		
chick-chick	0.259	0.805	chick-chick	0.597	1.134
chick-father	0.256	0.993	chick-father	0.588	1.344
chick-mother	1.128	2.618	chick-mother	1.667	3.345
father-chick	0.436	1.071	father-chick	0.588	1.283
mother-chick	1	1.878	mother-chick	1.627	3.059
father-mother	0.412	1.004	father-mother	1.091	2.467
mother-father	0.941	3.4	mother-father	1.727	4.267
Scramble condition			Week 3		
chick-chick	0.361	0.848	chick-chick	0.197	0.517
chick-father	0.28	0.605	chick-father	0.635	2.161
chick-mother	0.413	0.887	chick-mother	1.25	2.122
father-chick	0.36	0.71	father-chick	0.212	0.572
mother-chick	0.44	0.889	mother-chick	0.808	1.738
father-mother	0.625	0.751	father-mother	0.591	0.908
mother-father	0.375	0.609	mother-father	0.955	3.401

3.2.2 Model 2: Agonistic Interactions Frequency

The full model was significantly better than the null model (likelihood ratio test: $\chi^2 = 54.189$, $df = 10$, $P < 0.001$). Two predictors had a significant effect on the frequency of agonistic interactions, namely week of the experiment and dyad type. The frequency of agonistic interactions significantly increased with the week of experiment and was highest in week three (Table 6). Furthermore, there was a significant increase of the frequency between

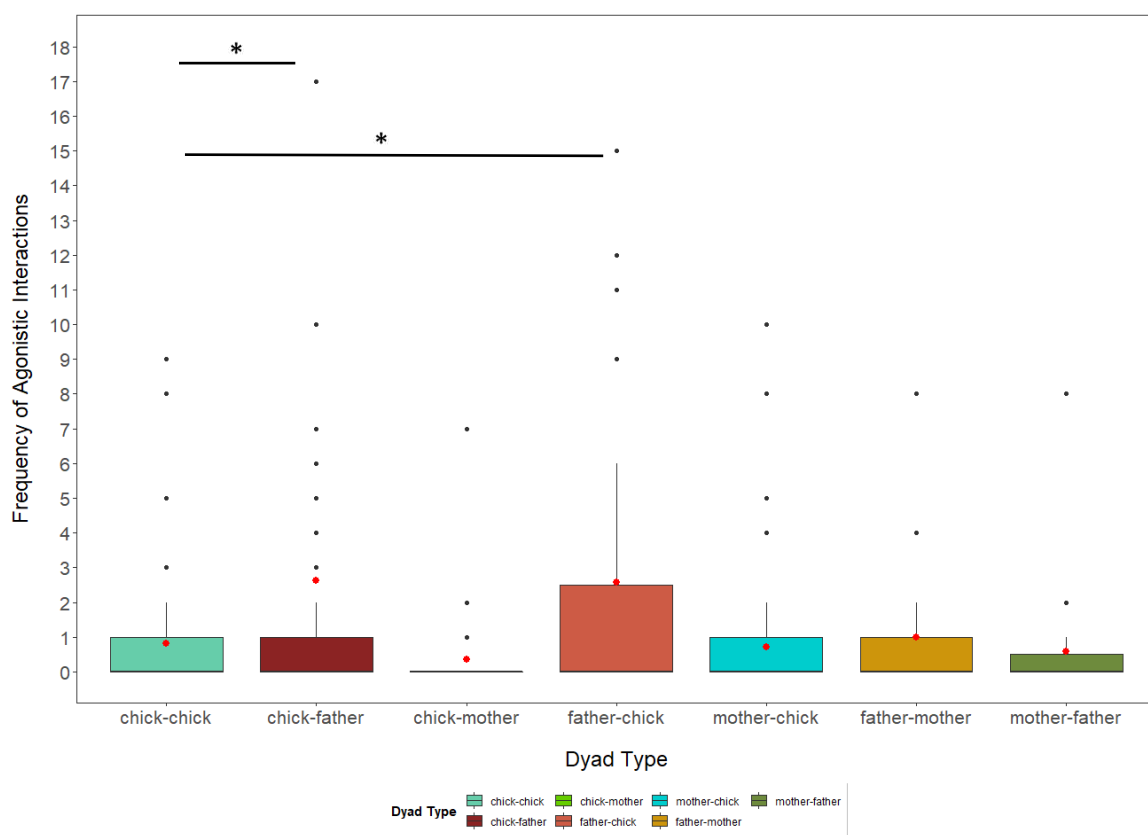


Figure 8: Boxplot of the agonistic interaction model showing the frequencies of agonistic interactions for the different dyad types. The plot focuses on the main data of the food sharing model, i.e., some outliers are not included in the plot (outliers: for chick-father at frequencies 23, 27 and 40; for father-chick at frequencies 29 and 35). Means are indicated in red. Boxplots indicate median (thick black line) and first and third quartile. Sample sizes for the dyad types: chick-chick = 74, chick-father = 165, chick-mother = 23, father-chick = 163, mother-chick = 45, father-mother = 27, mother-father = 16 cases.

particular dyad types, namely between fathers and chicks, with more agonistic interactions directed from fathers to chicks than the contrary (Table 4; Figure 8).

Descriptively, we observed most agonistic interactions between fathers and chicks during the Scramble condition (Table 5a, Figure S3 in the Supplementary Materials) and in the second and third week of the experiment, although this was not significant (Table 5b, Figure S4 in the Supplementary Materials). Between parents, most agonistic interactions seemed to occur during the OnePiece condition (Table 5a, Figure S3 in the Supplementary Materials) and the first week of the experiment, again not significant (Table 5b, Figure S4 in the Supplementary Materials). Overall, only few agonistic interactions seemed to happen between chicks and between mothers and chicks in most conditions (Table 5a, Figure S3 in the Supplementary Materials); and for these dyads, the frequencies of agonistic interactions seemed to peak in the third week, once more non-significant (Table 5b, Figure S4 in the Supplementary Materials). Between chicks, agonistic interactions increased with week of experiments, although again, this was non-significant (Table 5b, Figure S4 in the Supplementary Materials).

Table 4: Results of the agonistic interaction model (estimates, together with standard errors, confidence intervals, minimum and maximum of model estimates when excluding dyads one at a time, and sample size for each level of a factor).

term	estimate	SE	lower CI	upper CI	P-value	min	max	N
intercept	-1.947	0.438	-2.898	-1.207	²⁾	-2.234	-1.809	²⁾
week2	1.338	0.317	0.758	1.994	< 0.001	1.220	1.544	179
week3	1.923	0.32	1.383	2.551	< 0.001	1.791	2.129	285
conditionScramble	0.455	0.287	-0.068	1.072	0.113	0.372	0.587	264
conditionTwoPieces	0.105	0.298	-0.478	0.711	0.724	-0.033	0.244	132
dyad.typechick-father	0.94	0.470	-0.091	1.83	< 0.05	0.663	1.271	165
dyad.typechick-mother	-0.938	0.512	-2.104	0.035	0.067	-1.241	-0.728	23
dyad.typefather-chick	1.011	0.452	0.128	2.002	< 0.05	0.805	1.239	163
dyad.typefather-mother	1.202	0.635	-0.126	2.425	0.059	0.952	1.494	27
dyad.typemother-chick	-0.246	0.488	-1.269	0.764	0.614	-0.539	0.006	45

dyad.typemother-father 0.451 0.681 -0.921 1.622 0.507 -0.637 1.264 16
 2): P-value for Intercept not indicated due to limited interpretation; factors are dummy coded

with the Intercept composing the reference levels for the fixed effects of week (week 1, N = 49), condition (OnePiece, N = 117) and dyad.type (chick-chick, N = 74).

Table 5: Means and standard deviations for the frequency of agonistic interactions during the food experiment for a) the fixed effects of dyad type and condition, and b) the fixed effects of dyad type and week.

5a			5b		
Dyad Type	Mean	Standard Deviation	Dyad Type	Mean	Standard Deviation
OnePiece condition			Week 1		
chick-chick	0.133	0.571	chick-chick	0.067	0.254
chick-father	1.095	1.786	chick-father	0.429	0.926
chick-mother	0.476	1.537	chick-mother	0	0
father-chick	1.857	3.61	father-chick	0.429	1.076
mother-chick	0.524	1.75	mother-chick	0.095	0.301
father-mother	2	2.55	father-mother	1.778	2.682
mother-father	1.333	2.598	mother-father	1.222	2.635
TwoPieces condition			Week 2		
chick-chick	1.367	2.414	chick-chick	0.967	1.129
chick-father	1.333	3.916	chick-father	3.429	6.177
chick-mother	0.238	0.539	chick-mother	0.286	0.561
father-chick	1	2.49	father-chick	2.476	3.696
mother-chick	1.238	2.508	mother-chick	0.571	1.165
father-mother	0.889	1.364	father-mother	0.444	0.726
mother-father	0.333	0.707	mother-father	0.444	0.726
Scramble			Week 3		
chick-chick	0.967	1.033	chick-chick	1.433	2.388
chick-father	5.429	10.907	chick-father	4	10.159
chick-mother	0.381	0.669	chick-mother	0.81	1.569
father-chick	4.905	9.586	father-chick	4.857	9.738
mother-chick	0.381	0.921	mother-chick	1.476	2.857
father-mother	0.111	0.333	father-mother	0.778	1.302
mother-father	0.111	0.333	mother-father	0.111	0.333

3.2.3 Model 3: Frequency of Begging and Watching

The full model was significantly better than the null model (likelihood ratio test: $\chi^2 = 70.388$, $df = 10$, $P < 0.001$). Two predictors had a significant effect on the frequency of begging and watching behaviour, namely condition of the experiment and dyad type. The frequency of begging and watching behaviour was highest during the OnePiece condition (Table 8). Chicks directed most of their begging and watching to fathers. However, chicks directed almost as much begging and watching behaviour to their mothers as to their fathers (Table 6; Figure 9).

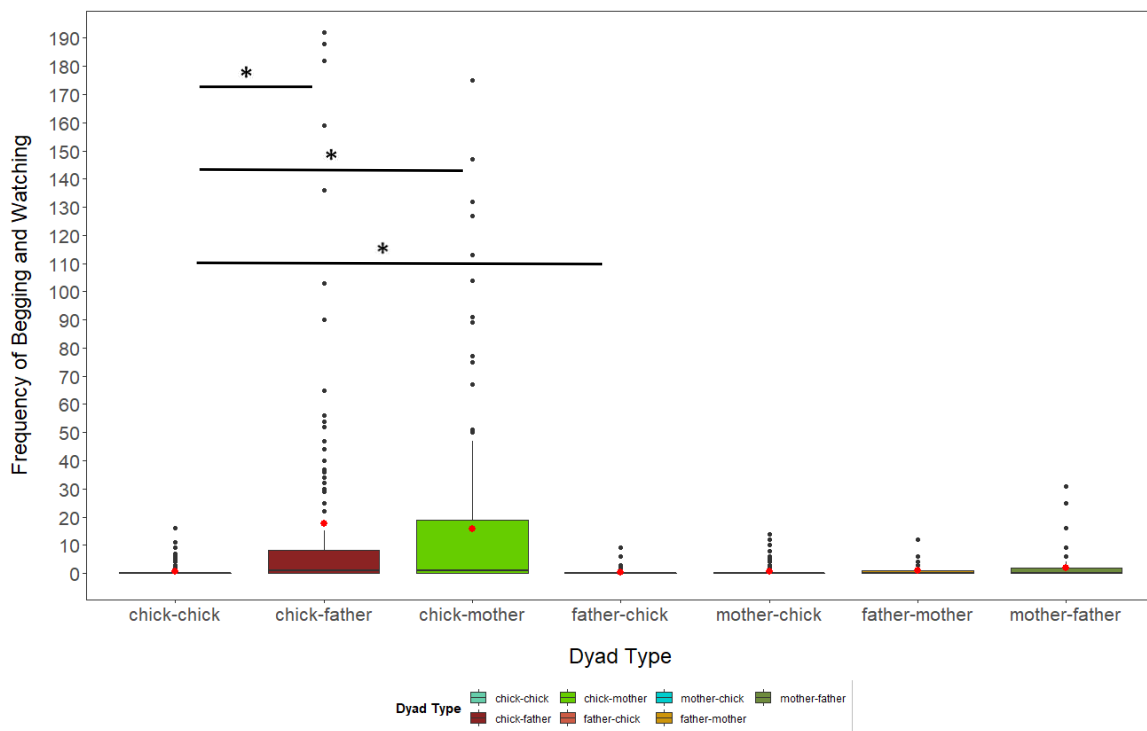


Figure 9: Boxplot of the begging and watching model showing the frequencies of begging and watching behaviours for the different dyad types. The plot focuses on the main data of the food sharing model, i.e., some outliers are not included in the plot (outliers: for chick-father at frequencies 263 and 288). Means are indicated in red. Boxplots indicate median (thick black line), first and third quartile, and the whiskers with 1.5 times the interquartile range. Sample size for the factor dyad type: chick-chick = 159, chick-father = 2696, chick-mother = 2380, father-chick = 46, mother-chick = 101, father-mother = 67, mother-father = 128 cases.

Although not significant, descriptively we can see an increase of begging and watching frequency with week of experiments (Table 6). Again descriptively, we see that chicks mostly begged and watched their parents in the OnePiece and TwoPieces condition (with similar frequencies in these two conditions) (Table 7a, Figure S5 in the Supplementary Materials) and frequencies peaked in the second week of the experiment, although this was not significant (Table 7b, Figure S6 in the Supplementary Materials). Between parents, little begging and watching was observed: mothers begged to and watched fathers at higher frequencies than the contrary; again, this was not significant. Frequencies of begging and watching behaviour were highest during the OnePiece condition (Table 7a, Figure S5 in the Supplementary Materials) and in the first week of the experiment (Table 7b, Figure S6 in the Supplementary Materials); once again, non-significant. Begging and watching behaviour between chicks peaked in the second week of experiments; although again, non-significant (Table 7b, Figure S6 in the Supplementary Materials).

Table 6: Results of the begging watching model (estimates, together with standard errors, confidence intervals, minimum and maximum of model estimates when excluding dyads one at a time, and sample size for each level of a factor).

term	estimate	SE	lower CI	upper CI	P-value	min	max	N
intercept	-0.565	0.503	-1.649	0.249	³⁾	-0.766	-0.342	³⁾
week2	0.072	0.304	-0.520	0.683	0.812	-0.095	0.302	2680
week3	0.1	0.310	-0.499	0.702	0.748	-0.117	0.223	1485
conditionScramble	-0.971	0.217	-1.367	-0.495	< 0.001	-1.107	-0.750	1459
conditionTwoPieces	-0.028	0.252	-0.524	0.443	0.912	-0.294	0.174	2127
dyad.typechick-father	3.068	0.646	1.785	4.278	< 0.001	2.778	3.449	2696
dyad.typechick-mother	2.962	0.643	1.733	4.209	< 0.001	2.695	3.458	2380
dyad.typefather-chick	-1.444	0.71	-2.893	0.018	< 0.05	-1.930	-1.140	46
dyad.typefather-mother	0.585	0.860	-1.181	2.238	0.496	0.288	0.853	67
dyad.typemother-chick	-0.911	0.687	-2.362	0.391	0.184	-1.377	-0.577	101
dyad.typemother-father	0.650	0.866	-1.144	2.283	0.453	0.001	1.468	128

3) P-value for Intercept not indicated due to limited interpretation; factors are dummy coded with the Intercept composing the reference levels for the fixed effects of week (week 1, N = 1412), condition (OnePiece, N = 1991) and dyad.type (chick-chick, N = 159).

Table 7: Means and standard deviations for the frequency of begging and watching behaviours during the food experiment for a) the fixed effects of dyad type and condition, and b) the fixed effects of dyad type and week.

7a			7b		
Dyad Type	Mean	Standard Deviation	Dyad Type	Mean	Standard Deviation
OnePiece condition			Week 1		
chick-chick	0.804	2.7	chick-chick	0.086	0.442
chick-father	23.395	57.956	chick-father	16.082	29.303
chick-mother	22.816	38.426	chick-mother	11.245	20.659
father-chick	0.474	1.409	father-chick	0.061	0.317
mother-chick	1.684	3.519	mother-chick	0	0
father-mother	2.188	2.287	father-mother	1.333	1.906
mother-father	4.563	8.294	mother-father	1.714	2.473
TwoPieces condition			Week 2		
chick-chick	1.259	2.381	chick-chick	1.431	2.852
chick-father	26	63.430	chick-father	23.294	55.908
chick-mother	23.923	39.943	chick-mother	24.51	41.076
father-chick	0.410	1.482	father-chick	0.412	1.314
mother-chick	0.795	1.794	mother-chick	0.745	1.917
father-mother	1.471	3.145	father-mother	1.273	2.848
mother-father	2.353	5.99	mother-father	2.364	6.114
Scramble condition			Week 3		
chick-chick	0.426	0.899	chick-chick	0.658	1.447
chick-father	10.573	24.376	chick-father	13.846	50.268
chick-mother	7.733	14.241	chick-mother	11.135	23.732
father-chick	0.16	0.466	father-chick	0.423	1.258
mother-chick	0.08	0.319	mother-chick	1.212	2.913
father-mother	0.219	0.553	father-mother	0.5	1.371
mother-father	0.469	0.95	mother-father	1.818	6.558

4. Discussion

To investigate food sharing in a parental care context, I observed parents' feeding behaviour at the nest and at one or two monopolisable food source(s) during the fledgling period. Main results show that mothers did most of the feeding during nestling and fledgling period while fathers were responsible for most aggressions toward the chicks. Agonistic interactions were in general more frequent in the Scramble condition. Chicks directed most of their begging and watching to fathers.

I will discuss below 1) the patterns of allo-feeding behaviour between parents and offspring during the nestling period, followed by 2) monopolisation (i.e., time spent at the food sources), 3) food sharing, 4) agonistic and 5) begging and watching behaviours during the food experiment. Finally, 6) I will shortly discuss general considerations on the methodology.

4.1 Parental Care and Food Sharing during the Nestling Period

The food sharing frequency during the nestling period decreased with week of observation between parents and between parents and offspring. As offspring gets older, they might not need so much food anymore. Also, parents may want to have their chicks leaving the nest to get their food themselves with time. This fits the phases of parental care described by Trivers (1974), in particular the one when parents more often refuse offspring's requests when they get older until the offspring finally becomes independent (Trivers, 1974). With respect to the reduced food transfers between parents, this might be because 1) mothers reduce their feeding effort to chicks, and therefore fathers do not need to bring as much food to the nest anymore, or 2) both parents generally did not need to be at the nest that often anymore because of reduced offspring care, and so food transfers between parents were not observable anymore (i.e., sampling bias).

Furthermore, fathers fed mothers at a higher frequency than the contrary. In general, males feeding their mates before and/or during copulation and incubation is known as courtship feeding, serving the nourishment of the mothers, but the main function is the maintenance of the pair bonding (Lack, 1940). In this study, fathers mostly fed mothers during the nestling period i.e., after incubation and hatching of the offspring, which means this behaviour cannot be defined as courtship feeding behaviour. However, fathers feeding mothers who spend a lot of time at the nest caring for offspring could still be an explanation for the observed pattern. In mammals, especially in cooperative breeding carnivores, lactating mothers are provided with food by the whole family (mainly aunts, uncles, and older offspring) (black-backed jackals *Canis mesomelas*: Moehlman, 1979; wolves *Canis lupus*: Harrington et al., 1983; African Hunting Dogs *Lycaon pictus*: Kuhme, 1965; Malcom and Marten, 1982). Finally, food transfers between raven parents could also partially be explained by the necessity to maintain a qualitative pair bond (Clayton and Emery, 2007).

Another reason why fathers transfer food to mothers could be to enable mothers to provide food to the offspring. This is in line with the result that mothers fed the offspring at higher frequencies than fathers. There are several hypotheses that could explain why mostly mothers are caring for the (mostly smallest) offspring. When mothers are the only ones incubating and brooding the offspring, they might simply continue caring for the (smallest) offspring (initial care hypothesis: Slagsvold, 1997). But mothers might also show specific care for offspring as they have already spent most of the time with the brood (time spending hypothesis: Stamps et al., 1985) and due to this they are also the ones having the best insight in the offspring's demands (best knowledge hypothesis: Gottlander, 1987). Another possibility is that differing behaviour of the chicks in the presence of high sibling competition causes a selective behaviour of the parents (sibling rivalry hypothesis: Slagsvold, 1997).

4.2 Food Experiment: Food Monopolisation

Interestingly, contrary to my expectations, mostly mothers were manipulating the food during the OnePiece condition. One explanation could be that mothers continued to provide more care than fathers and for that they need to be at the food source to get food not only for themselves, but also for the chicks. Another mutual but not exclusive explanation is that raven parents undergo a dominance reversal during the breeding season. In general, males are dominant over females in raven's social systems (Braun and Bugnyar, 2012; Boucherie et al. submitted). However, in many monogamous species dominance reversals can be observed during the breeding season, with females dominating males during this specific period. Outside the breeding season, mated males must maintain and defend their territory, while non-breeder males compete with others to find a mate. And in general, males of all age class compete with others to access food resources. However, during the breeding season, it might become beneficial for both partners that females become the dominant partner and more easily access valuable resources. Males can afford to be subordinate, and in the same way they are supporting their mate, because in monogamous species there is no doubt about paternity (Smith, 1980). The hypothesis that a dominance rank reversal occurs during breeding in common ravens is partly supported by my results, as mothers monopolised the single food sources which is the condition with the higher degree of competition. However, frequencies of agonistic interactions do not support this suggestion (agonistic interactions between fathers and mothers were similar). Further investigation would thus be needed to confirm a potential rank reversal between genders during breeding.

Chicks were able to manipulate food mostly during Scramble condition when competition was diluted with parents (and chicks) manipulating their own food sources. Maybe due to their lower rank (Braun and Bugnyar, 2012), they were not allowed by their

parents to access the single food source, but when two or more food sources were available parents were not able to monopolise all of them, so chicks were finally able to approach a food source. While mothers and fathers decreased their time spent at the food in all conditions during the experiment, chicks increased their time at the food source during the experiment. This could be explained by offspring becoming more and more independent from their parents and their ability to manipulate food themselves. Similar patterns were found in the Northern Wheatears, *Oenanthe oenanthe*, where young increased their foraging activity with age, while parents lowered their provisioning rate. Moreno related this behavioural pattern to fledglings' becoming independent (Moreno, 1984).

4.3 Food Experiment: Food Sharing Behaviour

Food sharing in general (as well as some agonistic interactions and begging and watching behaviour) were most frequently observed during the OnePiece condition. In this condition, individuals were concentrated in one location, and thus more likely to encounter and interact. In contrast, during the TwoPieces condition the birds could split up between two food sources reducing the probability of interactions.

Food sharing was most frequently observed during the second week of experiments, which only partly confirms my hypothesis that food sharing would be highest during the first week of experiment. A possible explanation could be that chicks stayed a lot in the nest during the first week of experiments (personal observation) and did not access the food source(s) at all, while from week two they started coming down and approaching the food source(s). The decrease of food sharing frequency in week three is in line with other studies. For example, in Montague's harriers, parents stopped providing their young with food at the end of the post fledgling period (Arroyo et al., 2002). Food sharing in young cockatiels, *Nymphicus hollandicus*, decreased within their first three years of live (Liévin-Bazin et al., 2019), and juvenile jackdaws,

Corvus monedula, decreased their food sharing behaviour when getting older, (de Kort et al., 2006; von Bayern et al., 2007).

Food sharing frequency between chicks remained equal for all conditions and peaked in the second week of experiments. A decrease of food sharing with age was found in juvenile jackdaws, *Corvus monedula* (e.g., de Kort et al., 2006; von Bayern et al., 2007), or young cockatiels, *Nymphicus hollandicus* (Liévin-Bazin et al., 2019). Liévin-Bazin and colleagues (2019) as well as von Bayern and colleagues (2004) additionally concluded that food sharing between siblings, but also non-siblings, serves the formation and maintenance of affiliative relationships between individuals (Liévin-Bazin et al., 2019; von Bayern et al., 2007; Boucherie et al. 2020; Loretto et al., 2012). According to my (descriptive) results, this could also be the case for common raven fledglings. Next to affiliative relationships, dominance ranks might play a role in food sharing between chicks, where chicks with high dominance might share food with their subordinate siblings (as it was found for example in siblings of the Atlantic salmon *Salmon salar*: Griffiths and Armstrong, 2002). However, it remains to be discussed whether raven fledglings even have stable dominance hierarchies already established (like e.g., European shags *Phalacrocorax aristotelis*: Velando, 2000; blue-footed boobies *Sula nebouxii*: Valderrábano-Ibarra et al., 2007) or if their dominance ranks are subject to constant change. Like between parents and offspring, food sharing between siblings could serve the offspring's inclusive fitness (Hamilton, 1964).

Food Sharing between parents and offspring is generally explained by inclusive fitness after Hamilton, describing that parents' fitness is benefitting from caring for their offspring (Hamilton, 1964), as especially in altricial bird species offspring would have no chance to survive without parents caring for them (Gonzalez-Voyer and Kolm, 2010). Like during the nestling period, during the food experiments mothers shared most food with chicks, which

might therefore be explained by the same theories: they are the ones incubating and brooding the offspring, so they might simply continue caring for the offspring (Slagsvold, 1997), they spent the most time with the offspring (Stamps et al., 1985) and they might have the best insight in the offspring's demands (Gottlander, 1987). Next to nutritional needs, food sharing between parents and offspring could also serve an informational need for the offspring, as they learn what they can eat and how they can manipulate the food (Brown et al., 2004). Primate mothers, too, are known to share with their offspring, more precisely 92% of food transfers between wild chimpanzee, *Pan troglodytes*, mothers and their offspring was directed from mothers to their offspring (McGrew, 1975).

In many biparental and monogamous bird species, mothers and fathers are known to feed their offspring and in context of parental care labour distribution they not only prefer different (pheno)types of their offspring but might also completely divide their broods. Parents can prefer different (pheno)types of their offspring, e.g., to impede selfish young and control allocations of food and other caring behaviours (Slagsvold, 1997). Different preferences of parents could be linked to sex and hatching rank. For example, fathers in crimson rosellas, *Platycercus elegans*, mainly fed large offspring and mothers feeding all offspring equally, and older males were preferred over females and young males (Krebs et al., 1999). However, there is also the possibility that both parents prefer a single sex (e.g., Red-winged black-bird *Agelaius phoeniceus*: Teather, 1992). Another factor is how fast chicks beg, e.g., parents can show preferences for chicks that beg quicker (e.g., Zebra Finches *Taeniopygia guttata*: Levrero et al., 2012) or beg the most (e.g., collared flycatchers *Ficedula albicollis*: Rosivall et al., 2005). Showing specific preferences might in the end lead to brood division, i.e., each parent showing specific preferences for different young during the post-fledging period (Draganoiu et al., 2006). Other species show labour distribution not by brood division, but by

fulfilling different aspects of care. For example, mothers of the Atlantic puffins, *Fratercula arctica*, invested more in caring for the offspring (i.e., parental effort), whereas fathers invested more in defending the territory and extra pair copulations (i.e., mating effort) (Creelman and Storey, 1991). Based on my results, I would suggest that raven parents do not divide their brood but divide their labour like observed in the Atlantic puffins, with mostly mothers caring for the offspring and fathers defending the territory. However, due to the experimental and statistical setup, I was not able to detect any parental preferences in the investigated raven families, thereby further studies should investigate possible parental preferences, but also include factors like territory defence and incubation/brooding effort in investigation of parental labour distribution in common raven parents.

4.4 Food Experiment: Agonistic Interactions

Agonistic interactions generally increased with week of experiment, and as expected, most agonistic interactions were directed from fathers to chicks. In general, adult ravens are known to direct agonistic behaviour to subadults trying to access food (Heinrich and Marzluff, 1995), because adult birds hold a higher dominance rank than subadults (Braun and Bugnyar, 2012) and in case of mates, they are defending food in their territory (Heinrich and Marzluff, 1995). Another explanation for agonistic interactions between fathers and offspring might be to initiate the fledgling's independence, not only by stopping provisioning of chicks (Moreno, 1984), but also by becoming more aggressive when chicks get older (Trivers, 1974).

While in the Scramble condition all types of dyads showed high rates of manipulation, they also showed high rates of agonistic interactions (at least some dyads). One explanation is that fathers tried to monopolise all scattered food pieces and therefore chased the chicks away. Similar patterns were observed in ruddy turnstones, *Arenaria interpres*, where in an experiment dominant individuals monopolised two food sources if close to each other (Vahl

and Kingma, 2007). However, this pattern differs from previous findings in a food monopolisation experiment with subadult ravens in a non-breeders group, where agonistic interactions increased when food was agglomerated and thus competition increased (Sima, 2012). Similarly, in alpine choughs, *Pyrrhocorax graculus*, agonistic interactions increased when food was patchily distributed compared to when it was randomly scattered and only some of the flock members could access the food (Delestrade, 1999). Female vervets, *Chlorocebus aethiops*, feeding at large and spatially clumped food sources encountered higher rates of agonistic interactions compared to female pata monkey, *Erythrocebus patas*, who feed at small and randomly distributed food sources (Pruetz and Isbell, 2000). One explanation lays in the way the scrambled food pieces were provided in the experiment of my thesis i.e., the pieces were put as heap in the aviary, and, at first glance, this heap could be viewed as agglomerated food source, too, leading to monopolisation and increased agonistic interactions.

4.5 Food Experiment: Begging and Watching

Contrary to my predictions, the frequency of begging and watching increased in all conditions with the week. I suggest that the experiments were conducted too early to show a decrease in begging as chicks were still dependent on their parents i.e., this would resemble the second phase of postnatal maternal care (Trivers, 1974).

Interestingly, chicks directed most of their begging and watching behaviour not only to their mothers, but also to their fathers. As especially begging behaviour and vocalizing can also be used as conciliation gesture after agonistic interactions, one explanation if that begging could be used by chicks to decrease the tension between father and chicks (Gwinner, 1964; von Boltzheim, 1993). Another explanation could be that because fathers received most

begging (perhaps because they provided less food) and therefore became aggressive to their chicks (personal suggestion and observation; comment by Boucherie, 2021).

Between parents, the frequency of begging and watching decreased with the week. This might be due to the dominance rank reversal. When the chicks get older, and breeding season comes to an end, fathers again become dominant over the mothers, and male common ravens never beg to their mates (Huber, 1991; von Boltzheim, 1993). Mothers, on the other side, do not need to feed chicks in the same extend as during the nestling period anymore and therefore I suggest they do not need to solicit for support and feeding of their mate anymore.

Begging and watching behaviour between chicks peaked in the second week of experiments. This could be due to chicks learning from each other (Schwab et al., 2008) or soliciting for food to strengthen their affiliative relationships with their siblings (Liévin-Bazin et al., 2019). However, begging could be used as conciliation gesture after agonistic interactions (Gwinner, 1964; von Boltzheim, 1993) reflecting competition between the chicks, because agonistic interactions increased with week of experiments, too, indicating competition between the siblings when getting older (e.g., Mock et al., 1990).

An in my opinion interesting aspect when investigating these behaviours is the combination of begging and watching (in contrast to the discussion above which mainly focused on begging behaviour). Watching their parents, on the one hand, could be part of begging behaviour (as often begging and watching could be observed in series, personal observation) to solicit food. On the other hand, chicks carefully watched their parents as long as they manipulated food but started begging as soon as the parents started moving away from the food possibly trying to get more food than the probably slower sibling. Similar results were found in the common redstart, *Phoenicurus phoenicurus*, where nestlings begged

quicker when they were hungry than when they were satiated (Porkert and Špinka, 2004). In general, begging and especially watching can have important social learning functions, i.e., chicks learn from their parents how to manipulate the food (Brown et al., 2004).

4.6 Methodology Discussion

Despite a thoroughly planned experimental design and interesting results, my findings were limited by several methodological constraints, which I aim to discuss here.

In the nestling period, the marking of chicks as early as in the nestling period would allow to further investigate the effects of sex-, age- or size-preferences on parents allo-feeding patterns during the nestling period. This would also allow to track down the chicks' weight and to include it in the analyses. Additionally, I would suggest quantifying the incubation and brooding effort of the parents to further assess their share in parental care.

In the food experiment during the fledging period, the chicks were known and marked with rings, but because of the small sample size and missing dyad types in the families it was not possible to have a look at sex-, age- or size-preferences of parents (e.g., in families with only female chicks it was not possible to investigate possible preferences of parents for male chicks), which is why I would suggest further studies focusing on parental preferences to include chicks' sex, age, and size (weight) in their analysis. Quite recently, Ersoy and colleagues (2021) actually investigated parental preferences in the post-fledging care in captive common ravens. They observed paternal preferences for male and heavy chicks, whereas mothers did not show any preferences (Ersoy et al., 2021). Additionally, I would suggest further studies investigating parental care and allo-feeding to focus not only on the post-fledging care, but also on the nestling period. To have a look at effects of brood size on parental care and offspring-preferences, families with more than three chicks should be compared to small

families with less than three chicks. Additionally, further studies investigating food sharing between raven fledglings should include all possible dyads for chick interactions. Furthermore, it would be interesting to find out something about the dominance hierarchy system for fledglings in common ravens. Regarding the dyads used for analysis, I would suggest to not only look at directions of interactions, but also at identities to investigate possible processes like “Tit-for-Tat” or reciprocity. Moreover, I would suggest altering the control condition (i.e., Scramble) in a way that the provided food pieces are not monopolisable, for example scatter them on a wider range in the aviary instead of providing them as a heap.

5. Conclusion

This study is the first attempt to investigate the nestling and fledgling parental care and labour distribution in the common raven using observations during the nestling period and at monopolisable food sources during the post-fledgling period. The focus of this investigation was on interactions between parents and between parents and offspring but also provides some hints on interactions between offspring. Results are suggesting a dominance-reversal in the raven parents and are indicating that mothers are the ones providing most of the care for the offspring, whereas fathers show the highest agonistic interactions frequency to chicks. Next to this, begging and watching behaviour of chicks directed to the parents could serve the solicitation for food, but also learning how to manipulate food. Due to the small dataset, the models excluded interactions of factors and therefore only few results showed significant differences between week, condition, or dyad type. But descriptive statistics revealed possible interactions between factors, which could be addressed in a future study using data of additional families. However, there is hardly anything known of fledgling-behaviour at a monopolisable food source in the family-context, but also about the fledgling behaviour itself especially in common ravens as well as in other bird species. Hence, this study could be viewed as a starting point of investigation not only regarding parental care and offspring-preferences in the common raven, but also regarding the food sharing and begging behaviour during post-fledgling period still in the context of the family.

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Ich habe mich bemüht, sämtliche Inhaber*innen der Bildrechte ausfindig zu machen und ihre
Zustimmung zur Verwendung der Bilder in dieser Arbeit eingeholt. Sollte dennoch eine
Urheberrechtsverletzung bekannt werden, ersuche ich um Meldung bei mir.

Supplementary Materials

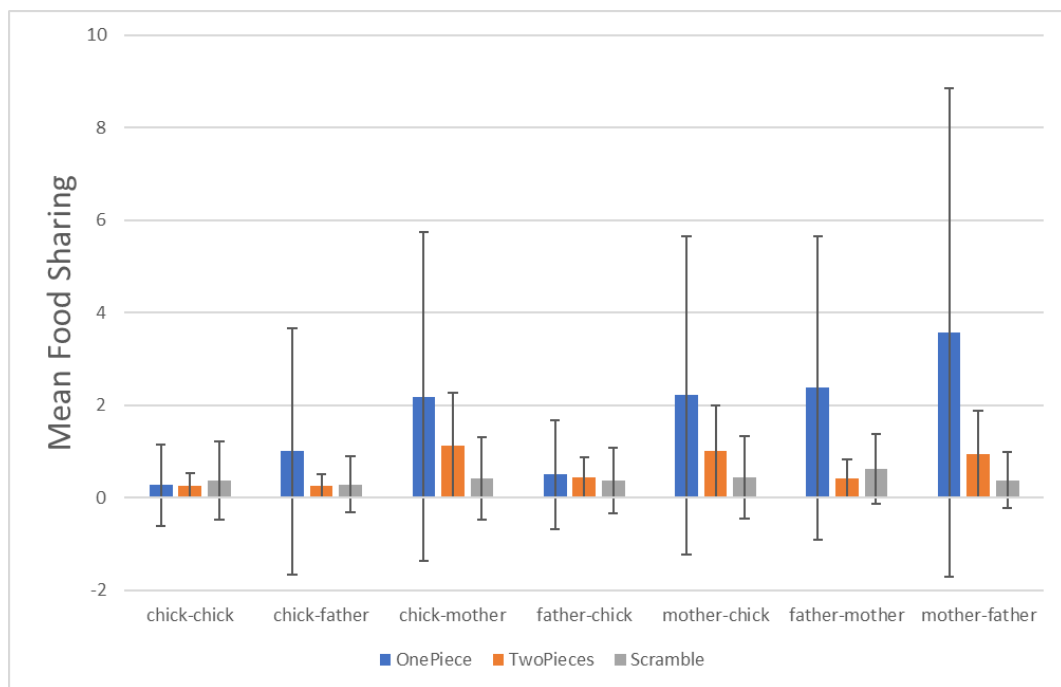


Figure S1: Bar plot illustrating the means and standard deviations for the food sharing frequency during the food experiment for dyad type and condition of experiment. Sample sizes for the dyad types: chick-chick = 68, chick-father = 69, chick-mother = 158, father-chick = 63, mother-chick = 156, father-mother = 65, mother-father = 85 cases. Sample size for the conditions of the experiment: OnePiece = 334, TwoPieces = 147, Scramble = 183 cases.

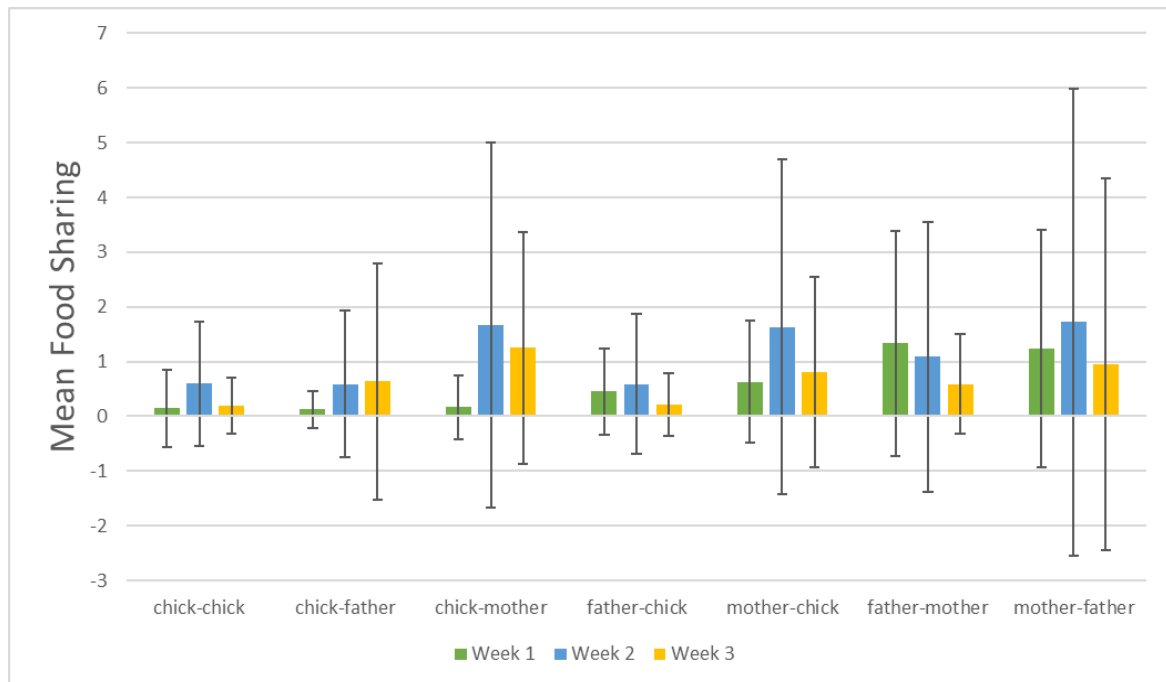


Figure S2: Bar plot illustrating the means and standard deviations for the food sharing rate during the food experiment for dyad type and week of experiment. Sample sizes for the dyad types: chick-chick = 68, chick-father = 69, chick-mother = 158, father-chick = 63, mother-chick = 156, father-mother = 65, mother-father = 85 cases. Sample sizes for the weeks of the experiment: week 1 = 131, week 2 = 333, week 3 = 200 cases.

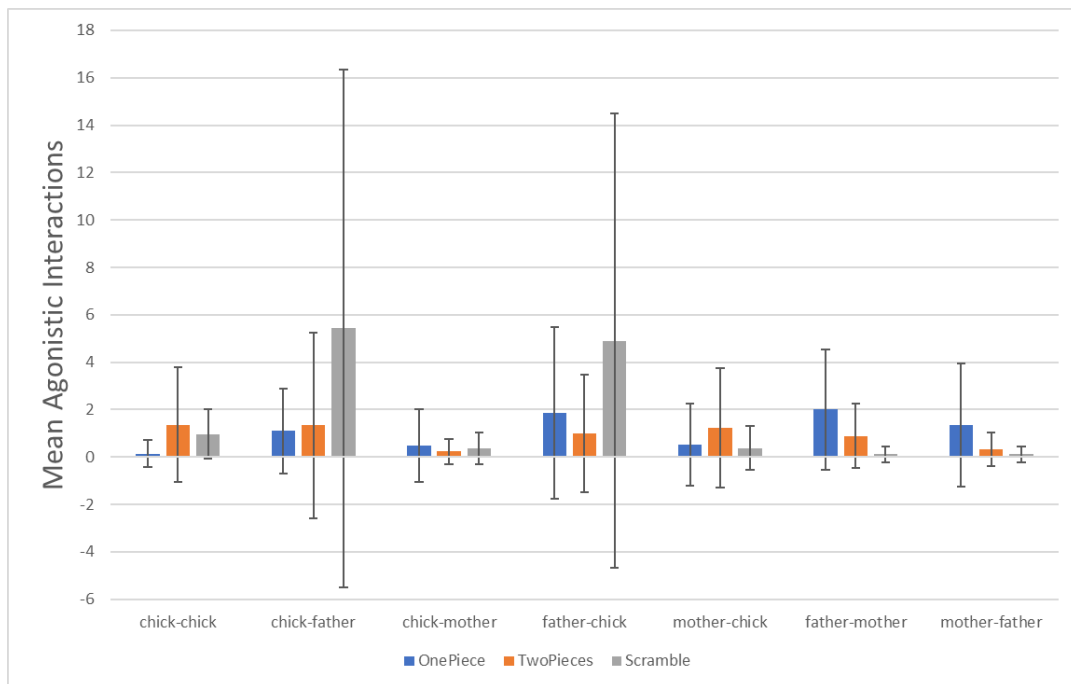


Figure S3: Bar plot illustrating the means and standard deviations for the frequencies of agonistic interactions during the food experiment for dyad type and condition of experiment. Sample sizes for the dyad types: chick-chick = 74, chick-father = 165, chick-mother = 23, father-chick = 163, mother-chick = 45, father-mother = 27, mother-father = 16 cases. Sample sizes for the conditions of the experiment: OnePiece = 117, TwoPieces = 132, Scramble = 264 cases.

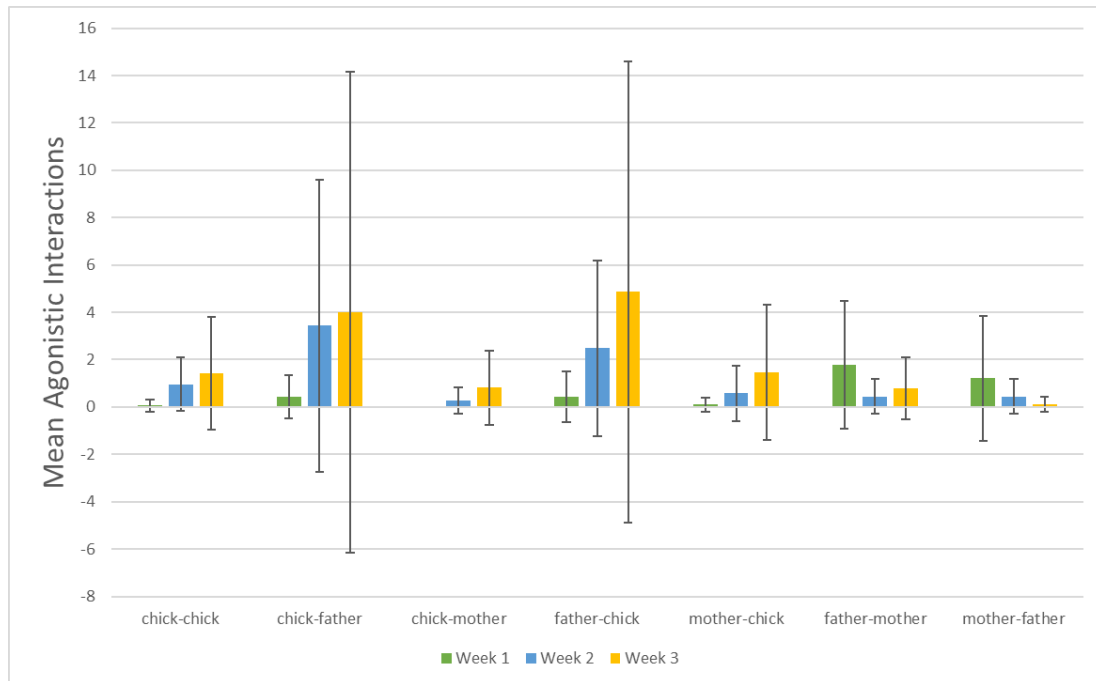


Figure S4: Bar plot illustrating the means and standard deviations for the frequencies of agonistic interactions during the food experiment for dyad type and week of experiment. Sample sizes for the dyad types: chick-chick = 74, chick-father = 165, chick-mother = 23, father-chick = 163, mother-chick = 45, father-mother = 27, mother-father = 16 cases. Sample sizes for the weeks of experiment: week 1 = 49, week 2 = 179, week 3 = 285 cases.

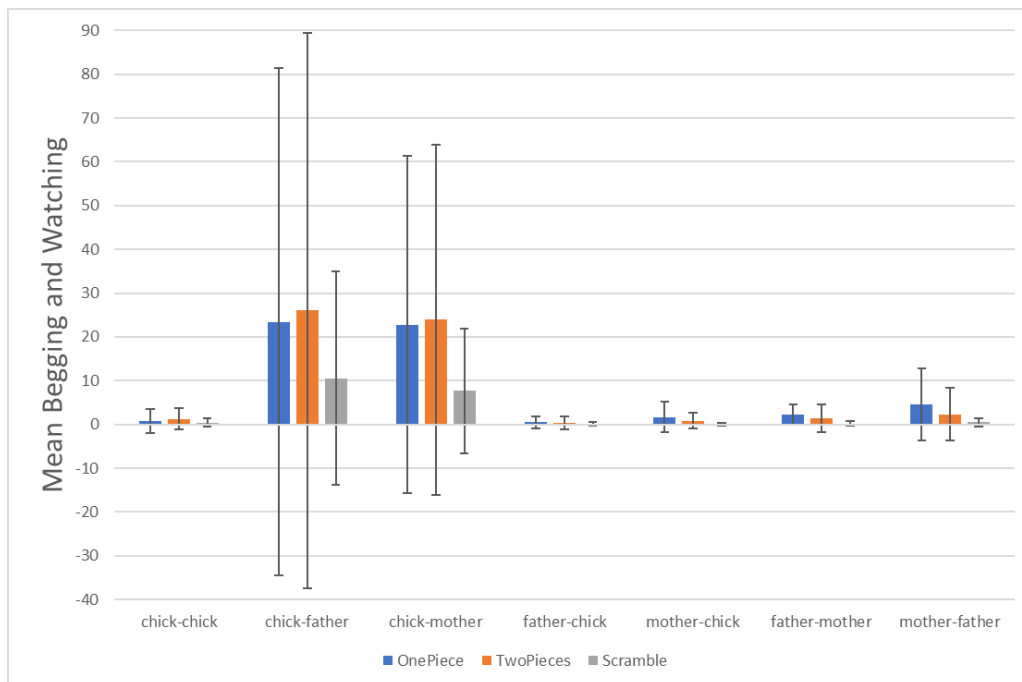


Figure S5: Bar plot illustrating the means and standard deviations for the frequencies of begging and watching behaviour during the food experiment for dyad type and condition of experiment. Sample sizes for the dyad types: chick-chick = 159, chick-father = 2696, chick-mother = 2380, father-chick = 46, mother-chick = 101, father-mother = 67, mother-father = 128 cases. Sample sizes for the conditions of the experiment: OnePiece = 1991, TwoPieces = 2127, Scramble = 1459 cases.

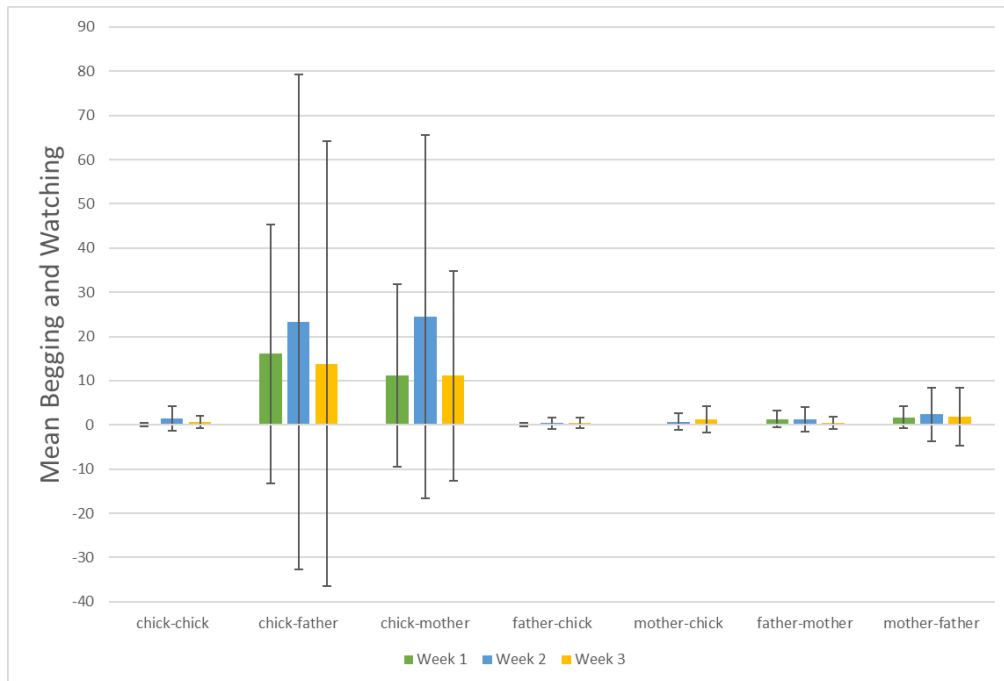


Figure S6: Bar plot illustrating the means and standard deviations for the frequencies of begging and watching behaviour during the food experiment for dyad type and week of experiment. Sample sizes for the dyad types: chick-chick = 159, chick-father = 2696, chick-mother = 2380, father-chick = 46, mother-chick = 101, father-mother = 67, mother-father = 128 cases. Sample sizes for the weeks of the experiment: week 1 = 1412, week 2 = 2680, week 3 = 1485 cases.

Table S1: Families used for observations of the nestling period and analysed in the food experiments in 2019 and 2020 (all families housed at Haidlhof Research Station).

Year	Family	Name	Parent/Chick	Sex	Treatment
2019	Joey-Rocky	Joey	Parent	Female	Food Experiment
2019	Joey-Rocky	Rocky	Parent	Male	Food Experiment
2019	Joey-Rocky	Hamlet	Chick	Male	Food Experiment
2019	Joey-Rocky	Juliet	Chick	Female	Food Experiment
2019	Joey-Rocky	Othello	Chick	Male	Food Experiment
2019	Nobel-George	Nobel	Parent	Female	Food Experiment
2019	Nobel-George	George	Parent	Male	Food Experiment
2019	Nobel-George	Hazel	Chick	Female	Food Experiment
2019	Nobel-George	Hickory	Chick	Male	Food Experiment
2020	Aramis-Paul	Aramis	Parent	Female	Food Experiment/Nestling Period
2020	Aramis-Paul	Paul	Parent	Male	Food Experiment/Nestling Period
2020	Aramis-Paul	Eragon	Chick	Male	Food Experiment/Nestling Period
2020	Aramis-Paul	Saphira	Chick	Female	Food Experiment/Nestling Period
2020	Astrid-Horst	Astrid	Parent	Female	Nestling Period
2020	Astrid-Horst	Horst	Parent	Male	Nestling Period
2020	Astrid-Horst	Hades	Chick	Male	Nestling Period
2020	Astrid-Horst	Nyx	Chick	Female	Nestling Period
2020	Joey-Rocky	Joey	Parent	Female	Nestling Period
2020	Joey-Rocky	Rocky	Parent	Male	Nestling Period
2020	Joey-Rocky	Ebony	Chick	Female	Nestling Period
2020	Joey-Rocky	Inky	Chick	Female	Nestling Period
2020	Nobel-George	Nobel	Parent	Female	Nestling Period
2020	Nobel-George	George	Parent	Male	Nestling Period
2020	Nobel-George	Maple	Chick	Female	Nestling Period
2020	Nobel-George	Oak	Chick	Female	Nestling Period

Table S2: Ethogram used to code the behaviours during the observations of the nestling period for the four families at Haidlhof Research Station in April and May 2020.

Parameter	Description of parameters
<u>Non-Social Behaviour at the Nest</u>	
Approach nest	ID enters nest and starts interacting immediately
Leave nest	ID goes out of nest and flies away
Visit nest	ID lands on/stays at nest platform without any interactions
Brood	ID sits on top of eggs/chicks, brooding
Stand	ID stands in the nest and over offspring without interacting
Clean	ID takes away faeces of chicks
Manipulate nest	ID interacts with material from the nest, e.g., branches

Auto-preen	ID goes through the own plumage with the beak
Social Behaviour at the Nest without Food	
Allo-preen	ID goes through the plumage of another ID with the beak
Touch	ID touches another ID with the beak
Force partner to retreat	ID displaces partner at the nest
Social Behaviour at the Nest with Food	
Feed	ID brings food and feeds it to another ID, either chick or mate
Transfer food	ID brings food and gives food to mate, who feeds it to the chicks
Begging	Directed from chicks to parents: with opened beaks and waving wings soliciting for food

Table S3: Ethogram for the food sharing experiments with the common raven *Corvus corax* in 2019 and 2020 (modified after Boucherie 2020).

Behaviour	Description
Agonistic Behaviour (Without Food)	
Agonistic (threat/peck/chase/charge)	<u>Threat</u> : One bird threatens another one, with display “thick head approach” and/or visual threat (the aggressor pecks in the direction of the victim without touching it), with or without vocalizations. <u>Peck</u> : One bird pecks another one with its beak. Pecking implies physical contact. <u>Chase</u> : One bird pursues another one, typically flying <u>Charge</u> : One bird pursues/rushes toward another one flying/running.
Fight	<u>Undirected</u> : Two birds hit each other with their feet/beaks, with one/both birds jumping in the air or with one bird down on the ground and one sitting on the top. <u>Directed</u> : One bird hit another bird with its feet/beak, with one/both birds jumping in the air or with one bird down on the ground and one sitting on the top.
Supplant	One bird enters in contact with another bird - who retreats/moves away in within 1-2s, 1m or more than 1m away, and takes its position. With or without vocalization of the emitter/receiver, and with or without direct physical contact between the two birds.
Avoid	One bird retreats/moves away (i.e., more than 1m away) from an approaching bird before it enters into its contact (approximately before the approaching bird is less than 1m away).
Submissive Display	One bird displays a submissive posture (e.g., step back and lean forward or bend over) after receiving an aggression from another bird (i.e., threat, peck, chase/charge), with or without vocalizations.
Retreat	One bird retreats/moves away after receiving an aggression from another bird (i.e., threat, peck, chase/charge), with or without vocalizations (i.e., more than 1m away).
Ignore/Protest	The victim (receiver) of an agonistic interaction (i.e., threat, peck, chase/charge) ignores the behaviour and stays in spatial associations with its aggressor (emitter) without reacting//stays in spatial associations and protest by posturing and/or vocalizing.
Retaliate	The receiver of an aggression responds by defending or counterattacking.
Agonistic Behaviour (Involving Food)	

Steal food	One bird steals a food item from another bird, and either stays or goes away with it. Contrary to passive and active item transfer, the transfer is this time initiated by the 'receiver'/bird stealing the item.
Try to steal food	One bird fails to steal the food item of another bird, either because the other bird left with the item, or because it threatened/aggressed the 'thief'.
Social Behaviour (Involving Food)	
Co-manipulate/co-feeding (same)	Two birds eat the same food item within a reaching distance (i.e., 0-0.5m).
Co-manipulate/co-feeding (distinct)	Two birds eat the different food items within a reaching distance (i.e., 0-0.5m).
Watch individual with food	One bird is in proximity or contact with another one and observes it handling a piece of food without any attempt to get it.
Follow individual with food	One bird walks or flies in the same direction as another individual that is manipulating a piece of food and with whom it was previously in proximity/contact and enters again in proximity/contact with it. The follower should move after the initiator has left, within four seconds maximum.
Approach with food	One individual coming closer to another individual while the approaching individual is carrying food in beak or claws.
Begging	One bird touches another's beak and vocalizes with/without wing flapping; or vocalizes with wing flapping in the direction of another bird to request an item. One bird flapping its wings in the direction of another bird without vocalization is also considered as one instance of begging (i.e., of low intensity).
Allofeeding/transfer food	<u>Allofeeding</u> : One bird actively transfers a food item from its beak to the beak of another bird. Occurs typically after begging (from the receiver). <u>Transfer</u> : During food manipulation, a food item is being transferred from one bird to another, either passively (the two birds are co-manipulating the food that gets transferred to only one of them) or actively (the bird possessing the food gives it to another bird).
Non-Social Behaviour	
Eat/manipulate food	One bird manipulates a food item with the beak or foot. A bird manipulates food also by holding it in its beak.
Move food (outside zone 2)	Used in the OnePiece and TwoPieces condition when an individual takes a food item out of food zone 2 or moves a food item that is already outside food zone 2. Used in the Scramble condition when an individual moves a food item in the aviary.
Bring food (in zone 2)	Used in One-Piece- and Two-Pieces-condition when an individual takes a food item out of food zone 1 into food zone 2.
Food Provided	Code the exact moment when the food is delivered into the aviary.
Food Zones	
Food Zone 1	Area within a radius of 0-0,5m around the food source. Used in all three conditions.
Food Zone 2	Area within a radius of 0,5-2m around the food source. Used in OnePiece and TwoPieces condition.
Spatial Associations – Food Zones	
Ground Proximity	Individuals being 0-1m away from each other while being on the ground.
Order of Access to Food (Zone 1)	Code the exact moment when an individual reaches food zone 1 and in which order individuals reach food zone 1. The range of the order is dependent on the number of individuals in the family. If an individual never reaches food zone 1 of a food source, then "No" is coded.

Out of Sight	When a bird in the Scramble condition manipulates food but either moves into the nest/shelter or the camera angle changes, and the bird is out of focus. Can also be used in the OnePiece or TwoPieces condition IF the focus-cam does not show the whole food zone 2. This behaviour is only to be used in cases where individuals are in food zone 1 for the Scramble condition, or food zone 1 or food zone 2 in the OnePiece and TwoPieces conditions (not when they are somewhere else in the aviary not interacting with food).
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Table S4: Sample sizes for a) week of observations and b) directed dyad of the observations during the nestling period.

S4a		S4b	
Week	Number Cases	Directed Dyad	Number Cases
Week 1	386	father-mother	55
Week 2	150	mother-father	9
Week 3	173	father-chick	224
Week 4	57	mother-chick	510
Week 5	32		

Table S5: Sample sizes for a) condition of experiment, b) week of experiment and c) type for the duration of the behaviour eat/manipulate during the food experiment, indicated in seconds.

S5a		S5b		S5c	
Condition	Sum of Seconds	Week	Sum of Seconds	Type	Sum of Seconds
OnePiece	13055,12	Week 1	19804,56	chick	22175,6
TwoPieces	19079,04	Week 2	20414,4	father	21347,04
Scramble	36565,2	Week 3	28480,4	mother	25176,72

Table S6: Sample sizes for a) condition of experiment, b) week of experiment, and c) dyad type of the food experiment.

S6a			
Condition	Food Sharing	Agonistic Interactions	Begging and Watching
OnePiece	334	117	1991
TwoPieces	147	132	2127
Scramble	183	264	1459

S6b			
Week	Food Sharing	Agonistic Interactions	Begging and Watching
Week 1	131	49	1412
Week 2	333	179	2680
Week 3	200	285	1485

S6c			
Dyad Type	Food Sharing	Agonistic Interactions	Begging and Watching
chick-chick	68	74	159
chick-father	69	165	2696
chick-mother	158	23	2380
father-chick	63	163	46
mother-chick	156	45	101
father-mother	65	27	67
mother-father	85	16	128