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„How Does Family Size Affect Foraging Success and Agonistic Behavior Within a Non-Breeding Group of Free-Flying Ravens?"

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2 Contents

3 Abstract

Social animals share their environment with a variety of conspecifics and heterospecifics. Each individual needs to acquire certain skills for the purpose of survival, such as finding and accessing food, sharing information with others, and climbing up the social hierarchy. To gain insight into how early life experiences can have an impact on some of these behaviors, I have investigated whether foraging success and agonistic behavior in juvenile ravens differs with family size (i.e., their upbringing) soon after joining a non-breeder group. In addition, I have also examined whether begging behavior of chicks and food provisioning by their parents differs in relation to family size in another group of ravens. **Methods:** Data was collected at the Cumberland Wildpark in the Alm Valley, Upper Austria. The focal observations in the non-breeder group were done on 18 individuals, born 2020 and 2021, and observed between September and December in their first year of life. The focal observations in the family group consisted of 25 chicks born in 10 different families in 2018 and 2019 and observed between May and July after leaving the nest but before their separation from the parents. All subjects were observed with a GoPro camera via focal and group sampling method. Statistical analysis was done using a generalized linear mixed model and R statistics (Version 4.2). **Results:** Male juvenile ravens showed more agonistic behavior during foraging than females. The frequency of donated and received agonistic behavior did not correlate with family size but the frequency of donated agonistic behavior showed a positive correlation with the number of male siblings within the brood. Similarly, the frequency of begging behavior did not correlate with family size but showed a negative correlation with the number of brothers. **Conclusion**: Sex composition in raven families may affect begging behavior in raven chicks and might also influence agonistic behavior in juveniles after joining non-breeder groups. For the future, it would be interesting to also investigate the begging behavior and the parental care in the first group of ravens (i.e., the juveniles), while integrating the data of my thesis, to study more directly if there might be any

potential carry-over effects from early childhood experiences into adulthood with respect to foraging and agonistic behavior.

Abstract

Soziale Tiere teilen sich ihre Welt mit Lebewesen der eigenen Art und fremder Arten. Jedes Individuum benötigt bestimmte Fähigkeiten um zu überleben, z.B. die erfolgreiche Nahrungssuche, das Teilen von Informationen mit anderen und der soziale Aufstieg innerhalb einer Hierarchie. Um einen Einblick darin zu erhalten, ob und inwiefern frühe Erfahrungen einen Einfluss auf die Ausbildung dieser Fähigkeiten haben können, habe ich untersucht ob Erfolg bei der Nahrungssuche und agonistisches Verhalten von jungen, nicht-brütenden Raben sich mit der Familiengröße (d.h. der Anzahl an Geschwistern) ändert. Des Weiteren habe ich in einer zweiten Gruppe von Raben (Familiengruppe) untersucht, ob das Bettelverhalten von Küken und die Bereitstellung von Futter durch die Eltern ebenfalls von der Familiengröße abhängt. **Methoden**: Die Daten wurden im Cumberland Wildpark im Almtal, Oberösterreich, gesammelt. Die Beobachtungen in den jungen, nicht-brütenden Raben fanden an 18 Individuen (geboren 2020) statt und diese wurden zwischen September und Dezember ihres ersten Lebensjahres beobachtet. Die Beobachtungen in der Familiengruppe wurden an 10 Familien mit insgesamt 25 Küken durchgeführt, welche zwischen Mai und Juli stattfanden, gleich nachdem sie das Nest verlassen hatten aber noch bevor sie von den Eltern getrennt wurden. Alle Individuen wurden mit einer GoPro Kamera und durch die „Focal Sampling“ und „Group Sampling“ Methode beobachtet. Die statistische Analyse wurde mit einem allgemeinen linearen Mixed Model und dem Statistikprogramm R (Version 4.2) durchgeführt. **Ergebnisse**: Männliche junge, nicht-brütende Raben zeigten während der Nahrungssuche mehr agonistisches Verhalten als Weibchen. Die Anzahl von gezeigtem und erhaltenem agonistischen Verhalten

korrelierte nicht mit der Familiengröße, aber es zeigte sich eine positive Korrelation mit der Anzahl an männlichen Geschwistern in der Familie. In ähnlicher Weise korrelierte das Bettelverhalten der Küken nicht mit der Familiengröße, wobei sich aber eine negative Korrelation mit der Anzahl an Brüdern zeigte. **Schlussfolgerung**: Die Geschlechtskomposition in Familien von Raben hat möglicherweise einen Einfluss auf das Bettelverhalten von Küken und auf das agonistische Verhalten in jungen, nicht-brütenden Raben. Für zukünftige Forschungsprojekte wäre es interessant das Bettelverhalten und das elterliche Fürsorgeverhalten in der ersten Gruppe von Raben (d.h. die jungen, nicht-brütenden Raben) ebenfalls zu untersuchen und mit den Daten meiner Thesis zu vergleichen, um herauszufinden ob es direkte „Carry-Over“ Effekte bzgl. frühkindlichen Erfahrungen und späterem jugendlichem Verhalten (Nahrungssuche und agonistisches Verhalten) gibt.

Key words: Feeding, foraging group, aggression, dominance, brood size, early life experience, survival strategies, begging, chick preferences.

4 INTRODUCTION

4.1 Social Behavior

Social behavior has been explored in many different animal species and has gained a lot of attention from researchers across the world (Alexander 1974; Boucherie et al., 2019). To fully grasp how social behavior has developed, it is necessary to understand how members of a social group might behave differently across contexts.

The social brain hypothesis proposes that living in a large group requires the management of complex relationships and the cooperation with other group members, which has resulted in the development of larger brains (Dunbar & Schulz, 2007). The act of cooperation involves the sharing of information during joint activities, such as foraging, predator avoidance, and territorial protection, which in turn may increase individual fitness (Lefebvre et al., 2004; Reader & Laland, 2002). In contrast, the ecological hypothesis suggests that brain development is the result of a high demand for decision-making as well as episodic memory during foraging activities, which may increase individual fitness arising from learning through one´s own errors by solving ecological problems at the individual and not at the group level (Dunbar & Schultz, 2007).

Group size differences may affect several components of social life and may shape behavior and fitness of group living animals in various ways (Isbell, 1991; Janson and Goldsmith, 1995; van Noordwijk and van Schaik, 1987; van Schaik, 1989). For example, time spent in vigilance while out foraging may be heavily influenced by the presence of others (Pulliam 1973; Elgar 1989; Lima 1990), which means that foraging behavior might connect both; the social brain and the ecological hypotheses. Typically, an individual must develop foraging skills based on trial and error while being guarded by other group members may lead them to be less exposed to predation and may therefore allow higher foraging success and higher survival. Individuals who are joining foraging groups have to adapt to current group dynamics that include the coordination of foraging strategies and conflict mitigation (Dunbar & Schultz 2007). Accordingly, foraging within a group introduces individuals into the complexity of social interactions and requires (at least) a basic understanding of relationships between group members.

4.2 Social Behavior Within Foraging Groups

4.2.1 From individual to group specific behavior

At the individual level, differences in foraging behavior could be the result of intraspecific competition connected to differences in sex or age (Bolnick et al., 2003; Durell, 2007; Phillips, Silk, Phalan, Catry, and Croxall, 2004; Votier et al., 2017). But with the aim to comprehend the evolutionary factors that influence collective decision-making, it is necessary to understand individual preferences as well as the behavior at the group level (Schloesser et al., 2021). More often than not, factors such as access to food, reproduction and survival are affected by dominance hierarchies in social groups (Sapolsky, 2005, Wingfield and Sapolsky, 2003).

Some foraging behaviors are site-specific (Baylis, Page, McKenzie, & Goldsworthy, 2012; Hillen, Kiefer, & Veith, 2009; Wakefield et al., 2015) while foraging groups may often consist of mainly familiar individuals visiting the same site but may also include individuals who tend to visit only occasionally (Loretto et al., 2007). As foraging is essential for survival and reproduction, complex behaviors have evolved to cope with the current environmental conditions and the protection of valuable resources (Zjacic and Scholz 2022). One of these behaviors is the exchange of information on food sources (Danchin et al. 2004), which facilitates the discovery of food (Giraldeau & Caraco 2000; Grüter & Leadbeater 2014). Hence, activities like collective foraging will affect group dynamics, especially if individuals feed from the same source (Conradt & Roper 2005).

4.2.2 Competition within foraging groups

Living together in a group often results in competition for limited resources (Alexander, 1974; Clutton-Brock and Harvey, 1977; Terborgh & Janson, 1986; van Schaik, 1989) and conflict mitigation is important for many social animals. Agonistic behavior is another adaptive component of social behavior that enables animals to secure as well as defend food, mates, and territories (Maney and Goodson., 2011). In this context, there are two types of competition; scramble competition and contest competition (Isbell, 1991; Janson & van Schaik, 1988; Lomnicki, 1988; Nicholson, 1954; Varley et al., 1973). In case of contest competition, an individual defends a resource and excludes others from access based on a social dominance hierarchy; often inducing aggressive behavior. In case of scramble competition, competitors just want the same resource (not regulated by a social chain) and, therefore, it is less likely that any dominance hierarchy increases aggressive behavior within this context. Hence, the formation of

groups characterized by fission-fusion dynamics should induce less aggressive behavior (cf., Koenig and Borries, 2006; Sterck et al., 1997).

4.2.3 Early Life Experience as a Predictor for Social Competences in Foraging Groups

Social behavior in many groups is described by the quality of relationships between individuals (Loretto et al., 2012). The family, consisting of parents and siblings, is the first group with which an individual interacts at the beginning of their life. There are numerous studies that have investigated the impact of early life experiences and they are generally seen as primary factors which drive the development of future behavior. John Bowlby postulated with his famous attachment theory that the nature and quality of the relationship between infant and caretaker heavily affects adult social behavior in humans and non-human's primates (Shaver and Mikulincer, 2009).

Parents are usually the first individuals who provide care to their offspring while siblings are the first individuals with whom newborn chicks compete. If the quality of early life experiences is one of the major factors that drive behavioral development, the question of whether differences in parental care, family size and composition may also have an impact emerges. Some parents may provide more food or may spend more time with specific offspring individuals than with others. In reverse, it is also interesting to ask why some offspring receives more care from their parents than others, how they process this experience and what they learn from it. For example, in captive ravens, the offspring of larger broods was fed less and begged more often, but at the same time the offspring who begged more was also fed more frequently from their parents (Ersoy et al., 2021).

Social plasticity is the ability to adapt behavior to specific conditions in complex environments. One genotype may produce different behavioral phenotypes, which has been described as the evolution of a plastic responses (Oliveira, 2009; Taborsky and Oliveira, 2012). For example, ants show complex foraging strategies and develop adaptive behaviors based on information they receive from other group members integrating information they have processed from their own past experiences (Kolay et al., 2020). Within the family unit, not only protective and affiliative behaviors can be observed between members, but also competition (Trivers 1974., Royle et al., 2002). In the case of sibling competition, males from dimorphic species tend to be more successful in scramble competition and are more sensitive to nutritional deprivation (Uller, 2006), probably due to higher energy costs for survival (Bonisoli-Alquati et al., 2011). Thus, it

could be that individuals, who were raised in bigger families with more siblings, learn to be more competitive from early life on and would therefore show more dominant or agonistic behavior as juvenile individuals towards others within and outside the family unit.

Begging behavior is characterized as a competition strategy between siblings (Mock & Parker 1997; Wright & Leonard 2002) and could be recognized from parents as a signal of need, (Kilner & Johnstone 1997), whereas body size could be recognized as a signal of quality (M. Calo et al.,2016). There is an ongoing scientific debate about whether increased begging frequency may be a signal of need or a signal of quality, respectively whether stronger or weaker offspring begs more or less. Corticosterone is produced either in the egg or endogenously by the nestlings and can affect their begging calls (Bowers et al 2016a; Kitaysky et al. 2001; Love and Williams 2008; Schwabl and Lipar 2002; Smiseth et al. 2011). Acute stress that occurs during food deprivation is often associated with emotional distress and an increase in corticosterone production. Parents provide and distribute food to offspring based on the type and quality of signals they receive from the offspring. The frequency or the amount of food provided by parents may be influenced by begging frequency of the offspring as an honest signal of need (Godfray 1991, 1995). Early life conditions may predict social competence, as for example seen in ravens where offspring raised in larger brood's value social information differently as individuals raised in smaller broods (Gallego-Abenza et al., 2022). However, foraging behavior within groups is a key component for many species, which requires successful task performance on the individual level and continuous adaptation to the environment at the group level.

4.3 Corvus corax as a Study Model for the Development of Social Behavior from an Early Life Stage in the Family Until Adulthood in a Social Foraging Group

To study the development of complex social behavior, the common raven (*Corvus corax*) is an appropriate model. This large-brained songbird forms individual relationships in social environments and sometimes has to deal with unpredictable conditions which may require high cognitive capacities (Aureli et al., 2008). The raven is known for its high ecological flexibility and scavenging abilities (Ratcliffe, 1997) as well as the formation of long-term monogamous pair bonds with biparental care that often persist after the offspring has become independent (Boarman & Heinrich, 1999). Life expectancy in ravens ranges between 10-30 years (Frannson et al.,2010; Haffer and Kirchner 1993). The offspring stays with the parents for about 10 weeks and then joins non-breeder groups, where they come into first time contact with individuals who are not their family members (Ratcliffe, 1997) and who may even be competitors at feeding sites

(Braun & Bugnyar, 2012; Bugnyar et al., 2007). Despite of this, ravens become territorial defenders once they have chosen a partner and show sexual dimorphism with males being larger than females (Boarman & Heinrich, 1999; Ratcliffe, 1997).

Ravens show social dominance hierarchies in captivity as well as in the wild (Huber, 1991). Relationships among males and between males and females are usually stronger than relationships among females (Fraser & Bugnyar, 2010). Dominance hierarchies regulate access to food sources while heavier ravens usually have better foraging success (Boarman & Heinrich, 1999; Stowe et al., 2006). Ravens spend a significant amount of time as part of non-breeder groups). During this time ravens inform others about food sources with food-associated calls ("ha a calls"; Heinrich 1988) while they are part of foraging groups with sometimes more than 100 individuals, who aggregate at food sources such as a carcass of a large animal or at garbage dumps (Boarman and Heinrich 1999). Yet, in general they aggregate in smaller foraging groups with less than 30 birds (Heinrich 1989; Dall and Wright 2009). Aggressive behavior of young ravens during competition for food can also be influenced by the sex steroid hormone testosterone (Adkins Regan 2005), therefore it can be expected to see sex differences in aggression levels especially during that early period of life. Hence, the quality of parental care received at an early age is likely to affect juveniles' future fitness (e.g., through body mass), with a stronger effect for males than females (Ersoy et al., 2021).

To better understand the causes for social behavior within social living animals, my goal was to study the impact of family size and composition on early life behavior as well as adult behavior in groups of ravens. Inspired by research on the effects of early life experience on the development of future social behavior, I have investigated (1) whether family size (i.e., brood size) affects feeding success and the display of agonistic behavior in juvenile ravens during foraging activities after joining nonbreeder groups, (2) whether family size affects the frequency of begging behavior of raven chicks towards their parents and the probability of chicks being fed within the family, (3) whether male and female chicks differ in their begging frequency towards the parents, (4) whether parents prefer to feed chicks that beg more or less and if they discriminate between sons and daughters with respect to the provisioning of food (Fig. 1). I hypothesized that having experienced more conflicts with siblings in bigger families, an individual might continue to display more aggressive behavior outside of the family when exposed to competitors in foraging nonbreeder groups and that individuals raised in bigger families might be more successful during foraging at the feeding site. Additionally, males might

also display more aggressive behavior than females within nonbreeder groups and show more begging behavior as chicks towards their parents and are also fed more often within the family in comparison to females. Moreover, increased family size might be associated with a decrease in individual fitness, due to a lower chance of an individual to be fed from its parents, which may lead to more stress, as more conflicts with siblings arise.

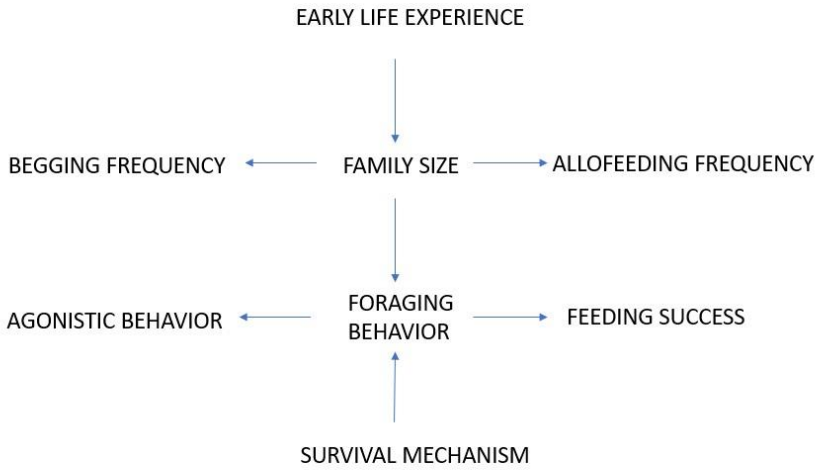

Figure 1: Possible cause and effect relationships between family size and several behaviors.

5 METHODS

5.1 Non-Breeding Raven Group in the Wild

Data was collected in the northern Austrian Alps, Grünau im Almtal in the Cumberland Wildpark (latitude: 47.807° N, longitude: 13.950°E). The ravens were observed with a GoPro camera via group sampling method at a wild boars' enclosure during their morning feeding time. Group sampling was conducted six days per week, in the morning between 8:00 and 9:00 am. The enclosure where the wild boars were fed, are also a hot-spot for foraging of a group of juvenile non-breeding ravens. The feeding is performed throughout the year on a daily basis and often attracts approximately 30 wild ravens during summer and up to 120 ravens during winter (Beck et al., 2020). The foraging group in the park consists of about 90% non-breeders; 20% of them are juveniles in their first year, 60% are sub-adults with age 1-3 years and 20% are adults older than 3 years (Boucherie et al., 2019). All the observed individuals in the non-breeding group were born in families in captivity (within separated aviaries of 80-120 m^2) either at the Research Center Haidlhof (four families), the Konrad Lorenz Research Center (two families) or the Zoo of Vienna (one family). Family size was determined by manipulating the number of eggs. The chicks originating from different families were usually located in the same station. They could not see but hear each other by vocalizations. Chicks hatched between late March and the beginning of April in Year 2020 and 2021 and were fed from the parents approximately 10 weeks post-fledging. In the middle of July, chicks from all families were separated from their parents and put into non-breeder aviaries at the Konrad Lorenz Research Station (Wildpark Cumberland, Grünau im Altmal). Group composition was controlled for, and some siblings had to be split up into two non-breeding groups. Both non-breeder aviaries were about 60 m^2 in size. Individuals were fed twice a day with a mixture of pellets, meat, vegetables, and fruits while having access to water all day. All ravens stayed in the non-breeder groups for six weeks and were released into the wild by the beginning of September. During week five each raven was separated from the group for measurements, blood samples, being marked with rings from the Austrian Ornithological Center, being colored with wing tags, and equipped with a GPS logger (Gallego-Abenza et al., 2022).

5.1.1 Agonistic Behavior at the Foraging Site in the Wild

The sample for behavioral analysis consisted of 18 individuals. 17 individuals born in the year 2020, of which one individual escaped from captivity and one individual died in the family place

before gender determination, which is why the gender of two individuals is not known. The rest of the sample consisted of nine males and six females. Eight males and six females were released because one male died during the family phase. Five males were observed, as one male died shortly after release, and two males were not often present at the wild boar feeding site; that is why they were excluded from the analysis. Of six females, two females were observed consistently, two females died shortly after release and two females were not present at the feeding site often enough and were therefore excluded from the analysis. 25 individuals born in year 2021, 13 males, seven females. No gender was identified for the remaining five individuals; four died in during the family phase and one escaped. A total of twelve males and seven females were released. One male died in the first month after release, and one male was not often enough at the feeding site for observation. Accordingly, ten males were observed. Six females died in the first month after release, one female was observed consistently. The ravens were observed between September and December in their first year of life. One of these ravens was only present once during the observation period and did not engage in foraging or agonistic behavior. Therefore, it was also removed from the analysis. Consequently, the analysis consisted of 17 ravens, three ravens (17.6%) were female, and 14 ravens (82.4%) were male. The ravens had between zero to three siblings of the same age; most often it was three siblings (in 47.1% of cases), only one raven was a single chick, 76.5% of the ravens had one brother and 17.6% had two brothers. Behavioral data analysis consisted of individual and behavioral scan analysis with the Solomon coding software.

Seven agonistic types of behavior were recorded and subsequently analyzed. Whenever an individual engaged in a specific type of agonistic interaction, it was noted if it was the donor or the receiver. Observations were conducted with a GoPro camera. Each observational video was 600 seconds long and was analyzed in full. In total, 21 videos of individuals born in the year 2020 and 30 videos of individuals born in the year 2021 were analyzed. Agonistic events were recorded as binomial data; value “1” event occurred, value “0” event did not occur. Presence at the feeding site was noted down in a list, which is available on the internal data platform at the research station. Additionally, data on the presence of individuals at the feeding site was integrated into the analysis of behavioral data to calculate the frequency of occurred agonistic events (Table 2). The occurrence of agonistic behavior was rare and in almost all individuals below 20% of observations. Threat was the most common behavior displayed in 12,7% of times as the donor and 19,7% of times as the receiver (Table 3 & 4). The second and third most

frequent behavior was displacement, with 7.0% of times as the donor and 6.0% of times as the receiver, and forced displacement, with 7,6% of times as the donor and 4.8% of times as the receiver (Table 3 & 4). Displacement from food and forced displacement from food occurred at a much lower frequency, with 0.6% of times as the donor and 1.9% as the receiver as well as 1.6% of times as the donor and the receiver, respectively (Table 3 & 4). Agonistic behavior types related to the stealing of food occurred in about 5% of times or less (Table 3 & 4).

5.1.2 Feeding Success in the Wild

For the calculation of foraging success, every 30 seconds of every 600 s video was checked during the wild boar feeding and subsequently analyzed (scan sampling method). Each individual present at the 30 second mark, was noted as "present", holding food in its beak or with the head looking down towards the ground as "feeding". In total 23 videos from the year 2020 and 32 videos from the year 2021 were used for the analysis of agonistic behavior.

5.1.3 Statistical Analysis of Agonistic Behavior and Feeding Success in the Wild

Statistical analysis was done in R statistics (Version 4.2) using a generalized linear mixed effect model and the lme4 package (Bates et al., 2016). The IDs of each raven ("Ravenname") was used as a random effect. A significance level of $p > .05$ was used as a cut-off value for hypothesis testing. Analysis was done with two data sets, one extracted from the "Behavioral Scan Analysis" analyzing agonistic interactions between individuals while foraging, and a second one from the "Individual Scan Analysis" calculating individual feeding success while foraging. The dependent variables for agonistic behavior were coded as binomial data, i.e., six types of agonistic behavior namely "Threat", "Displacement", "Displacement from food", "Forced Displacement from Food", "Steal Success" and "Steal Failed". Two new variables were created, giving information on who actually initiated the observed conflict by coding "Dconflict" when the focal animal was the donor and "Rconflict" when the focal animal was the receiver of agonistic behavior. The independent variables were "Sex", "Time since release", "Number of siblings", "Number of brothers" and "Number of sisters"; coded as categorial variables and analyzed as absolute and relative frequencies (percentages). Effects of independent variables been calculated in two generalized linear mixed effect models, for two dependent variables, donated ("Dconflict") and received ("Rconflict").

Number of feedings was calculated by the number of times an individual was observed when it had food in their beak or when they had their head looking down towards the ground, divided

by the number of times present at the feeding site, which resulted in a response variable called “Feeding success”. Independent variables “Sex”, “Time”, “Number of siblings”, “Number of brothers” and “Number of sisters” were included in one statistical generalized linear mixed effectmodel which analyzed feeding success. Using the formula Y = m*X+b, a linear regression was calculated to test for a correlation between agonistic behavior and feeding success.

5.2 Family Raven Group in Captivity

This sample consisted of 10 pairs of captive ravens and 25 chicks born in April 2018 and 2019 in the research station Haidlhof in Bad Vöslau (47°58´07.6´´N, 16°08´34.9´´E), the Zoo Schönbrunn (48°10´55.51´´N, 16°18´10.026´´E) and the Wildpark Cumberland at Konrad Lorenz research station in Grünau im Almtal (47°48´27.4´´N, 13°56´52.4´´E). Parents and chicks were observed in the post-fledgling phase from May until middle of July in the years 2018 and 2019. Each family was kept in an aviary with the size of 10m*8m*5m. Each pair of parents bred in a separate aviary where the chicks fledged after a 37-day nestling period. All chicks were captured and fitted with colored leg rings in week six post-hatch, when the birds started to learn how to fly and before the observations started. Sex was determined genetically based on blood samples (Ersoy et al.,2021). After 73 days since fledging, the juvenile chicks got captured and were separated from their parents. They are put together for six weeks with juveniles from other families to form nonbreeder groups in enclosures of the Wildpark Cumberland. In the beginning of September, the juveniles were released from the nonbreeder aviaries and joined the resident free-flying groups of wild ravens.

5.2.1 Begging and Parental Care Behavior in Captivity

Each chick and parent were observed with a 5-minutes focal sampling method, once in the morning and once in the afternoon (five days per week during the post fledging phase). Sample size for data analysis then consistent of 24 chicks. Eleven ravens (45.8%) were female, and thirteen ravens (54.2%) were male. The ravens had one to three siblings of the same age; the mode was 1 sibling (33.3% of the ravens). Six individuals (25%) had zero brothers within the same breeding sample, ten individuals (41.7%) of ravens had one brother, seven individuals (29,2%) had two brothers and one individual (4.2%) three brothers (Table 4).

Behavioral analysis of the interactions between offspring and parents was done in the coding software “Loopy” using an ethogram for begging, affiliative and agonistic behaviors. “Allo-feeding” describes behavior when one bird transfers food from its own beak to another bird, in

this analysis the following behaviors were observed: “Allo-feeding” from parents to offspring; “haa-call” vocalizations with wings flapping in direction to the parents, which was defined as “begging” and individuals within a radius of 100 cm were classified as individuals in “proximity”. All three variables were measured as the frequency of occurrences between each offspring and its parents. Behavioral data was observed in 2018 and consisted of 25 days in May, 26 days in June, and 15 days in July including five families as well as in 2019 and consisted of 22 days in May, 12 days in June and 13 days in July including five families.

5.2.2 Statistical Analysis of Begging and Parental Care in Captivity

The total number of observations was divided with the number of each observed behavior (allo-feeding, begging and proximity) for each individual and each dyad (mother-son, mother-daughter, father-son, and father-daughter) to create mean values for the statistical analysis. Information about offspring’s sex, number of siblings, number of brothers, number of sisters and parent sex was extracted from available data. Statistical analysis was done in “R” statistics software (Version 4.2.) using a generalized linear mixed effects model. “Number of siblings”, “Number of brothers”, “Number of sisters” “Sex of chick” were categorical independent variables. Dependent metric variables “Begging to mothers”, “Begging to fathers”, “Feedingbymother”, “Feedingbyfather”, “Proximity with mother” “Proximity with father” were created after each individual number of behaviors was divided by the number of observations. Note that the number of observations was not the same for each individual and each behavioral event. Dataset “feedbeggprox” consisted of behavioral values extracted from the Loopy software after behavioral analysis. “Family Group” was used as a random effect. Each independent variable was tested with dependent variable in separated model. In total I runed 21 general linear mixed effect models with repeated measures ANOVA methods.

6 RESULTS

6.1 Family Size and Agonistic Behavior and Foraging Success in the Wild

During group foraging at the wild boars feeding site, male ravens initiated agonistic behavior more often than females, p = <0.001 (Table 3, Fig. 2). Feeding success decreased over time $\chi 2$ = 7.746, p = 0.005 (Table 3, Fig. 3), whereby juvenile ravens had better feeding success right after release when joining the foraging group (i.e., within the first month), whereas feeding success decreased consistently thereafter. There was no correlation between time after release and initiated p = 0.619 or received conflicts p = 0.291 (Table 3). Number of siblings did not correlate with agonistic behavior p = 0.403 (Table 3) but number of brothers correlated positively with agonistic behavior, p = 0.011 (Table 3, Fig. 4), but not with number of sisters p = 0.646 (Table 3, Fig. 5) in the non-breeder group. Linear regression analysis showed no correlation between feeding success and initiated (Table 3, Fig. 6) or received conflicts (Table 3, Fig. 7).

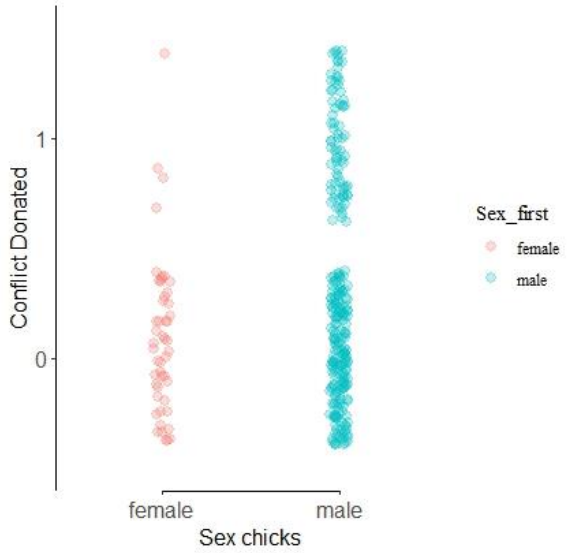

Figure 2: Sex differences in the rate of initiated conflicts during group foraging at the wild boar feeding site (Estimate Std. 2.44, p< 0.001)

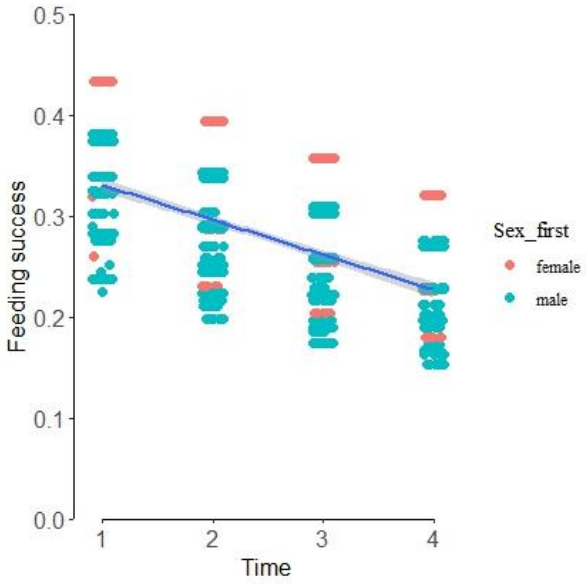

Figure 3: The line indicates a decreasing rate of feeding success over time (in months) during foraging at the wild boar feeding site and after joining the foraging group ($\chi 2 = 7.746$, $p = 0.005$).

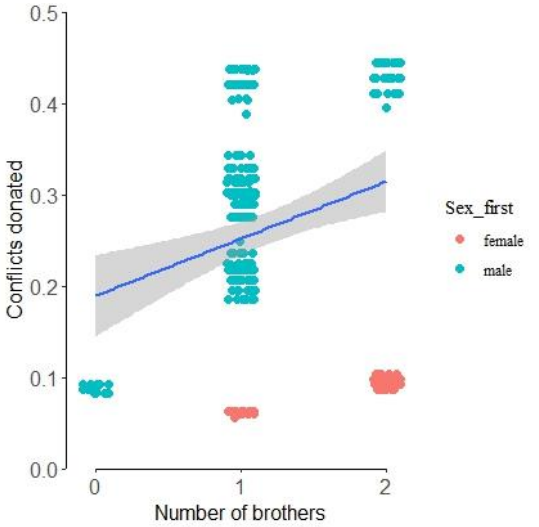

Figure 4: Effect of number of brothers on the rates of initiated conflicts with group members during foraging at the wild boar feeding site (Estimate Std. Error 0.94, $p = 0.011$). The line indicates alinear positive relationship between frequency of initiated agonistic behavior and the number of brothers.

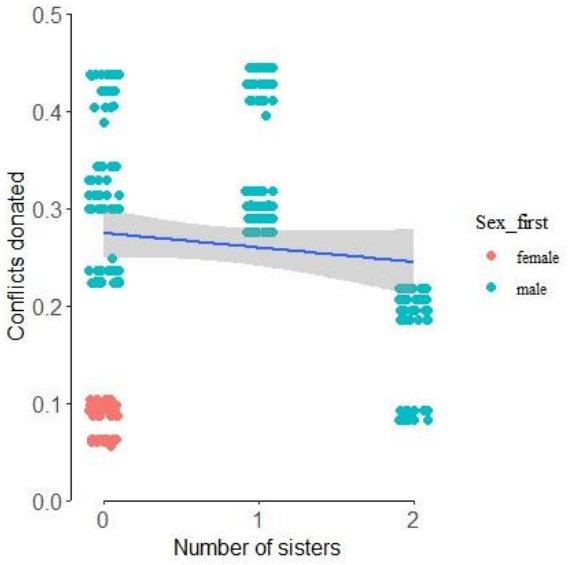

Figure 5: Effect of the number of sisters on the rates of initiated conflicts with group members during foraging at the wild boar feeding site (Estimate Std. Error -0.12, p= 0.646). The line indicates no linear relationship between the frequency of initiated conflicts and the number of sisters.

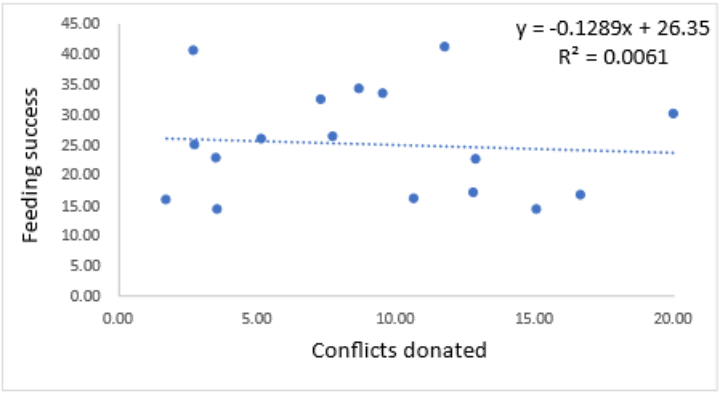

Figure 6: This scatter plot is a visualization of the raw data and shows the regression line between the factors feeding success and conflicts initiated.

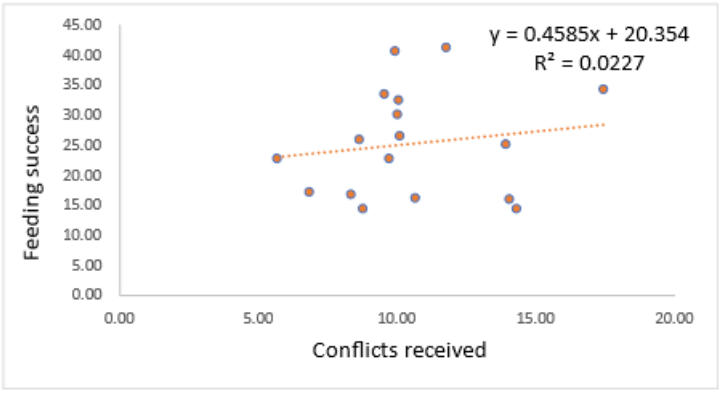

Figure 7: This scatter plot is a visualization of the raw data and shows the regression line between feeding success and conflicts received. In this case, the line indicates a slight positive slope, but there is no significant correlation.

6.2 Offspring Begging Behavior and Parental Care in Captivity

Male chicks beg more often for food than female chicks ($p = 0.019$ (Table 4, Fig. 8). Chicks beg more often towards the mother than the father ($p = 0.024$ (Table 4, Fig. 9.) There was no effect on individual begging frequency towards the parents related to number of siblings $p = 0.271$ (Table 4). Chicks raised with more brothers begged less towards the parents $p = 0.012$ (Table 4, Fig. 10), whereas chicks with more sisters begged more often towards the parents ($p = 0.01$, (Table 4, Fig. 11). Chicks raised with more brothers begged less often towards the father, $p = 0.020$ (Table 4, Fig. 12) but there was no effect of number of sisters on begging frequency towards the father $p = 0.290$ (Table 4). Similarly, there was no effect of number of brothers, $p = 0.316$ (Table 4, Fig. 13) or sisters, $p = 0.200$ on begging frequency towards the mothers (Table 4). Chicks who begged more often, were fed more often from fathers $p < 0.001$ (Table 5, Fig. 14), but not from the mother $p = 0.140$; Table 5, Fig. 15). Mothers fed chicks more often than fathers $p = 0.012$; (Table 5, Fig 16). Fathers fed male chicks more often than female chicks $p = 0.044$ (Table 5, Fig 17), whereas mothers did not show any preference for a specific sex while providing food $p = 0.232$(Table 5, Fig. 18). Male chicks who directed their begging behavior more often towards the father were also fed more frequently by the father $p = 0.001$ (Table 5, whereas female chicks who begged more often towards the father were not fed more frequently by the father $p = 0.136$; Table 5). Chicks raised with more brothers, were less frequently fed from the father in comparison to those who were raised with less brothers $p = 0.002$ (Table 5, Fig. 19). And mothers fed chicks who were raised with more brothers also frequently less often $p = 0.027$; Table 5, Fig. 20). Number of sisters did not influence feeding frequency by mothers $p = 0.159$; Table 5).

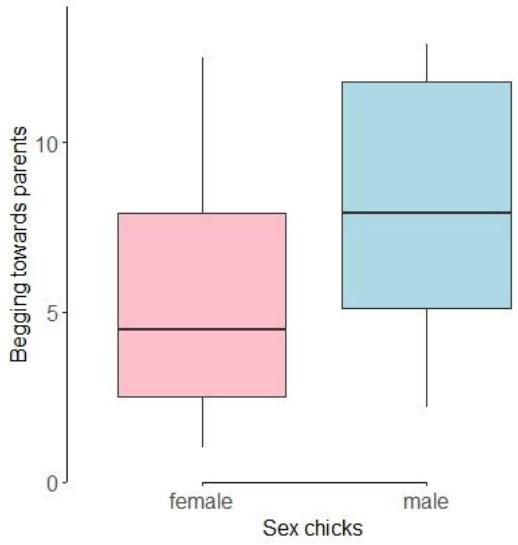

Figure 8: Boxplot representing effect of sex of chicks on begging frequency towards the parents (Estimates Std = 3.23, $p = 0.019$).

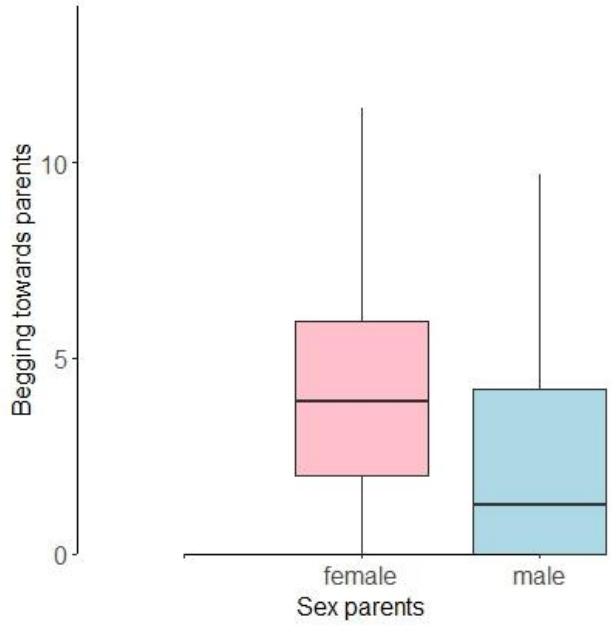

Figure 9: Effect of sex of parents on begging frequency towards the parents (Estimate Std -1.854, $p = 0.024$).

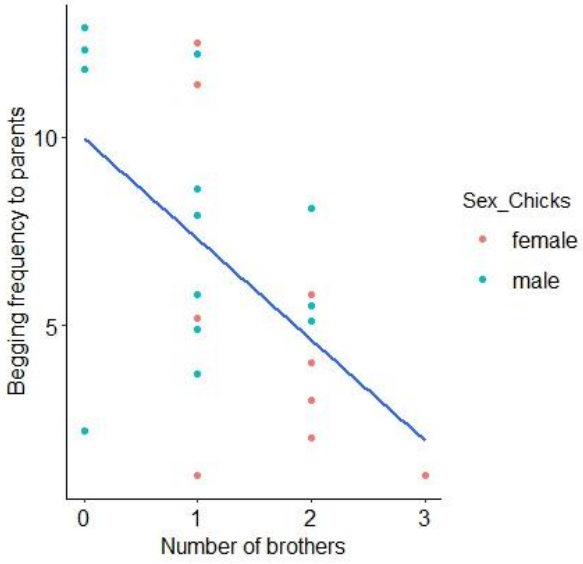

Figure 10: Effect of number of brothers on begging frequency towards the parents. The line indicates a negative linear relationship between the number of brothers and the rate of begging frequency towards the parents (Estimates Std -2.630, p = 0.012).

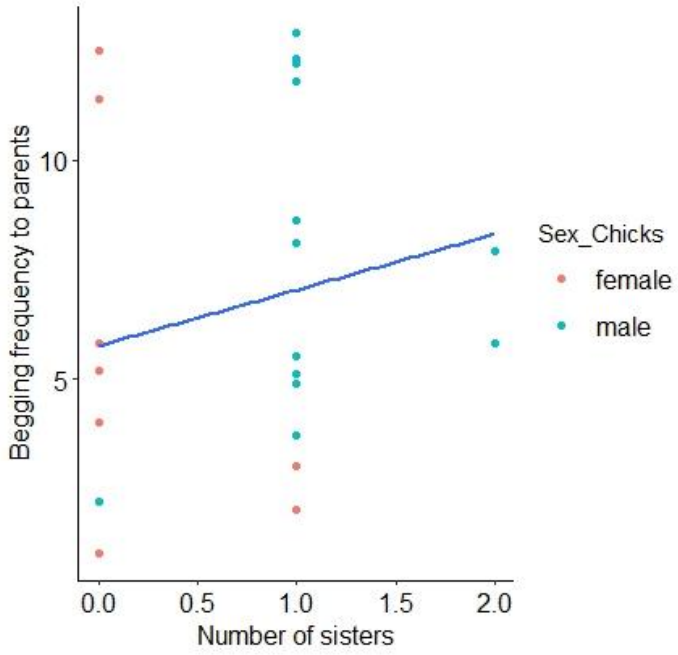

Figure 11: Effect of number of sisters on begging frequency towards the parents. The line indicates a positive linear relationship between the number of sisters and the rate of begging frequency towards the parents Estimates Std 3.134, p = 0.014).

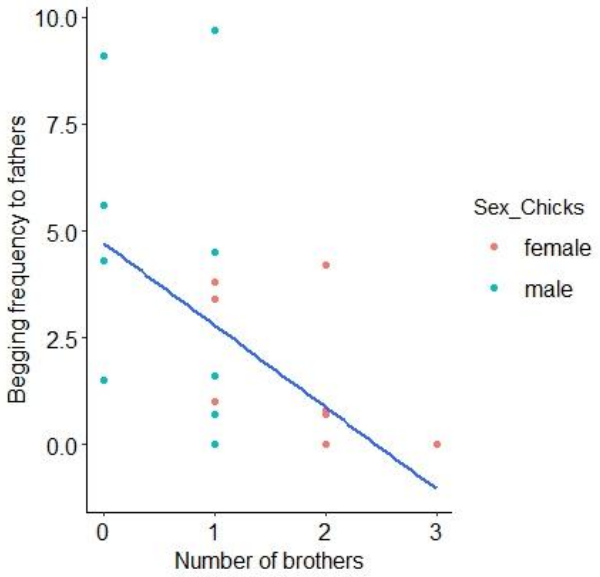

Figure 12: Effect of number of brothers on begging frequency towards the fathers. The line indicates a negative linear relationship between the number of brothers and begging frequency towards the fathers (Estimates Std -1.67, $p = 0.020$)

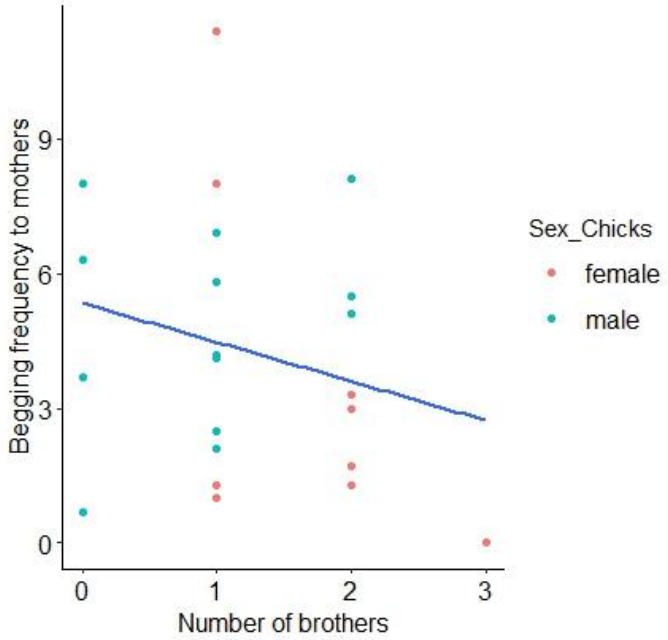

Figure. 13: Effect of number of brothers on begging frequency towards the mothers. The line indicates a negative linear relationship between the number of brothers and begging frequency towards the mothers (Estimates -0.72, $p = 0.316$).

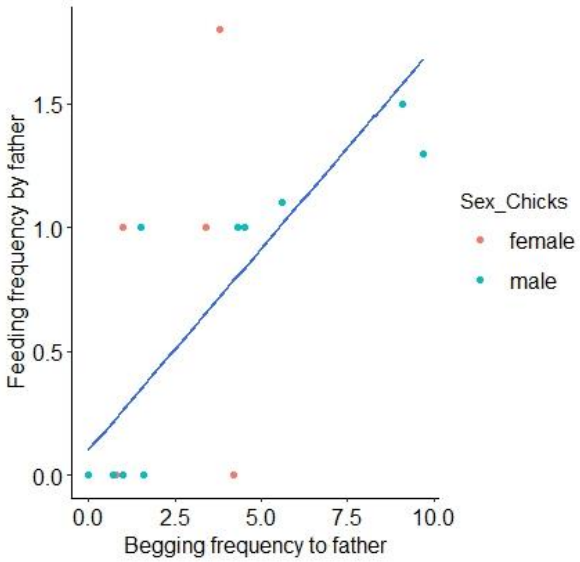

Figure 14: Effect of begging frequency towards the father on feeding frequency by the father. The line indicates a positive linear relationship between begging frequency towards the fathers and feeding frequency from the fathers towards the chicks (Estimates Std 0.011, $p < 0.001$).

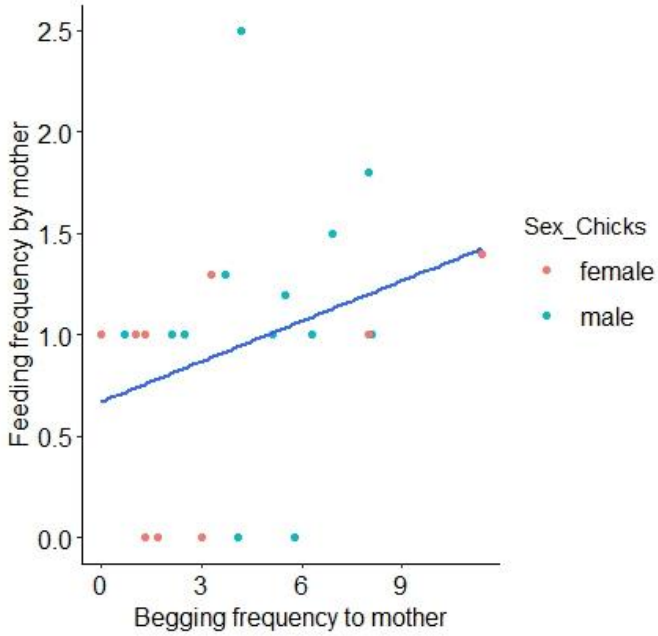

Figure 15: Effect of begging frequency towards the mother on feeding frequency by the mother. The line indicates a positive but not significant linear relationship between begging frequency towards the mothers and feeding frequency from the mothers towards the chicks (Estimate Std 0.065, $p = 0.140$).

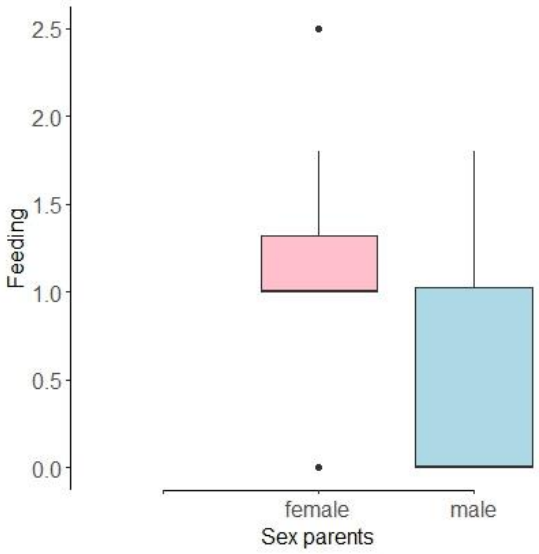

Figure 16: Boxplot representing feeding frequency of parents towards the chicks (Estimates Std -0.525, $p = 0.012$).

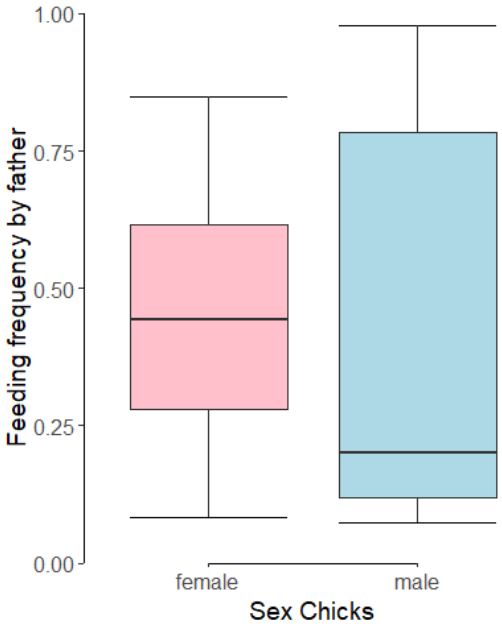

Figure 17: Feeding frequency from fathers towards male and female chicks (Estimate Std 0.2994, $p = 0.044$)

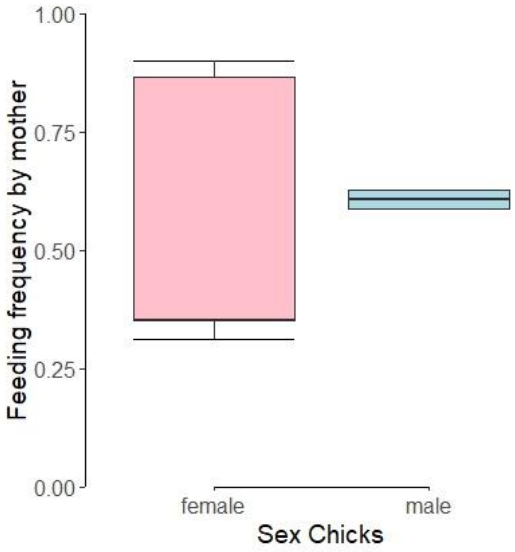

Figure 18: Boxplot representing feeding frequency from mothers towards male and female chicks (Estimate Std 0.0277, $p = 0.232$).

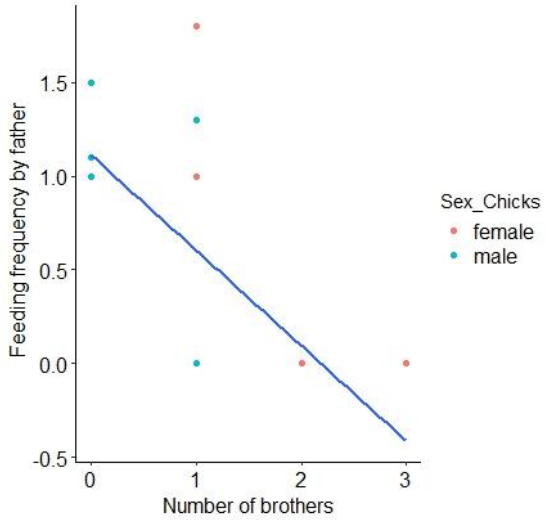

Figure 19: Effect of number of brothers on feeding frequency by the father. The line indicates a negative linear relationship between number of brothers and feeding frequency by fathers towards the chicks. (Estimates Std -0.411, $p = 0.002$).

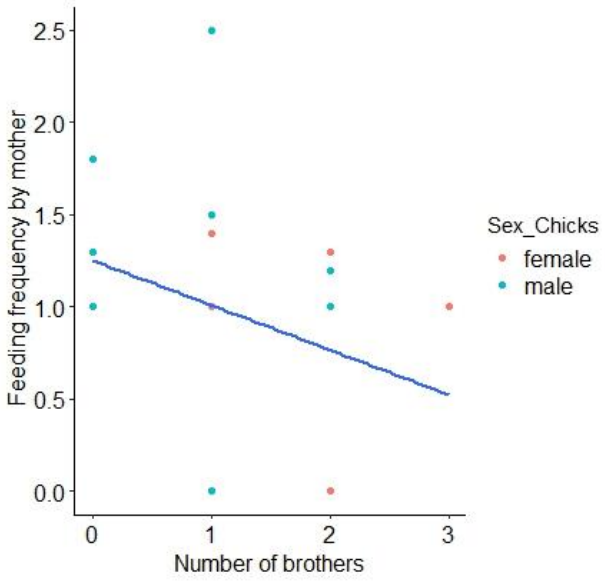

Figure 20: Effect of number of brothers on feeding frequency by the mother. The line indicates a negative linear relationship between number of brothers and begging frequency to the mothers (Estimates Std -0.411 $p = 0.027$).

7 DISCUSSION

Ravens raised in larger families (i.e., with more siblings) showed no differences in the display of agonistic behavior outside of the family (i.e., after joining the non-breeding group) compared to ravens raised with less siblings. My first hypothesis was thus not supported. However, the frequency of agonistic behavior displayed outside of the family correlated positively with an increased number of brothers, in the sense that ravens raised with more male siblings initiated more conflicts towards other group members at the feeding site. In contrast, ravens raised with more sisters started conflicts less often.

There was no effect of family size on feeding success at the foraging site. Similarly, there was no correlation between agonistic behavior and feeding success. Surprisingly, feeding success correlated negatively with the time since joining the foraging group. At the beginning, just after joining the nonbreeding group, the juveniles were observed more often with food in the beak than at later times. The observation period for foraging behavior spanned from an immediate release into the wild (in September) to 5 months post-release. In this period juvenile ravens usually increase their levels of socio-positive behavior and decrease levels of aggression while they begin to establish a dominance hierarchy, which makes them more adaptable in interactions with conspecifics (Loretto et al., 2012).

Findings from ravens in captivity show that young ravens increase the food-caching frequency during the first six month after fledging while food is often stored further away from conspecifics (Bugnyar et al., 2007). If the same is true for food caching behavior in the wild, it could explain the results observed in this study – that (observed) feeding success decreases over time. In particular, if juvenile ravens are caching their food more often at later months, they may not be seen feeding on site as frequently as before because they would spend more time out of view of the camera. Furthermore, the frequency of ravens taking off and flying away to consume food in distance to others correlates positively with age (Gallego Abenza et al., 2019).

It could also be that older ravens, who are senior foraging group members and are often the more dominant individuals on site, are helping juvenile ravens to survive their first period as independent individuals in the wild and therefore grant them more access to food when joining the group.

The results of my study indicated that male ravens at the feeding site initiated agonistic behavior more often than females – which supports my third hypothesis. Consistent with the findings of

Boucherie et al. (2022) were males who usually had higher dominance ranks started aggressive behavior much more frequently than females. Note that the sample size was not balanced with three females and 15 males, which could bias this observation. In the first month of release into the Wildpark Cumberland, 62% females did not survive; all of them died outside of the park. Of 15 released males, two males (10%) did not survive. One male died in wolf enclosure in the park and the second one died outside of the park (within a radius of 35 km). This observation could support a hypothesis about sex related bias in dispersal, which claims that in monogamous species, the females benefit from leaving the territory to increase their chance to find more competitive breeding partners. At the same time, males who stay territorial may have a better chance to avoid predation and secure food sources (Payevski, 2005). Juveniles released into the Wildpark Cumberland are not sexually mature, what could indicate that the time for dispersing is too early. After joining the feeding group, female ravens received more aggression than males (Boucherie et al., 2022). Mentally mature ravens reach a level of dominance ranks recognition, remembering which individual has a higher rank than them (Massen et al., 2014). Females in the family phase were discriminated from their fathers, what lead that females became less food in general during this phase, but they also begged less. Following this finding it may be that females learned to be submissive during the family phase and that they repeat submissive behavior in the wild too. On the other hand, females might need less care from their parents and therefore they might beg less for food. Growing up with more brothers, being exposed to higher competition or even food deprivation may be less critical for a female raven´s survival during the family phase as for male survival. It may be that the higher mortality rate after release into the wild and a higher dispersion rate of females is explained by early life experiences and not by a sex bias based on evolution. Surprisingly, the data in my study indicated also that females had a better survival chance during the family phase as males. All hatched females survived the family phase and were released into the wild, whereas 10% of hatched males did not survive the family phase, despite that male chicks seemed to be treated better from their parents, in particular, were fed more often than female chicks consistent with finding of Ersoy et al. (2021). But why do male ravens show more dominant behavior? In spotted hyenas, females show more dominance behavior than males in case social support exists (Vullioud et al., 2008). While in contrast, female raven chicks seem less supported by their parents during early life by their parents, so it may be that this supported the display of submissive behavior and led female juvenile ravens to leave the familiar territory which caused a lower survival chance. There was

also a difference in begging behavior with male chicks begging more often than female chicks, which led the father to feed the sons more often than the daughters, whereas the mother showed no difference in food allocation. In general, chicks who beg more often were also fed more and raven mothers feed all chicks more often than fathers (Ersoy et al., 2021) so it could be that the observed differences in benefits of begging might be driven by the behavior of the father. In my study, I have found that chicks, who were raised with more brothers than sisters, begged less often towards their parents and were also fed less. Corticosterone is a glucocorticoid that drives dominant behaviour in avian species (Crino et al., 2014) and given the chance that having more brothers led to higher corticosterone levels, this might be an important contributing factor to why ravens raised with more brothers show more agonistic behaviour.

This could carry-over into more aggressive behavior in adulthood. Food deprivation as well as sibling competition are strong stressors during early life development, which might result in increased excretion of stress hormones (Saino et al., 2003). In summary, being raised with more brothers leads to a lower feeding probability from parents, and may elevate corticosterone levels, which may induce more aggressive behavior as adults but may also lead to more behavioral flexibility when interacting with conspecifics and joining larger foraging groups. Note that during the developmental period ravens' socio positive interactions increase over time and aggressive behaviors decrease, especially after forming a stable dominance hierarchy (Loretto et al., 2012).

Growing up in a larger brood might decrease nestlings' fitness because they are in a stronger competition for limited resources (Crino et al., 2014). Moreover, the males in zebra finches exposed to developmental stress via corticosterone manipulation, had higher reproductive success when reaching adulthood (Crino et al., 2014). If the individuals raised with more brothers have poorer fitness and are prone to experience higher competition, it could mean that the response of the fathers to an elevated begging frequency of the chicks is an evolutionary adaptive behavior. This may lead fathers to recognize a higher begging frequency as a signal of higher need. But the question remains, why do offspring with more brothers beg less in general? Individuals with more brothers are fed less often from the father because the food needs to be distributed among more male individuals and, therefore, begging may be less likely to be

rewarded in total for every individual, whereas this is might not the case in broods with more sisters.

Being raised with more brothers could also foster the development of cognitive skills with food and object caching competition. A larger brood with more male individuals might be a more stressful environment. For example, corticosterone treated zebra finches solve foraging tasks a lot faster than untreated siblings (Crino et al., 2014). Individuals with a higher corticosterone level might be faster at foraging in the wild, which could explain the lacking association between aggression and feeding success in my study. As such individuals would spend less time on the feeding site and reduce the probability of being observed.

Conclusion and further directions

The findings of this study, in particular, that males begged more than females could indicate that begging is interpretated as signal of need from fathers in ravens. However, the question remains if a signal of need should be considered the same throughout life or if that might change over time? Male ravens are larger compared to females (Ersoy et al., 2021) and are more competitive and physically stronger (Boucherie et al., 2022), so it could be that the more competitive individuals require a higher amount of food to satisfy their energetic needs. Growing up with more brothers, lead to more competitive behavior outside of the family place and could qualify for a higher dominant rank in juveniles in non-breeding stage. It would be interesting to compare data of the sample of nonbreeding ravens (i.e., the first group) taken during the family phase and integrating the data of adult agonistic behavior and feeding success of the current study to examine the effects of early life experiences on future adult behavior directly. The observational videos have been taken in the past but were not yet coded to be analyzed at the time of commencing my study.

8 TABLES

Table 1.
Effect of sex, time, number of siblings, number of brothers, number of sisters on initiated and received conflicts with group members during foraging at the wild boar feeding site.

Variable	**Estimate Std.**	**Error**	**z value**	**Pr(>|z|)**
Intercept	-3.50	0.83	-4.20	<0.001***
Conflict donated vs. sex_firstmale	2.44	0.60	4.06	<0.001***
Conflict donated vs. time	0.07	0.13	0.50	0.619
Conflict donated vs. number of siblings	-0.39	0.29	-1.36	0.172
Conflict donated vs. number of brothers	0.94	0.37	2.53	0.011*
Conflict donated vs. number of sisters	-0.12	0.26	-0.46	0.646
Intercept	0.45	0.57	0.79	0.432
Conflict received vs. sex_firstmale	-0.87	0.86	-1.01	0.310
Conflict received vs. time	0.16	0.13	1.27	0.205
Conflict received vs. number of siblings	-0.44	0.37	-1.18	0.239
Conflict received vs. number of brothers	0.35	0.45	0.78	0.434
Conflict received vs. number of sisters	-0.15	0.34	-0.43	0.664

Observed juveniles (N = 18) male juveniles (N = 15), female juveniles (N = 3)

Conflict received (received conflict from another group member at the foraging site).

Time (first, second, third and fourth month after joining the foraging group)

Sex_firstmale (sex of raven's individual)

Table 2.
Effect of sex, time, number of siblings, number of brothers, number of sisters on feeding success during foraging at the wild boar feeding site.

Feeding success (frequency of how many times a raven was observed with food in the beak at foraging site).

Variable	y=	R^2
Feeding success vs. conflict donated	-0.1289x + 26.35	0.006
Feeding success vs. conflict received	-0.4585x +20.354	0.023

Table 3: Correlation between the rate of conflicts and feeding success during foraging at the wild boar feeding site with regard to donated and received conflicts.

Variable	Chisq	Df	Pr(>Chisq)
Intercept	1.2841	1	0.257143
Feeding success vs. sex_firstmale	1.4656	1	0.226034
Feeding success vs. time	7.7459	1	0.005384 **
Feeding success vs. number of siblings	0.2069	1	0.649219
Feeding success vs. number of brothers	0.0349	1	0.851869
Feeding success vs. number of sisters	0.0478	1	0.826864

Time (first, second, third and fourth month after joining the foraging group)

Sex_firstmale (sex of raven's individual)

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Table 4: Effect of sex, number of siblings, number of brothers, number of sisters on begging frequency of chicks towards parents in the family group in captivity

Variable	Estimate Std.	Error	z value	Pr(>|z|)
Begging to parents vs. Sexchicks				
Intercept	5.23	1.27	13.05	4.12	0.001 **
Sex_male	3.22	1.23	14.62	2.63	0.019 *
Begging to parents vs. sex parents				
Intercept	4.33	0.62	19.16	6.96	<0.001***
Sex_male	-1.85	0.79	36.93	-2.35	0.024 *
Begging to parents vs. number of siblings				
(Intercept)	9.49	1.33	12.98	7.13	<0.001***
	-1.25	m0.95	18.75	-2.76	0.271
Begging to parents vs. number of brothers				
(Intercept)	9.49	1.33	12.98	7.13	<0.001***
	-2.63	0.95	18.75	-2.76	0.012 *
Begging to parents vs. number of sisters				
(Intercept)	4.85	1.37	15.26	3.55	0.003 **
	3.13	1.15	17.92	2.74	0.014*
Begging to father vs. number of brothers				
(Intercept)	4.30	0.88	16.69	4.91	0.000***
	-1.67	0.64	15.36	-2.62	0.020 *
Begging to father vs. number of sisters				
(Intercept)	1.95	0.97	18.25	2.00	0.061
	1.02	0.94	20.90	1.09	0.290
Begging to mother vs. number of brothers				
(Intercept)	5.08	0.99	22.00	5.15	< 0.000 ***
	-0.72	0.70	22.00	-1.03	0.316

Table 5: Effect of sex, number of siblings, number of brothers, number of sisters and begging freqency on feeding frequency of paretns towards chicks in the family group in captivity

Variable	Estimate	Std. Error	df	t value	Pr(>|t|)
Feeding by parents vs. begging by chicks					
Intercept	0.71	0.24	19.58	2.99	0.007 **
	0.05	0.03	21.35	2.00	0.056
Feeding by parents vs. sex parents					
Intercept	1.08		0.14	7.60	<0.001 ***
	- 0.53		0.20	-2.60	0.012 *
Feeding by father vs. sex chick					
Intercept	0.60	0.23	10.34	2.65	0.024 *
	0.29	0.13	13.54	2.22	0.044 *
Feeding by mother vs. sex chick					
Intercept	1.01	10.25	13.53	4.08	0.001 **
	0.28	0.22	15.34	1.24	0.232
Feeding by father as response on begging by chicks					
Intercept	0.44	0.17	10.47	2.60	0.026 *
	0.11	0.02	13.95	5.80	<0.001 ***
Feeding by father as response on begging by sons					
Intercept	0.06	0.01	4.04	8.03	0.001 **
	0.51	0.16	7.19	3.13	0.016 *
Feeding by father as response on begging by daughters					
Intercept	0.13	0.04	1.19	3.70	0.136
	0.34	0.22	8.87	1.56	0.155
Feeding by mother as response on begging by chicks					
Intercept	0.88	0.27	18.46	3.26	0.004 **
	0.07	0.04	17.98	1.55	0.140
Feeding by father vs. number of brothers					
Intercept	1.11	0.18	13.70	6.02	<0.001 ***
	-0.41	0.12	20.77	-3.56	0.002 **
Feeding by father vs. number of sisters					
Intercept	0.58	0.24	10.73	2.45	0.033 *
	0.27	0.13	14.17	2.09	0.056
Feeding by mother vs. number of brothers					
Intercept	1.54	0.25	16.53	6.24	<0.005 ***
	-0.41	0.17	21.71	-2.38	0.027*
Feeding by mother vs. number of sisters					
Intercept	0.95	0.26	15.68	3.72	0.002 **
	0.31	0.21	18.16	1.40	0.159

9 REFERENCE

Alexander D. (1974) The evolution of social behavior

Assensio N., Korstjens A.H., Schaffner C.M., Aureli F. (2008) Intragroup aggression, fission-fussion dynamics and feeding competition in spider monkeys

Aureli F., Schaffner M., Boesch C., Bearder K., Call J., Chapman A., Connor R., Di Fiore A., Dunbar I. M. , Henzi P., Holekamp K., Korstjens H. , Layton R., Lee P., Lehmann J. , Manson H. , Ramos-Fernandez G., Strier B., van Schaik C.P. (2008) Fission-fussion dynamics: new research framework

Baylis A., Page B., McKenzie J., Goldsworthy S. (2012) Individual foraging site fidelity in lactating New Zealand fur seals: Continental shelf vs. oceanic habitats

Boarman WI., Heinrich B. (1999) Common raven (Corvus corax)

Bolnick D.I., Doebeli M. (2003) Sexual dimorphism and adaptive speciation: two sides of the same ecological coin

Bolnick D.I., Svänback R., Fordyce JA. (2003) The ecology of individuals: incidence and implications of individual specilizations

Boncoraglio G., Martinelli R., Saino N. (2008) Sex-related asymmetry in competitive ability of sexually monomorphic barn swallow nestlings

Boncoraglio G., Saino N. (2008) Barn swallow chicks beg more loudly when broodmates are unrelated

Bonisoli-Alquati A., Boncoraglio G., Caprioli M., Saino N. (2010) Birth order, individual sex and sex of competitors determine the outcome of conflict among siblings over parental care

Bonisoli-Alquati A., Møller P., Rudolfsen G., Saino N., Caprioli M., Ostermiller S., Mousseau A. (2011) The effects of radiation on sperm swimming behavior depend on plasma oxidative status in the barn swallow (*Hirundo rustica*)

Bonisoli-Alquati A., Rubolini D., Caprioli M., Ambrosini R., Romano M., Saino N. (2011) Egg testosterone affects wattle color and trait covariation in the ring-necked pheasant

Boogert N.J., Farine D.R., Spencer K.A. (2014) Developmental stress predicts social network position

Boogert N.J., Nightingale G.F., Hoppitt W., Laland K.N. (2014) Perching but not foraging networks predict the spread of novel foraging skills in starlings

Boucherie H., Gallego-Abenza M., Massen J. M., Bugnyar T. (2022) Dominance in a socially dynamic setting: hierarchical structure and conflict dynamics in ravens' foraging groups

Boucherie H., Loretto C.M., Massen J.M., T. Bugnyar (2019) What constitutes “social complexity” and “social intelligence” in birds? Lessons from ravens

Bowers K., Jenkins B., Mueller J., Miller D., Thompson F., Sakaluk K. Condition-Dependent Begging Elicits Increased Parental Investment in a Wild Bird Population

Braun A., Bugnyar T. (2012) Social bonds and rank acquisition in raven nonbreeder aggregations

Bugnyar T. (2015) Social cognition in ravens

Bugnyar T., Schwab C., Schloegl C., Kotraschal K. (2007) Ravens judge competitors trough experience with play caching

Bugnyar T., Stoewe M., Heinrich B. (2007) The ontogeny of caching in ravens, Corvus corax

Chin H., Love P., Clark M., Williams D. (2005) Brood size and environmental conditions sex-specifically affect nestling immune response in the European starling *Sturnus vulgaris*

Clutton-Brock T., Harvey P. (1977) Primate ecology and social organization

Cockrem J.F. (2007) Stress, corticosterone responses and avian personalities

Conradt L., Roper T.J. (2005) Consensus decision making in animals

Crino L., Prather T., Driscoll C., Good M., Breuner W. (2014) Developmental stress increases reproductive success in male zebra finches

Crino O.L., Driscoll S.C., Breuner C.W. (2014) Corticosterone exposure during development has sustained but not lifelong effects on body size and total and free corticosterone responses in the zebra finch

Crino O.L., Breuner C.W. (2015) Developmental stress: evidence for positive phenotypic and fitness effects in birds

Dall S., Wright J. (2009) Rich Pickings Near Large Communal Roosts Favor 'Gang' Foraging by Juvenile Common Ravens, Corvus corax

Danchin E., Giraldeu A., Valone J., Wagner H. (2004) Public information: from nosy neighbors to cultural evolution

Dunbar R.I.M., Schulz S. (2007) Evolution in the social brain

Elgar M.A. (1989) Predator vigilance and group size in mammals and birds

Ersoy S., Maag N., Boehly T., Boucherie H., Bugnyar T. (2021) Sex-specific parental care during postfledging in common ravens

Fraser O., Bugnyar T (2010) The quality of social relationships in ravens

Fraser O.N., Bugnyar T. (2010) Do ravens show consolation? Responses to distressed others

Gallego-Abenza M., Boucherie P., Bugnyar T. (2022) Early social environment affects attention to social cues in juvenile common ravens, *Corvus corax*

Giraldeau L.A., Caraco T. (2000) Social foraging theory

Glassey B., Forbes S. (2002) Begging and asymmetric nestling competition

Greggor L., Spencer A., Clayton S., Wild T. (2017) jackdaws' reproductive success and their offspring's stress hormones are connected to provisioning rate and brood size, not to parental neophobia

Grueter C., Leadbeater E. (2014) Insights from insects about adaptive social information use

Heinrich B. (1988) Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, *Corvus corax*

Hillen J., Kiefer A., Veith M. (2009) Foraging site fidelity shapes the spatial organisation of a population of female western barbastelle bats

Hull K.L., Cockrem J.F., Bridges J.P., Candy E.J., Davidson C.M. (2007) Effects of corticosterone treatment on growth, development, and the corticosterone response to handling in young Japanese quail (*Coturnix coturnix japonica*)

Isbell L.A. (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates

Janson C.H., Goldsmith ML. (1995) Predicting group size in primates: foraging costs and predation risks

Killner R., Hinde C. (2012) Parent-offspring conflict

Kilner R., Johnstone R.A. (1997) Begging the question: are offspring solicitation behaviours signals of need?

Kitaysky AS., Kitaiskaia EV., Piatt JF., Wingfield JC. (2003) Benefits and costs of increased levels of corticosterone in seabird chicks

Lefebvre L., Reader M., Sol D. (2004) Brains, Innovations and Evolution in Birds and Primates

Lima L. (1990) Back to the basics of anti-predatory vigilance: the group size effect

Loretto M.C., Fraser O., Bugnyar T. (2012) Ontogeny of social relations and coalition formation in common ravens *(Corvus Corax)*

Loretto M.C., Schuster R., Bugnyar T. (2016) GPS tracking of non-breeding ravens reveals the importance of anthropogenic food sources during their dispersal in the Eastern Alps

Love P., McGowan O., Sheriff J. (2012) Maternal adversity and ecological stressors in natural populations: the role of stress axis programming in individuals, with implications for populations and communities

MacCormick H., MacNulty D., Bosacker A., Lehman C., Bailey A., Collins A., Packer C. (2012) Male and female aggression: lessons from sex, rank, age, and injury in olive baboons

Maney D.L., Goodson JL. (2011) Neurogenomic mechanisms of aggression in songbirds

Mock W., Parker A. (1997) Evolution of sibling rivalry

Mock W., Dugas B., Strickler A. (2011) Honest begging: expanding from Signal of Need

Moretz J.A., Martins E.P., Robison B.D. (2007) Behavioral syndromes and the evolution of correlated behavior in zebrafish

Moretz J.A., Martins E.P., Robison B.D. (2007) The effects of early and adult social environment on zebrafish (Danio rerio) behavior

Payevsky V., (2015) Sex-biased survival and philopatry in birds: Do they interact?

Phillips R.A., Silk J.R.D., Phalan B., Catry P., Croxall J.P. (2004) Seasonal sexual segregation in two Thalassarche albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence

Pulliam H.R. (1973) On the advantages of flocking

Reader S., Laland K. (2002) Social intelligence, innovation, end anhanced brain size in primates

Regan A. (2005) Neuroendocrinology of social behavior

Russ J. (2018) Differences in Behavioral and Physiological Responses to Stress in Zebrafish

Saino N., Ferrari R., Romano M., Martinelli R., Møller P. (2003) Experimental manipulation of egg carotenoids affects immunity of barn swallow nestlings

Saino N., Suffritti C., Martinelli R., Rubolini D., Møller P. (2003) Immune response covaries with corticosterone plasma levels under experimentally stressful conditions in nestling barn swallows (*Hirundo rustica*)

Sapolsky R. (2005) The influence of social hierarchy on primate health

Shaver P.R., Mikulincer M. (2009) An overview of adult attachment theory

Taborsky B., Oliveira R. (2012) Social competence: an evolutionary approach

Terborgh J., Janson C.H. (1986) The socioecology of primate groups

Uller T. - Biological Reviews (2006) Sex-specific sibling interactions and offspring fitness in vertebrates: patterns and implications for maternal sex ratios

Van Noordwijk M.A., Van Schaik C.P. (1987) Competition among female long-tailed mcaques, Maca fascicularis

Van Schaik C.P. (1989) Social rank and sex ratio of captive long-tailed macaque females (Macaca fascicularis)

Votier S., Fayet A., Bearhop S., Bodey W., Clark L., Grecian J., Guilford T., Hamer K., Jeglinski J., Morgan G., Wakefield E., Patrick S. (2017) Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator

Vullioud C., Davidian E., Wachter B., Rousset F., Courtiol A., Höner O. (2008) Social support drives female dominance in the spotted hyaena

Wada H. (2008) Glucocorticoids: mediators of vertebrate ontogenetic transitions

Wingfield J.C., Sapolsky R.M. (2003) Reproduction and resistance to stress: when and how

Wright J., Leonard L. (2002) The Evolution of Begging- Competition, Cooperation and Communication

Zjacic N., Scholz M. (2022) The role of food odor in invertebrate foraging

10 APPENDIX

Table 1A. Characteristics of the ravens that were released into the wild

Characteristic	Value	Absolute (relative) frequency
Number of siblings	*1*	4 (23,5%)
	2	5 (29,4%)
	3	8 (47,1%)
Number of brothers	*0*	1 (5,9%)
	1	13 (76,5%)
	2	3 (17,6%)
Sex	*female*	3 (17,6%)
	male	15 (82,4%)

Table 2A. Information about the frequency of agonistic behavior with regard to donor and receiver

Type of agonistic behavior	Donor	Receiver
Threat	40 (12,7%)	62 (19,7%)
Displacement	22 (7,0%)	19 (6,0%)
Displacement from Food	2 (0,6%)	6 (1,9%)
Forced Displacement	24 (7,6%)	15 (4,8%)
Forced Displacement from Food	5 (1,6%)	5 (1,6%)
Steal Success	6 (1,9%)	17 (5,4%)
Steal Failed	13 (4,1%)	17 (5,4%)

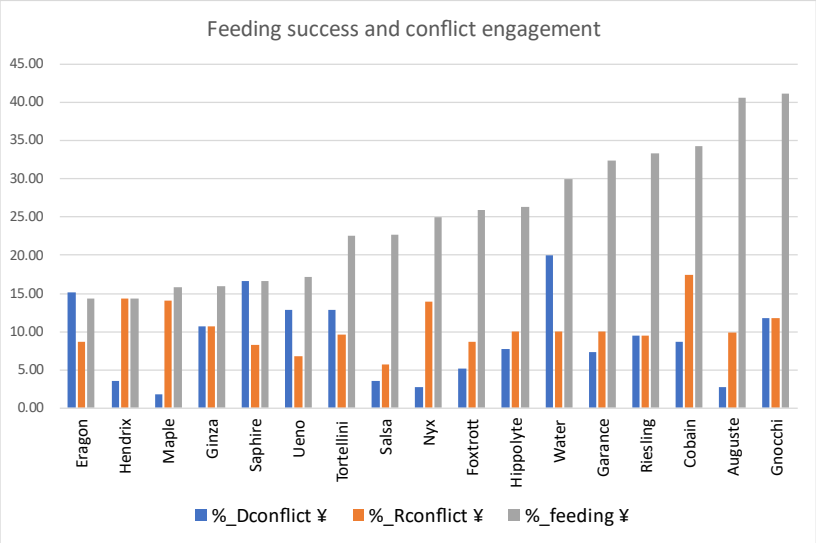

Figure 21. Raw data of feeding success started and received conflicts of each observed juvenile individual in the wild at feeding site. Feeding success (frequency of how many times a raven was observed with food in the beak at foraging site).

Table 3A. *Characteristics of the sample that was kept in captivity.*

Characteristic	**Value**	**Absolute (relative) frequency**
Number of siblings	*0*	1 (4,2%)
	1	8 (33,3%)
	2	7 (29,2%)
	3	8 (33,3%)
Number of brothers	*0*	6 (25%)
	1	10 (41,7%)
	2	7 (29,2%)
	3	1 (4,2%)
Sex	*Female*	11 (45,8%)
	Male	13 (54,2%)

Table 4A. *Characteristics of the chicks sample size that was born in captivity in Years 2020 and 2021.*

Characteristic	**Value**	**Males**	**Females**	**Sex_Unknown**
Year 2020				
Number of born chicks	*17*	*9*	*6*	*2*
Number of released chicks	*14*	*8*	*6*	*0*
Number of died chicks in family phase	*3*	*1*	*0*	*2*
Number of died chicks in first two months in the wild	*5*	*1*	*4*	*0*
Year 2021				
Number of born chicks	*25*	*13*	*7*	*5*
Number of released chicks	*19*	*12*	*7*	*0*
Number of died chicks in family phase	*4*	*0*	*0*	*4*
Number of died chicks in first two months in the wild	*7*	*1*	*6*	*0*