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„Sex-specific variation of parental care in common ravens,  
*Corvus corax*:  
Offspring body mass affects male investment“

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Selin Ersoy

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## Abstract

Parents face a trade-off when allocating limited resources into reproduction and self-maintenance, and this generally results in differential investment in individual offspring when rearing multiple offspring simultaneously. Offspring sex and body mass influence future reproduction and, therefore, these traits may influence differential parental care. Many species show different patterns of sexual size dimorphism and sex-specific parental investment, but the underlying causes remain poorly understood. I investigated the effect of individual and social factors on differential parental investment in common ravens, sexually dimorphic songbirds that provide bi-parental care. Specifically, I assessed the effect of offspring body mass, sex, begging intensity, and parent sex on feeding probability by parents. I further investigated the individual factors that influence offspring begging behaviour, and affiliative and agonistic interactions between parent and offspring. My results showed that fathers fed and affiliated more with heavy sons, whereas mothers showed no preference. I found that begging increased the likelihood of offspring to get fed from both parents, and light females and heavy males preferentially begged more to the fathers. My results suggest that in common ravens, offspring body mass serves as a signal in father-offspring interactions.

**Keywords:** Common raven, Parental care, Parent-offspring interaction, *Corvus corax*, Offspring body mass, Offspring sex





## **Zusammenfassung**

Eltern sind generell mit dem Konflikt konfrontiert, wieviel Ressourcen sie in Selbsterhaltung investieren sollen und wieviel in Fortpflanzung. Dieser Konflikt wird verstärkt, wenn die Ressourcen knapp sind. Wenn mehrere Nachkommen gleichzeitig aufgezogen werden, wird dann oft nicht gleichmässig in alle Nachkommen investiert. Da das Geschlecht und Körpergewicht der Nachkommen deren zukünftige Reproduktion beeinflusst, kann davon ausgegangen werden, dass die Eltern ihre limitierten Ressourcen selektiv nach diesen Eigenschaften verteilen. Diese selektive Verteilung von Ressourcen abhängig von Eigenschaften der Nachkommen wird in vielen verschiedenen Arten beobachtet, jedoch versteht man die zugrundeliegenden Mechanismen bislang nur sehr schlecht. In meiner Studie habe ich den Einfluss von individuellen und sozialen Faktoren auf die selektive Ressourcenverteilung von Eltern des Kolkraben untersucht. Kolkraben sind eine soziale Singvogelart mit geschlechtsspezifischem Grössenunterschied und beide Eltern investieren in die Aufzucht der Nachkommen. Ich habe den Einfluss des Körpergewichts, Geschlechts und der Bettelintensität der Nachkommen, und des Geschlechts der Eltern auf die Fütterungswahrscheinlichkeit der Eltern untersucht. Ausserdem habe ich den Einfluss der oben genannten individuellen Faktoren auf das Bettelverhalten, und auf die affiliativen und agonistischen Interaktionen zwischen den Eltern und Nachkommen, untersucht. Meine Resultate zeigten, dass Väter schwere Söhne bevorzugten. Dies zeigte sich in vermehrtem Füttern und mehr affiliativen Interaktionen. Mütter hingegen zeigten keine Präferenz für Geschlecht und Körpergewicht der Nachkommen. Erhöhtes Bettelverhalten erhöhte die Fütterungswahrscheinlichkeit von beiden Eltern, und leichte Weibchen und schwere Männchen bettelten selektiv häufiger zum Vater. Meine Resultate suggerieren, dass Kolkraben-Väter das Körpergewicht und Geschlecht von ihren Nachkommen als Signal nutzen und ihre Investition darauf abstimmen.

**Schlagwörter:** Kolkraben, Brutpflege, Eltern-Nachwuchs-Interaktion, *Corvus corax*, Körpergewicht, Geschlecht



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# 1 Introduction

## 1.1 Definitions of Parental Care and Parental Investment

Parental care and investment are crucial for the survival of many species. These are well established concepts and generally appreciated as adaptive strategies to increase fitness through investment of valuable resources of parents into their offspring (Clutton-Brock, 1991). However, among species there is a wide variation in the type of care and amount of resources that parent invest in their offspring. One strategy adopted by some species is that parental care is limited to producing eggs or live offspring, which are then left to fend for themselves. Another strategy involves one or both parents investing in a considerable amount of parental care, sometimes even after nutritional independence, as in some bird species and some mammals including humans (Gonzalez-Voyer & Kolm, 2010).

Any form of parental behaviour directed towards the offspring that increases the fitness of the offspring is defined as parental care (PC). Preparation of the nests and burrows, production of eggs, care of eggs or the young inside or outside the parent's body, provisioning of young before and after birth and care of the offspring after nutritional independence can be included in the term of parental care. It is important to note that PC includes only post-mating parental investment (Gonzalez-Voyer & Kolm, 2010). There are two types of PC: depreciable and non-depreciable. Depreciable care is defined as instances in which an increase in the brood or litter size decreases the benefit of parental care for individual offspring; such as provisioning food. On the other hand, non-depreciable care is defined as instances when an increase or decrease of the brood or litter size does not affect the offspring's individual benefits; such as parental vigilance to detect potential predators.

Trivers introduced Parental Investment Theory (PIT) in 1972 and he defined parental investment (PI) as any parental expenditure (time, energy, etc.) on an individual offspring that reduces the parent's potential to invest in other components of fitness, for example, the well-being of existing offspring, their own future sexual reproduction, and inclusive fitness through aid to kin (Clutton-Brock, 1991; Trivers, 1972). It is important to highlight that during PI, parents face a trade-off between investing resources to increase their current offspring's chance of survival and future reproduction, and using these resources for their own survival and future reproduction. PI can be split into two main categories: mating investment and rearing

investment. Mating investment involves the sexual act and the production of sex cells invested therein, whereas rearing investment is the time and energy expenditures used to raise the offspring.

## 1.2 Sexual Conflict over Care

Trivers (1972) presented an argument on parental investment and sexual selection based on anisogamy which is form of sexual reproduction that involves different size and/or form of gametes. He suggested that anisogamy is the reason for differential investment between sexes. Because eggs have larger gametes than sperm, females produce eggs, therefore, Trivers suggested that females make a larger parental investment prior to mating. Males, on the other hand, have smaller gametes, therefore, they can replenish their gamete supply and return to the mating pool sooner than females. For that reason, female care would be favored because producing an egg is costly, therefore, they would stand more to lose if they did not invest in the offspring. On the other hand, males care would not be favored because producing sperm is cheap and, they can return the mating pool. Therefore, Trivers put forward two arguments: 1) females should invest heavily in parental care because they stand to lose more than males, 2) male-male competition diminishes the likelihood of male parental investment.

The first argument, that females are more committed than males to providing care because they stand to lose a greater initial investment, was contradicted by Kokko and Jennions (2008). The authors argued that Trivers' argument commits the Concorde fallacy, which is a cognitive illusion that compels you to continue to invest in a (failing) asset in order not to waste the effort you already put into it. It dictates that abandoning a past investment is costly and, hence, it is the more beneficial continue this course of action. However, decisions based only on past investment would lead parents to never abandon their current brood, which is not what we observe in nature.

The second argument by Trivers (1972) stated that "male-male competition will tend to operate against male parental investment, in that any male investment in one female's young should decrease the male's chances of inseminating other females". The idea that anisogamy leads to males competing for mates is argued against by many scientists (Ah-King, 2013; Kokko & Jennions, 2008). One counterargument explores whether the marginal gains made from increased investment in competition are greater than those made by caring for offspring. After

all, if offspring die due to a reduction in parental care, it is detrimental to both parents. Ah-King (2013) states that anisogamy is not evidence for the differential sex roles. Gowaty and Hubbell (2005) modelled sex-related behavior stochastically and presented an evidence that gamete size has no influence on behavior. The findings of an integrative model by Kokko and Jennions (2008) also refute any suggestion that anisogamy on its own lead to divergent sex roles. They showed the role of anisogamy on sex roles and on parental investment in a more sophisticated model where they show sperm competition leads to greater female care by influencing the certainty of parentage.

An alternative explanation for why males often care less is the uncertainty of paternity (Gonzalez-Voyer & Kolm, 2010). The risk of caring for someone else's offspring increases the cost of caring. In species where the females mate with many males, uncertainty of paternity favors less care from males. This indicates an asymmetry in parental certainty; unlike females, who are always certain of maternity, males can never be certain of paternity. Under this hypothesis, we can also explain the bi-parental care system (both males and females care). In species with bi-parental care, adult sex ratio is often equal and level of sexual selection is low. Hence, investment in care by both sexes would be favored because of the low probability of encountering other mates. Furthermore, there is an evidence that in bi-parental care system, male care can increase his certainty of paternity (Ah-King et al., 2005; Kvarnemo, 2006) and even that sometimes, females prefer males that provide care (Reynolds & Jones, 1999).

### 1.3 Post-mating Conflict between Sexes

The difference in contribution to parental care between sexes varies among taxa. In mammals, female-only care occurs in approximately 90% of the species (Clutton-Brock, 1991). In birds, 75-90% of the species show bi-parental care, but in most cases females invest more heavily than males (Birkhead & Moller, 1993). In reptiles, parental care is provided either by the female or by both parents (Reynolds et al., 2002). In amphibians, male-only and female-only care is equally common, and bi-parental care rarely occurs (Beck, 1998). In invertebrates, female-only care is common and male-only care is rare. (Zeh & Smith, 1985). The list of the differences in parental care between taxonomic groups show that parental care systems vary considerably between species. In general, however, female care is more common than male care.

Parental care requires resources from parents which they cannot invest in their own growth, survival or future reproduction. Parents are limited by time and resources, and, therefore, face a trade-off between investment in themselves and in their offspring. From an evolutionary point of view, parental care should be favoured only when it benefits the parent but not necessarily to the offspring. Natural selection optimises parental behaviour to gain maximum benefit for minimum costs (Kilner, 2002a). Parent and offspring interests generally coincide, although not always without conflict. If the costs of parental care exceed the benefits for the parent, the parent will reduce the care, even if it is fatal for the offspring.

Trivers (1974) presented the theory of parent-offspring conflict and suggested that conflicts between parent and offspring arise over the amount and distribution of care and resources. He argued that offspring are selected to demand more investment than parents are selected to give. Accordingly, he suggested that the conflict between parent and offspring is caused by a genetic conflict of interest: whereas parents are equally related to all their current and future offspring, the offspring are only half related to their siblings and for that reason, they are selected to demand more investment even at their siblings' expense. As each parent has limited resources to divide among reproduction and self-maintenance (C. M. Lessells, 2002a) and some offspring demand more investment, this generally results in differential investment in offspring.

#### 1.4 Differential Investment in Offspring

Differential investment in offspring can occur by varying the ratio of sons and daughters produced (investment before birth), or through differential investment of energy in offspring after birth or hatching.

##### 1.4.1 Differential Investment before Birth

Trivers and Willard (1973) hypothesized that females can manipulate the sex of their offspring to maximize their reproductive success. Depending on parents' condition such as body size and hierarchical status, they can either produce more sons or daughters. Parents in good condition (e.g. dominant) would invest more in producing sons, as sons will increase the parents' fitness by producing more offspring than daughters. On the other hand, parent in poor condition are likely to produce more daughters because females have higher chance to reproduce than males however, females produce larger gametes and they are limited in quantity of offspring they



produce. The hypothesis was then tested and supported in the red deer (*Cervus elaphus*) study, where they showed that dominant mothers produces significantly more sons than daughters compared to deer who held a subordinate position in the herd (Clutton-Brock, Albon, & Guinness, 1981). Another recent study analysed 90 years of breeding records of different mammal species, and showed that some mammalian species can manipulate the sex of their offspring in order to produce extra grandchildren (Thogerson et al., 2013).

#### 1.4.2 Differential Investment after Birth

Bi-parental care, where males and females participate in offspring care, is common in many bird species (Cockburn 2006; Lack 1968). For this group, provisioning by both parents is often necessary to guarantee successful offspring rearing, but males and females may differ in their investment (Creelman & Storey, 1991). Differential investment in offspring can further occur by differential investment of energy in offspring after birth or hatch. The level of investment may depend on the offspring's sex, body mass, begging intensity, or parent sex.

##### 1.4.2.1 Sex-specific Parental Care

Selection may favour differential investment in sons and daughters by male and female parents after birth or hatch (Clutton-Brock et al., 1981; Trivers, 1972; Weimerskirch et al., 2000). There are three different types of sex-specific parental care (C. Lessells, 1998): i) Depreciable PC that depends on the sex of the parent but not of the offspring, ii) Depreciable PC that depends on the sex of the offspring but not of the parent, iii) Includes an interaction between parent and offspring sex.

i) Both sexually dimorphic and monomorphic bird species showed parent sex-specific PC and numerous studies showed different patterns; fathers provided more food in wandering albatrosses (*Diomedea exulans*, Weimerskirch et al., 2000), black-billed magpies (*Pica pica*, Buitron, 1988), manx shearwaters (*Puffinus puffinus*, Gray & Hamer, 2001); mothers provided more food in mediterranean storm-petrel (*Hydrobates pelagicus melitensis*, Albores-Barajas et al., 2015), great tits (*Parus major*, Kolliker et al., 1998), eastern bluebirds (*Sialia sialis*, Ligon & Hill, 2010a) and, no difference between sexes were found in Wilson's storm petrels (*Oceanites oceanicus*, Gladbach et al., 2009); and females of in atlantic puffins (*Fraterecula arctica*) invested more in the direct care of offspring, whereas males invested more in nest defence (Creelman and Storey 1991).

ii) It is generally not clear that if parents are able to discriminate the sex of individual offspring before the offspring attain adult plumage. Some empirical studies have found parental preferences for offspring sex (Gowaty & Droge 1991; Ligon & Hill 2010a; Mainwaring et al. 2011), and other studies have failed to find support (Teather 1992; Leonard et al. 1994; Michler et al. 2010). Bias in parental care depending on offspring sex generally occurs in species that exhibit size dimorphism, where cost of parenting towards one or the other sex differs. This can affect the parent's ability to provision the offspring, and the offspring of the larger sex might need more food allocation (Stamps, 1990). In most raptor species, females are on average bigger than males and, therefore, females cover most of the parental investment, and investment for the male offspring is higher because they are smaller and, therefore, males do not need as much as feeding that females need (Newton, 1978).

iii) Some studies showed that parental care was influenced by the interaction of parent sex and offspring sex. In the wandering albatross, fathers invested more in the sons, thereby increasing their own fitness because it increased sons' juvenile survival, and it came at no cost to future breeding performance (Cornioley et al., 2017). In zebra finches (*Taeniopygia guttata*), mothers preferentially provisioned sons over daughters (Mainwaring, Lucy, & Hartley, 2011), in humans (*Homo sapiens*), fathers invest more time in sons than daughters (Mammen, 2011), and in eastern bluebird, fathers were more likely to provision daughters whilst mothers showed no preference (Gowaty and Droge 1991).

#### 1.4.2.2 *Effect of Offspring Quality on Parental Care*

Offspring body mass can influence the parental decision in terms of differential investment because, body mass is a good indicator of an organism's body condition that reflects the amount of energy reserved to survive (Labocha & Hayes, 2012). Since the environmental resources are limited and parents are expected to adjust their expenditure, offspring body mass can affect the amount of care a parent provides. Young offspring with low body mass and slow growth are often the first to be discarded by the parents (Gottlander, 1987). Studies on pied flycatchers (Gottlander, 1987) and eastern bluebirds (Ligon & Hill, 2010a) showed that parents invested more in the bigger and heavier offspring. Other studies showed sex-specific variation in parents, where fathers tended to preferentially feed larger offspring, but females tended to favour small offspring (Lessells, 2002b). Hierarchies among siblings are often defined by individuals' body mass, and it is generally assumed these hierarchies are mediated by selective

feeding through the parents (Gottlander, 1987; Shaw, 1985). However, the hierarchy can also be established through sibling competition (Dickens et al., 2008). For example larger nestlings can dominate by positioning themselves closer to the parents or through their begging behaviour (Cotton, Kacelnik, & Wright, 1996).

#### *1.4.2.3 Offspring Begging Strategies*

Signalling of “need” by offspring offers a resolution to the parent offspring conflict. Parents can use the information transmitted by offspring begging as a signal of the offspring’s level of need and, adjust the investment towards specific offspring. An honest signalling model performed by Kilner and Johnstone (1997) suggests that offspring begging intensity reflects the level of offspring need, that parents should provision young in relation to begging intensity, and that begging is costly. Begging signals may have fitness cost to offspring in terms of energy expenditure and predator attraction, and therefore, it should therefore only be performed if the offspring is in “honest need”. Both theoretical and empirical studies show that intense begging has an important effect on parental feeding (Cotton et al., 1996; Dickens & Hartley, 2007; Gottlander, 1987; Levrero et al, 2012). In birds, offspring use both vocal and visual displays to signal their “need” to the parents. Parental decisions can be influenced by the behaviours of nestlings when parents rely on the begging intensity as an indicator of which nestling has the highest needs (Kilner et al., 1999). While many studies support the idea that begging is a reliable indicator of offspring condition and also parental feeding (Cotton et al., 1996), there are some studies that question the honesty of begging as a signal (see Kilner, 2002a; Kilner et al., 1999). Larger nestlings may be dominant over their siblings and use higher begging intensity to receive more food from the parents (Cotton, Kacelnik, & Wright, 1996). In several species, adult males are found to be more responsive to begging intensity than females (Stamps et al. 1985; Sasvari 1990), and as shown in a recent study on whilst canaries (*Serinus canaria*) mothers paid decreasing attention to begging behaviours as chicks aged, but fathers’ responsiveness remained constant (Kilner 2002b).

### **1.5 Socio-Behavioural Interaction between Parent and Offspring**

Several kinds of social interactions are known to be important for the survival of group living social species. These interactions can be affiliative (e.g., allo-grooming and helping behaviours) or agonistic (e.g., aggressive conflicts and fights). In many animals, social interactions between the group members do not follow random patterns of association, but

reflect social bonds (affiliative interactions) and dominance rank hierarchies (agonistic interactions), respectively. In several primate (e.g., Kutsukake & Clutton-Brock, 2006; Missakian, 1974) and bird (e.g., Fraser & Bugnyar, 2010) species, factors such as age, social rank, dominance relationship, and kinship affect the social interactions between individuals.

Allo-grooming (or allo-preening in birds, Figure 1) is one of the behaviours that plays an important role in maintaining social relationships (Kutsukake & Clutton-Brock, 2006). Removing the ecto-parasites from the body of a peer, especially from those parts that are impossible to reach by the peer itself, improves the peer's condition and strengthens the social relationships between groomer and peer. Allo-grooming or allo-preening further provides benefits through 'relaxation', in the form of decreasing heart rate (Aureli et al., 1999) and altered beta-endorphin levels (Keverne et al., 1989). Studies on birds (Clayton & Krebs, 1994), primates (Maestripieri, 1998; Parker & Maestripieri, 2011), and rodents (Liu et al., 2000) show that grooming interactions between mother and offspring have an important effect on the infant's hormonal and neural development. In house wrens, parents initiate allo-preening more than their offspring, and reciprocation never occurs (Gill, 2012), whereas in cooperatively breeding mammals, offspring reciprocates grooming (Kutsukake & Clutton-Brock, 2006). Furthermore, the amount of grooming given from parent to offspring can also vary between different offspring (e.g., in rodents Liu et al., 2000). A study on tamarins showed a sex-specific grooming interaction between parent and offspring that fathers huddle and contact affiliate more with their adult sons than daughters (Ginther & Snowdon, 2009).



**Figure 1.** Common raven pair showing allo-preening (Picture: Matthias Loretto).

## **2 Interdisciplinary Approach for Parental Care**

While human developmental psychology and behavioural ecology differ in their basic conceptualizations of parental care, they arguably study the same phenomena despite this difference. In psychology, the studies started to research parent and offspring interaction in the 1950s and these studies mostly conduct experiments on animals and compare to human subjects. Harry Harlow's experiment (1958) on maternal deprivation in rhesus monkeys is one of the cornerstones for developmental psychology.

In the experiment, Harlow separated infant monkeys from their mothers after birth and then moved the young monkeys to monkey mother machines. These machines were equipped to dispense milk but whether one was made of bare wire mesh, the other one was a wire mother covered with soft teddy cloth. When the experimental subjects were frightened by strange, loud objects, monkeys raised by terry cloth surrogates made bodily contact with their mothers, rubbed against them, and eventually calmed down. On the other hand, monkeys raised by a wire mesh did not go to their mothers instead, they threw themselves on the floor, clutched themselves, rocked back and forth, and screamed in terror. Harlow's study suggested that infant

need was not simple physiological needs, it could not be reduced to nursing. Infant and mother attachment was shown as emotional rather than physiological. After Harlow's study, the area of developmental psychology became a branch in psychology and has been focused on parent infant interaction and development of infant.

Both developmental psychology and behavioral ecology already has a well-developed theoretical framework proposing an explanation for the underlying mechanisms on parent and offspring interaction. While developmental psychology has been focusing on humans, it has been also using animals as a model to explain phenomenon. Therefore, these two fields have not been completely separated from each other.

My goal in this study has been to take a holistic approach to study the phenomena of parental care, integrating theoretical knowledge and important concepts from both developmental psychology and behavioral ecology on common ravens.

### **3 Common Ravens**

Common ravens, *Corvus corax*, are a long-lived (~15 years in the wild, ~40 years in captivity; Sherman, 2010) and large brained songbird species, widely distributed across the Northern Hemisphere (Haring, 2007). They have one of the longest periods of socio-cognitive development of any avian species, while they become sexually mature with three years of age, they often become reproductively successful not before the age of five years (Fraser & Bugnyar, 2010b). Pairs are characterized by long-term monogamy with mates remaining together. Breeding and egg laying occurs between mid-February and late March, they lay between 3 and 7 eggs per nest, and females incubate for 20-25 days (Berg, 1999). Chicks fledge between 5 and 7 weeks of age and the parents take care of their offspring after nutritional independence until offspring are 6 months old. Once independent from their parents, juvenile ravens join non-breeder groups until they find their partner and establish a breeding territory. The non-breeder groups are large social groups living with fission-fusion dynamics, meaning that these social groups are prone to constant change in respect to group size and composition. During that time, young ravens may be exposed to strong competition at feeding sites that leads to various caching behavior changes according to the presence and the knowledge of conspecifics and includes hiding food from others, caching food behind objects that might

obstruct the others' view (Bugnyar & Kotrschal 2002), and even considering conspecifics' knowledge of cache location when protecting and pilfering caches (Bugnyar & Heinrich 2005). This sophisticated caching and pilfering skills suggests that raven possess elements of a theory of mind, which allows them to make choices not only based on the memory of their own perspective but, they can also take into account the others' perspective (Bugnyar, 2013).

Friendly affiliative bonds with other conspecifics are important in raven social life for survival and reproductive success (Braun & Bugnyar, 2012). Bonded ravens tend to resolve conflicts between each other (Fraser & Bugnyar, 2011), support each other in conflicts with conspecifics (Fraser & Bugnyar, 2012), and console each other after severe conflicts with other group members (Fraser & Bugnyar, 2010a). Social bonds are further critical when achieving and maintaining higher dominance ranks, which in return increases an individuals' chance to access food (Bugnyar, 2013). The quality of raven social relationships resembles the ones of chimpanzees and other mammals, as the value of their bonds becomes apparent in alliance formation and conflict management (Fraser & Bugnyar, 2010b; Güntürkün & Bugnyar, 2016).

The socio-cognitive behaviours of ravens have been in the centre of the attention over the last decade, studies on ontogeny focused on hand-raised birds in their same-aged peer groups (Loretto et al., 2012). However, it is still unknown how the young ravens do in their 'natural' early social environment, i.e. family groups. In my study, I aimed to understand the dynamics of parent-offspring interactions and the socio-cognitive development of the young ravens.

## **4 Objectives**

The aim of this study was to disentangle the dynamics between parent and offspring interaction on common ravens and identify the individual and social drivers that effect differential parental investment. I collected detailed data on parent-offspring interactions from five captive raven families and measured body mass of the offspring at the time of fledging and (experimentally controlled) dispersal from the family. My specific objectives were: 1) To investigate the effect of offspring body mass, sex, age, begging intensity, and parent sex on parental feeding probability. I expected that begging would increase the probability of feeding, and that male and/or heavy offspring would receive more food from their parents. I further expected that young offspring would be fed more than old ones and that fathers would feed their offspring

more. 2) To investigate the influence of offspring body mass, sex, age, and parent sex on begging behavior. I expected that the offspring with lighter body mass would beg more and, I further expected that offspring would beg less with increasing age. 3) To investigate the effect of offspring body mass, sex, age and parent sex on positive social (affiliation) given by parent to offspring. I expected that heavy and/or male offspring would receive more affiliative behavior, that mothers would show more affiliation to the offspring than fathers, and that parents would affiliate more with old offspring than young. 4) To investigate the influence of offspring body mass, sex, and parent sex on negative social behaviors (agonistic) given by parent to offspring. I expected that parents would show more agonistic behaviors towards male and heavy offspring, that fathers would show more agonistic behaviors towards offspring than mothers, and that parents would show more agonistic behavior to old offspring than young. 5) To investigate the effect of feeding on offspring daily growth rate, depending on parent sex and offspring sex. I expected that male offspring would have higher growth rates than female offspring and that fathers would have a higher impact on offspring growth than mothers.

## 5 Methods

### 5.1 Data Collection

The study was conducted between May 2016 and July 2016 at the Haidlhof research station in Bad Völsau and the Konrad Lorenz research station in Grünau, Austria (Figure 2). The Haidlhof station is operating since 2010 and is co-owned by the University of Vienna and the Veterinary Medicine University of Vienna. The Konrad Lorenz station is operating since 1973 and is funded by the University of Vienna and the federal state of Upper Austria. Both stations provide housing for ravens, whereby most of the aviaries of the Konrad Lorenz station are situated in the adjacent Cumberland Wildpark. The raven aviaries are all similar size (each 50-80 m<sup>2</sup>; and a height of 5-7 m), located outdoor, and contain trees, stones, tree trunks, and shallow pools for bathing. Food is provided for all captive ravens twice per day and includes meat, milk products, vegetables and fruits and, water is provided ad libitum. The ravens in both stations are marked with colored leg rings for individual identification.

I collected data from five pairs of common ravens and their offspring (Table 1). All five pairs were kept at the Haidlhof research station for the first three years in non-breeder groups of 8 to 12 individuals. When the individuals became sexually mature, they chose a partner from



these groups. After this voluntary mate choice, the pairs were moved to separate aviaries where they are allowed to breed. Two pairs were moved to the breeding aviaries in Konrad Lorenz station and, three pairs remained in the Haidlhof station (Figure 2). The pairs were housed in similar aviaries in both station. Nest boxes were located in the aviaries and tree branches were provided as nestling material than the pairs built their nest. The pairs started breeding and laying eggs between mid-February and late March. They laid 4 to 6 eggs per nest and females incubated for 20-25 days. After incubating period, four eggs hatched from each nest.



**Figure 2.** Location of the study areas in Austria.

At both research stations, captive ravens were habituated to visitors and close observations by humans, allowing me to record behaviors with a video camera. To minimize disturbance and not to alter behaviors of the animals, observer and camera did not move during the observations. Although common ravens are known to be neophobic (Kijne & Kotrschal, 2002), study animals were not disturbed by the observer or the camera. Each raven family was filmed for a period of 30 min twice a day, in the morning and afternoon. Observations were conducted from fledging of the chicks, until the end of the parental care, when chicks were 110 days old and got transferred to a separate aviary in the Cumberland Wildpark (appr. 200 m<sup>2</sup>), forming a non-breeder group.

After filming, the video footage was played back and all social interactions between family members were labelled using the software Cyber Tracker (Cyber Tracker Conservation 2013) on a smartphone (Samsung Galaxy s6). I followed a strictly defined ethogram (Table S2): i) Food provisioning from parent to offspring was labelled as *feeding*. This behavior comprised that a parent carried food in its beak and placed it in the offspring's beak. ii) *Begging* (Figure 4). behaviors were divided in two types of begging; *low intensity* and *high intensity* begging. *Low intensity* begging included the offspring's auditory signal of hunger, which was a short "ha" call. *High intensity* begging included a combination of auditory and visual signals, which consisted of an individual flapping its wings, displaying its brightly colored mouths to the parent, and "ha" calls. While *low intensity* begging was not directed to the parents, *high intensity* begging was directed to either one of the parent. iii) Affiliative behaviors included *allo-preening* (Figure 1)., where one bird touched the feathers of another bird with its beak for longer than two seconds; *touch*, where one bird touched another bird's body with its beak; and *contact sit*, where two birds sat near to each other (Figure 3). Affiliative behaviors could be directed from parent to offspring or from offspring to parent. iv) *Agonistic* behavior included physical aggression (pecking and kicking) from parent to offspring. When none of the behaviors in the ethogram occurred, animals were considered idle. For each behavioral observation of 30 min, the occurrence of each behavior was counted and summarized per chick.



**Figure 3.** Common raven pair in contact sit (Picture: JB).

Chicks were captured two times; at the start of the observation period, when chicks were fledging, and at the end of the observation period, when parental care stopped and juveniles were transferred to group housing. During the first capture, fledglings were marked with colored leg rings for individual identification and fledgling body mass ( $m_F$ ) was recorded. During the second capture, blood samples were collected for gender analysis, and juvenile body mass ( $m_J$ ) was measured.



**Figure 4.** Raven chicks are begging to the father from the nest (Picture: JB).

## 5.2 Statistical Analysis

To investigate the effects of individual offspring traits and parent sex on parent-offspring interactions, I used four separate generalized linear mixed models (GLMM) implemented in the R library *lme4* (Bates et al., 2016): (1) feeding probability, (2) begging frequency, (3) affiliation probability (4) agonistic probability. To investigate the effect of parental investment on offspring's daily growth rate (5), I used a linear mixed effect model (LMM) implemented in the R library *lme4*. Model selection based on Akaike's Information Criterion for small sample sizes (AICc) was performed using the *dredge* function in the R library *MuMin* (Barton, 2016). To control for pseudo-replication, individual identity and family identity were included as random effects in all models. All parameter calculations and statistical analysis were done in R (R Core Team 2014). Details of all full models and outcomes of model selections are given in the supplementary information (Table M1-M5).

To test for collinearity between explanatory variables, I used the variance inflation factor (VIF). Offspring sex and fledgling body mass were found collinear in models 1-4, and fledgling body mass was therefore dropped from the models. To investigate the effect of fledgling body mass, I conducted two separate GLMM analyses (a and b) in addition to each of the models 1-4, for which I split female and male chicks into two groups. In these sub-models a and b, I only

included those variables that were identified as in the model selection of models 1-4 and added fledgling body mass. Since the most important variables were already identified in during model selection of the main models 1-4, used the hypothesis testing approach based on *P*-values for the sub-models a and b.

As mentioned above, begging behaviour consisted of two different types; *low* and *high intensity*. *Low intensity* begging was discarded from all models after preliminary analyses showed that it had no effect on any of the response variables. Therefore, *low intensity* begging was not reported in any of the full model descriptions in the supplementary information and *high intensity* begging was renamed to *begging* for the rest of the analyses.

### 1) Feeding

I investigated the effects of offspring traits, parent traits, and behaviours between parents and offspring on the feeding probability (Table M1). In 1126 observations of feeding counts, only nine were larger than one (two feedings occurred five times, three feedings occurred four times). Therefore, I used a binomial GLMM with the binary response variable *Fed*: no feeding occurred vs. feeding occurred. I included the continuous variable *Age*, the age in days since hatch of the offspring. I included the sex of the offspring that was fed as binary response variable *Sex*: female vs. male. I included the sex of the parent that fed the offspring as binary response variable *Parent*: mother vs. father. I included the number of intense begging from the offspring to a parent prior to feeding as integer variable *Beg*. I included the number of affiliative behaviours from a parent to an offspring as integer variable *AffP*. I further included an interaction term between *Sex* and *Parent*.

*1a)* As described above, due to collinearity of sex and fledgling body mass, females and males were split into two data set to investigate the effect of body mass on feeding probability for each sex separately. In this analysis, I used a binomial GLMM to assess the effect of female fledgling body mass on feeding probability (Table M1a). I included the explanatory variables of the best model identified by model selection of the main *Feeding* (1) model: *Age*, *Parent*, and *Beg*. I further included the female fledgling body mass as continuous variable *MassFledge*, and the interaction term between *MassFledge* and *Parent*.

*1b)* Here, I used a binomial GLMM to investigate the effect of male fledgling body mass on feeding probability (Table M1b). I included the same explanatory variables than in model 1a

(interactions are represented by *var<sub>x</sub>:var<sub>y</sub>*): *Age*, *Parent*, *Beg*, *MassFledge*, and *Parent:MassFledge*. The only difference was that the analysis was performed with the male data subset and, therefore, *MassFledge* refers to male fledgling body mass.

## 2) *Begging*

I investigated the effects offspring traits, parent traits, and behaviours between parents and offspring on the begging frequency of chicks (Table M2). In 1126 observations of begging counts, 82 of them were larger than one and showed Poisson distribution. To handle the zero inflation in the data (914 of 1126 observations were zeros), I used a Hurdle model with two steps. In the first step, I concluded a binomial GLMM *BeggingBinom* with the binary response variable *BegBin*: no begging occurred vs begging occurred. In the second step, using only non-zero observations, I performed a Poisson GLMM *BeggingPoiss* (2.1) with the integer response variable *BegPoi*.

2.1) In the first step (model *BeggingBinom*, Table M2.1) with the binary response variable *BegBin*. I included the continuous variable *Age*, the age in days since hatch of the offspring. I included the sex of the offspring that begged as binary response variable *Sex*: female vs. male. I included the sex of the parent that was begged by the offspring as binary response variable *Parent*: mother vs. father. I included the number of affiliative behaviours from a parent to an offspring as integer variable *AffP*. I included the number of affiliative behaviours from an offspring to a parent as integer variable *AffC*. I included the number of agonistic behaviours from a parent to an offspring as integer variable *Ago*. I further included an interaction term between *Sex* and *Parent*.

2.2) In the second step (model *BeggingPoisson*, Table M2.2) with the integer response variable *BegPoi*, I included the explanatory variables that were not identified by the model selection to be important to explain variance of the binomial relationship of begging in the *BegBinom* (2.1) model, which were *Sex*, *Parent*, and *Sex:Parent*.

2.1a) I used a binomial GLMM to investigate the effect of female fledgling body mass on begging probability (Table M2.1a). I included the explanatory variables of the best model identified by model selection of the *BeggingBinom* (2.1) model: *Age*, *Ago*, and *AffC*. I further included the female fledgling body mass as continuous variable *MassFledge*.



2.2a) Here, I used a Poisson GLMM to investigate the effect of female fledgling body mass on begging frequency (Table M2.2a). I included the explanatory variables of the best model identified by model selection of the *BeggingPoisson* (2.2) model: *Parent*, *MassFledge*, and *Parent:MassFledge*.

2.1b) In this analysis, I used a binomial GLMM to investigate the effect of male fledgling body mass on begging probability (Table M2.1b). I included the same explanatory variables as in model 2.1a: *Age*, *Ago*, and *AffC*. The analysis was performed with the male data subset and, therefore, *MassFledge* refers to male fledgling body mass.

2.2b) Here, I used a Poisson GLMM to investigate the effect of male fledgling body mass on begging frequency (Table M2.2b). I included the same explanatory variables in model 2.2a: *Parent*, *MassFledge*, and *Parent:MassFledge*.

### 3) *Affiliation*

I investigated the effects of offspring traits, parent traits, and behaviours between parents and offspring on the affiliation probability of parent towards offspring (Table M3). In 1126 observations of affiliative behaviour counts, only 39 occasions were larger than one (two affiliation occurred 20 times, more than three affiliation occurred 19 times). Therefore, I used a binomial GLMM with the binary response variable *AffP*: no affiliation occurred vs. affiliation occurred. I included the continuous variable *Age*, the age in days since hatch of the offspring. I included the sex of the offspring that was affiliated as binary response variable *Sex*: female vs. male. I included the sex of the parent that affiliate with the offspring as binary response variable *Parent*: mother vs. father. I included the number of affiliative behaviours from an offspring to a parent as integer variable *AffC*. I included the number of agonistic behaviours from a parent to an offspring as integer variable *Ago*. I further included an interaction term between *Sex* and *Parent*.

3a) Here, I used a binomial GLMM to assess the effect of female fledgling body mass on the affiliation probability of parent towards offspring (Table M3a). I included the explanatory variables of the best model identified by model selection of the main *Affiliation* (3) model: *Age*, *Parent*, *AffC*, *MassFledge* and *Parent:MassFledge*. Here, *MassFledge* refers to female fledgling body mass.

3b) Here, I used a binomial GLMM to investigate the effect of male fledgling body mass on the affiliation probability of parent towards offspring (Table M3b). I included the same explanatory variables than in model 3a: *Age*, *Parent*, *AffC*, *MassFledge* and *Parent:MassFledge*. Here, *MassFledge* refers to male fledgling body mass.

#### 4) Agonistic

I investigated the effects of offspring traits, parent traits, and behaviours between parents and offspring on the probability of agonistic behaviour from parent to offspring (Table M4). In 1126 observations of agonistic behaviour counts, only 50 occasions were larger than one (two agonistics occurred 29 times, more than three agonistic occurred 21 times). Therefore, I used a binomial GLMM with the binary response variable *Ago*: no agonistic occurred vs. agonistic occurred. I included the continuous variable *Age*, the age in days since hatch of the offspring. I included the sex of the offspring that was agonised as binary response variable *Sex*: female vs. male. I included the sex of the parent that show agonistic behaviour towards the offspring as binary response variable *Parent*: mother vs. father. I further included an interaction term between *Sex* and *Parent*.

4a) I used a binomial GLMM to investigate the effect of female fledgling body mass on the agonistic behaviour probability from parent to offspring (Table M4a). I included the explanatory variables of the best model identified by model selection of the main *Agonistic* (4) model: *Parent*, *MassFledge* and *Parent:MassFledge*. Here, *MassFledge* refers to female fledgling body mass.

4b) I used a binomial GLMM to investigate the effect of male fledgling body mass on the agonistic probability behaviour from parent to offspring (Table M4b). I included the same explanatory variables than in model 4a: *Parent*, *MassFledge* and *Parent:MassFledge*. Here, *MassFledge* refers to male fledgling body mass.

#### 5) Parental investment

To investigate if feeding influenced the growth rate of offspring, I calculated the relative daily growth rate of each offspring as follows:

$$Growth = \frac{\frac{m_J - m_F}{m_F}}{\Delta t}$$



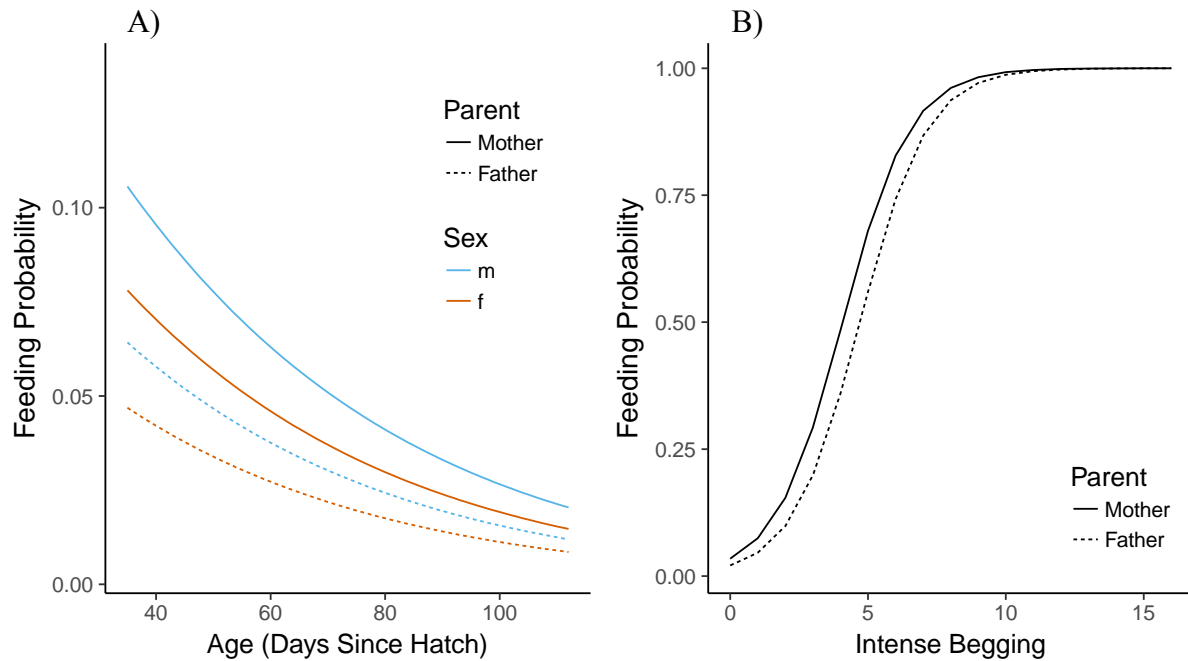
where  $m_F$  was fledgling body mass in gramm,  $m_J$  was juvenile body mass at the time of dispersal in gramm, and  $\Delta t$  was the number of days elapsed between time of fledging and time of dispersal. I used a linear mixed effect model (LMM) to investigate the effect of parental feeding on offspring daily growth rate (Table M5). In this analysis, *Growth* was a continuous response variable and, I included the sex of the offspring as binary response variable *Sex*: female vs. male. I calculated the mean of all feeding frequency across all observations for each offspring and by mother and father separately. I included the mean of the feeding by mother as continuous variable: *Fed.Mother* and, the mean of feeding by father: *Fed.Father*. I further included the interaction terms *Sex:Fed.Mother*, and *Sex:Fed.Father*.

## 6 Results

I followed five pairs of common ravens ( $N=10$ ) with four offspring each ( $N=20$ ). The average number of observation sessions recorded per family was  $\mu = 71.36$ . Fledgling body mass were collected from all 20 chicks. One male chick died three weeks before end of the data collection, and his juvenile body mass was collected when he died. For the rest of the 19 chicks, juvenile body mass was collected at the end of the behavioral data collection. A complete list of the individuals and model descriptions is given in the supplementary information (Table 1, M1-M5).

### 1) Feeding

Mothers were more likely to feed the offspring than fathers (Est= 0.58, SE= 0.002, Figure 5A, Table M1). Intense begging had an increasing effect on feeding probability by parents (Est= 0.90, SE= 0.002, Figure 5B). Parents were more likely to feed younger offspring than older offspring (Est= -0.56, SE= 0.002, Figure 5A). The model selection did not reveal any effect of offspring sex, interaction between offspring sex and parent, and affiliation from parent to offspring on feeding probability by parents.



**Figure 5. A)** Effect of offspring age depending on parent sex and offspring sex on feeding probability by parents. **B)** Effect of intense begging on feeding probability by parents. The lines show the relationship predicted by the averaged model. Grey shaded areas show standard errors.

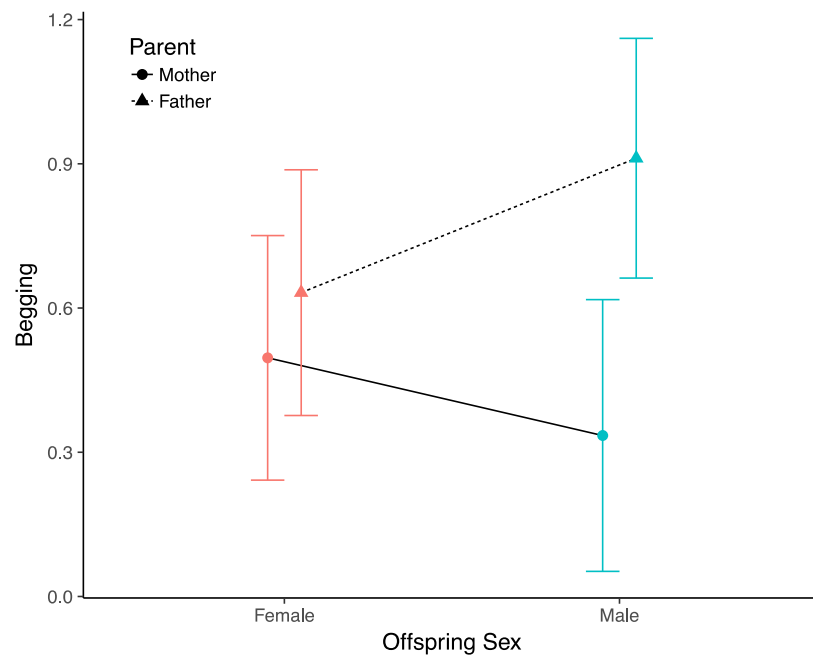
*1a)* Light females were more likely to be fed by their mothers than fathers (Est= -1.16, SE= 0.61,  $P = 0.06$ , Figure 7B, Table M1a). Female subset analysis revealed the same results than the main analysis with mothers being more likely to feed than fathers (Est= 1.03, SE= 0.57,  $P = 0.07$ ), and intense begging had an increasing effect on female offspring feeding probability by both parents (Est= 1.20, SE= 0.20,  $P < 0.001$ ). Opposite to the main analysis, female offspring age did not have effect on female feeding probability.

*1b)* Heavy males were more likely to be fed by the fathers than mothers. (Est= -0.83, SE= 0.41,  $P = 0.04$ , Figure 8B, Table M1b). Both parents were more likely to feed heavy males than light males (Est= 0.80, SE= 0.39,  $P = 0.06$ ). Male subset analysis revealed the same results than the main analysis such that intense begging had an increasing effect on male offspring feeding probability by both parents (Est= 0.80, SE= 0.14,  $P < 0.001$ ), and parents were more likely to feed younger males than older males (Est= -0.58, SE= 0.23,  $P = 0.01$ ). Different than the main analysis, here, parent sex did not have an effect on male feeding probability.

## 2) Begging

2.1) Younger offspring were more likely to beg to parents than older offspring (Est= -0.60, SE= 0.09, Table M2a). The offspring affiliation to the parent increased the likelihood of offspring begging to the parent (Est= 0.20, SE= 0.07). Agonistic interactions from parents to offspring increased the likelihood of intensive begging (Est= 0.42, SE= 0.09). The model selection did not reveal any effect of offspring sex, parent sex, interaction between offspring sex and parent, and affiliation from parent to offspring on offspring begging probability.

2.2) Male offspring begged more often to their fathers than mothers (Est= -0.44, SE= 0.20, Figure 6, Table M2b). Male offspring begged more often than female offspring (Est= 0.28, SE= 0.13), and both female and male offspring begged more often to their fathers than mothers (Est= -0.14, SE= 0.28).

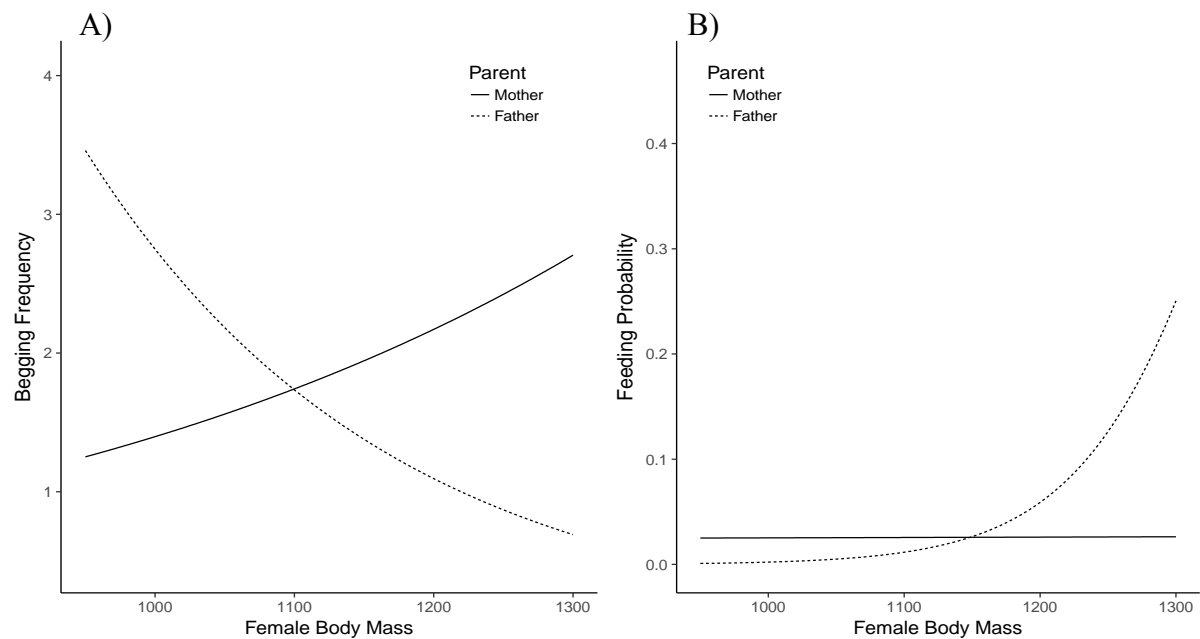


**Figure 6.** Effect of offspring sex on begging frequency depending on the sex of the parent. The lines show the relationship predicted by the averaged model. Grey shaded areas and error bars show standard errors.

2.1a) Light female offspring were more likely to beg than heavy females (Est= -0.46, SE= 0.24,  $P = 0.05$ , Table M2.1a). Female subset analysis confirmed the results of the main analysis with younger females being more likely to beg to parents than older females (Est= -0.68, SE= 0.13,  $P < 0.001$ ), and agonistic interaction from parent to females increased the likelihood of intense begging from females (Est= 0.55, SE= 0.11,  $P < 0.001$ ). Different to the main analysis, female

offspring affiliation to the parent sex did not have an effect on offspring begging probability to the parent.

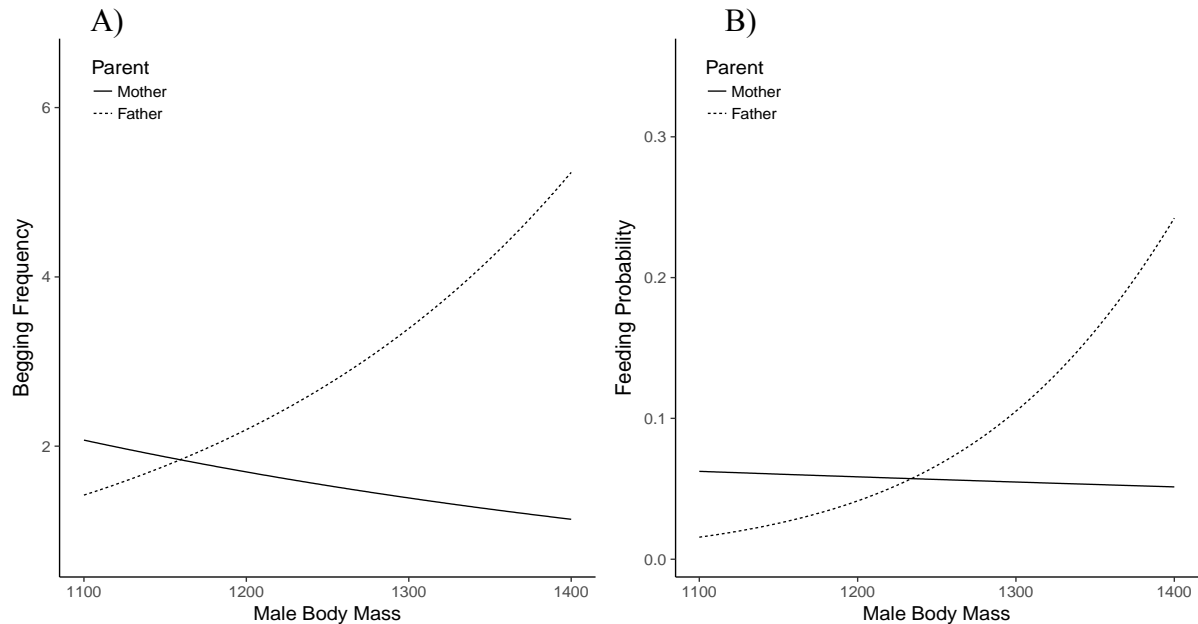
2.2a) Light female offspring begged more often to their fathers, and heavy females begged more often to their mothers (Est= 0.45, SE= 0.15,  $P = 0.002$ , Figure 7A, Table M2.2a). As in the main analysis, light females begged more often than heavy females (Est= 0.30, SE= 0.09,  $P < 0.001$ ). Different than in the main analysis, parent sex did not have an effect on female offspring begging frequency.



**Figure 7. A)** Effect of female fledgling body mass on begging frequency. **B)** Effect of female fledgling body mass on feeding probability. The lines show the relationship predicted by the averaged model. Grey shaded areas show standard errors.

2.1b) Here, the model did not reveal any effect of male body mass on begging probability. Male subset analysis confirmed the results of the main analysis and showed that younger males were more likely to beg to parents than older males (Est= -0.56, SE= 0.14,  $P < 0.001$ , Table M2.1b). Male offspring affiliation to the parent increased the likelihood of offspring begging to the parent (Est= 0.27, SE= 0.11,  $P = 0.01$ ). Agonistic interaction from parents to males increased the likelihood of intense male offspring begging (Est= 0.35, SE= 0.12,  $P = 0.003$ ).

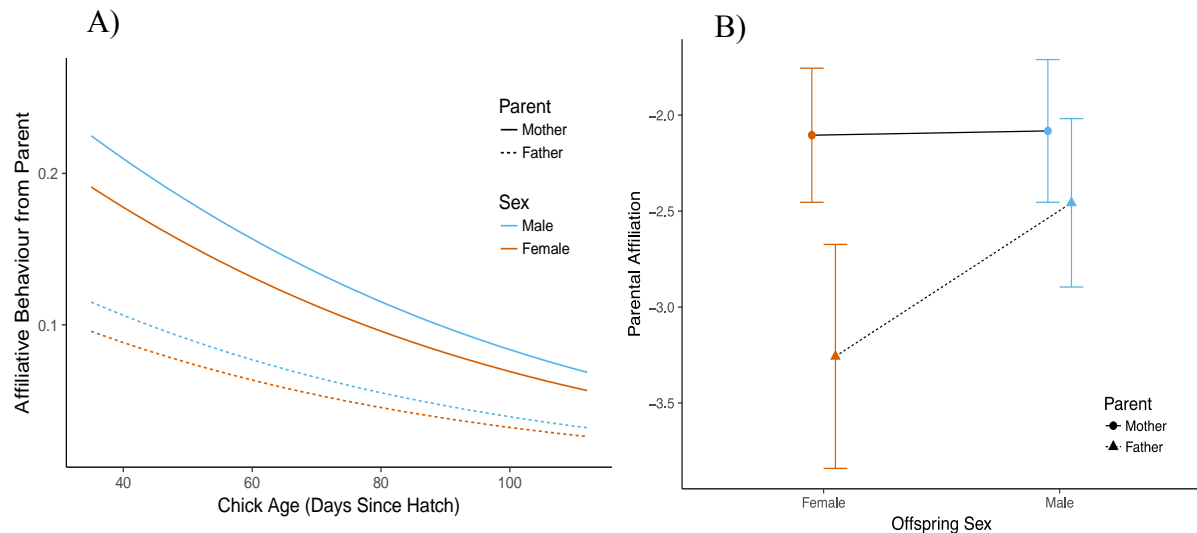
2.2b) Heavy male offspring begged more often to their fathers than mothers (Est= -0.38, SE= 0.15,  $P = 0.01$ , Figure 8A, Table M2.2b), and heavy males begged more than light males (Est= 0.22, SE= 0.11,  $P = 0.04$ ). Same than in the main analysis, males begged more often to their fathers than mothers (Est= -0.55, SE= 0.15,  $P < 0.001$ ).



**Figure 8. A)** Effect of male fledgling body mass on begging frequency. **B)** Effect of male fledgling body mass on feeding probability. The lines show the relationship predicted by the averaged model. Grey shaded areas show standard errors.

### 3) Affiliation

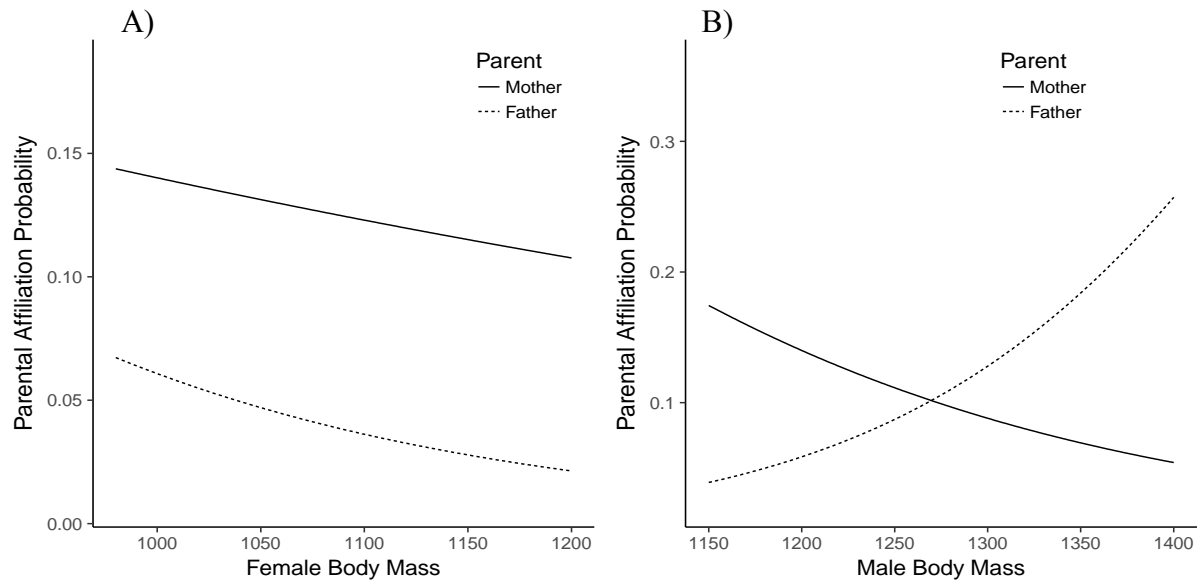
Mothers were more likely to affiliate with both male and female offspring than fathers (Est= 1.16, SE= 0.35, Figure 9A, Table M3). Fathers were more likely to affiliate with male offspring than female offspring (Est= -0.87, SE=0.46, Figure 9B). Both parents were more likely to affiliate with male offspring than female offspring (Est= 0.86, SE= 0.40, Figure 9A). Parents were more likely to affiliate with young offspring than older (Est= -0.43, SE= 0.12, Figure 9B). Parents were more likely to affiliate with offspring was more affiliative with parents (Est= 0.48, SE= 0.08). The model selection did not reveal any effect of parents to agonism from parent to offspring on the probability of parent to show affiliation towards the offspring.



**Figure 9. A)** Effect of offspring age on affiliation probability depending on parent and offspring sex. **B)** Effect of offspring sex on affiliation probability depending on the sex of the parent. The lines show the relationship predicted by the averaged model. Grey shaded areas and error bars show standard errors.

3a) Here, the model did not reveal any effect of female body mass on parent to offspring affiliation probability. Female subset analysis revealed the same results than the main analysis mothers were more likely to affiliate with female offspring than fathers (Est= 1.24, SE= 0.36,  $P < 0.001$ , Figure 10A, Table M3a). Parents were more likely to affiliate with young female offspring than older (Est= -0.64, SE= 0.18,  $P < 0.001$ ), and parents were more likely to affiliate with female offspring that affiliate with parents (Est= 0.43, SE= 0.12,  $P < 0.001$ ).

3b) Fathers were more likely to affiliate with heavy male offspring than mothers (Est= -0.84, SE= 0.31,  $P = 0.01$ , Figure 10B, Table M3b). Both parents were more likely to affiliate with heavy male offspring than light males (Est= 0.52, SE= 0.27,  $P = 0.06$ ). Same than in the main analysis, parents were more likely to affiliate with male offspring that affiliated with parents (Est= 0.54, SE= 0.11,  $P < 0.001$ ). Different to the main analysis, offspring age and parent sex did not have an effect on male offspring affiliation probability by parents.



**Figure 10.** **A)** Effect of female fledgling body mass on affiliation probability depending on the sex of the parent. **B)** Effect of male fledgling body mass on affiliation probability depending on the sex of the parent. The lines show the relationship predicted by the averaged model. Grey shaded areas show standard errors.

#### 4) Agonistic

Fathers were more likely to show agonistic behaviour to both male and female offspring than mothers (Est= -0.63, SE= 0.19, Table M4). Offspring age and offspring sex did not have an effect on agonistic probability from parents to offspring.

*4a-b)* Models did not reveal any effect of fledgling body mass on parent to offspring agonistic probability. Both male and female subset analyses revealed the same results than the main analysis that fathers were more likely to show agonistic behaviour to offspring than mothers (Females: Est= -0.72, SE= 0.28, Table M4a; Males: Est= -0.55, SE= 0.28, Table M4b).

#### 5) Parental investment

LMM growth analysis (Table M5) revealed the null model as the best model. Hence, I could not show a differential effect of parental investment on the daily growth of offspring.

## 7 Discussion

This study provides a comprehensive overview of the individual and social factors influencing parent-offspring interactions in the common raven, a songbird with bi-parental care and slight sexual size dimorphism. I found distinct differences in sex-specific interactions between parent and offspring: Fathers invested more feeding and affiliative behaviour into heavy males and less into light females. Mothers, on the other hand, invested most of their feeding into light females and generally showed more feeding and affiliation towards their offspring than fathers. I will first discuss my findings from the perspective of the parents and then from the perspective of the offspring.

### 7.1 Parents' point of view

My results suggest that mothers are more likely to follow the strategy of investing in quantity, whereas fathers are more likely to follow the strategy of investing in quality when rearing offspring (Fischer, Taborsky, & Kokko, 2011). As parental care is costly in terms of limited time and resources, parents can be expected to optimise their parental behaviour so that they gain maximum benefit (Kilner, 2002a). My results suggest that raven fathers adopted a strategy, where parents living in high-quality nest environments prefer sons over daughters because sons show greater variability in reproductive potential than daughters (Barrios-Miller & Siefferman, 2013). A recent study on wandering albatrosses showed that investing in sons is an efficient strategy for fathers to increase their inclusive fitness because it increases sons' juvenile survival (Cornioley et al., 2017). Several studies on other species also showed that heavier nestlings survive better as juveniles (Magrath, 1991). When juvenile ravens disperse from their parents' territory, they join non-breeder groups to find food, partner, and social affiliations. The ravens in these groups live in a social hierarchy with older and heavier males generally inhabiting higher ranks (Boarman and Heinrich 1999). Body mass increases male juveniles' competitive ability in the non-breeder group, where they are involved in agonistic interactions with other male group members to reach and defend their position (Braun and Bugnyar, 2012). Occupying a high rank allows them to gain better access to restricted resources, to affiliate with potential allies and to build social bonds without suffering interferences by others (Fraser & Bugnyar, 2012, Massen et al., 2014); ultimately, it facilitates finding a partner and defending a territory for reproduction. Therefore, investing in heavy sons might be an efficient strategy for raven fathers to increase their fitness. Female juvenile ravens,



on the other hand, tend to experience less competition in the non-breeder group, where they involve more in affiliative interactions with other female group members (*pers. observation*).

Experimental studies showed that honest signalling of nestling quality can influence parents' decision in terms of offspring investment. Because offspring traits like sex, body mass and ornamentation influence future reproductive value, these traits may function as signals and influence parental decision. In a study on eastern bluebirds, they experimentally manipulated the plumage coloration of offspring and found that fathers used feather coloration to discriminate between sons (Barrios-Miller & Siefferman, 2013). They further showed that only fathers, but not mothers, showed favouritism towards the offspring with the highest reproductive value. An experimental study on blue tits showed that fathers tended to favour larger and stronger offspring while mothers were less likely to discriminate between offspring (Slagvold et al., 1994). In my study on an un-manipulated system, I found evidence that this is also the case in common ravens. My results support the hypothesis that the parent that provides the least overall reproductive investment, is more likely to direct its investment to the most valuable offspring (Lessells, 2002b). In ravens, reproduction is likely to be more energetically costly for females than it is for males, as females lay eggs, incubate the eggs, brood hatchlings and provide ~50% of nestling care. My findings support Trivers' (1972) hypothesis in ravens, where females invest more into offspring than males prior to the period of parental care and may therefore be less willing to discriminate among their offspring.

An alternative explanation on sex-specific parental care on ravens can support an ongoing debate on whether parents can discriminate the sex of their offspring or not. Male and female offspring are visually not easy to discriminate when they hatch from the eggs. Therefore, parents may not discriminate some sex-specific characteristics. Hence, parents may face a choice whether to use the imperfect information about offspring sex and provide differential care on different offspring sex, or provide parental care indiscriminately (Lessells, 2002a). These two choices can alternatively explain the reason in ravens, why fathers invest more in heavy males and less in light females. 1) Common ravens are sexually dimorphic species; therefore, fathers might follow a strategy that is using information on offspring body mass to acquire the sex of the offspring (males on average heavier than females) and, eventually, fathers choose to invest more in male offspring. 2) Or, fathers might consider the size of the offspring as a quality information, and invest more on heavy offspring. However, the mechanisms which allow raven parent to discriminate the sex of individual offspring are currently unknown.

My results on affiliative interactions between parent and offspring revealed a similar pattern than the results from the feeding analysis. This shows that affiliative interactions are part of the parental investment and it is important to consider affiliation when studying parental care in social species. Thus far, the importance of affiliative behaviours in parental care was only studied in primates (Lazaro-Perea et al., 2004; Missakian, 1974; Stone Sade, 1963). A study on the bi-parental cooperatively breeding tamarins showed that huddling and contact affiliation between fathers and adult sons had the same pattern than I found in the common ravens (Ginther & Snowdon, 2009). The authors showed that fathers are more likely to affiliate with male offspring. However, I found that intensive begging had an increasing effect on agonistic behaviour from parent to offspring, with fathers being more agonistic than mothers. This suggests that if begging is getting too costly for fathers to respond, he show aggression to the offspring to cease begging.

## 7.2 Offspring's point of view

My results showed that begging increased the chances of offspring to be fed by parents. Light female and heavy male offspring begged more to the fathers than mothers. Fathers responded by providing more food to heavy sons but not to light daughters. The latter were fed more by their mothers instead.

There is a considerable evidence that chick begging reflects their current state of hunger (Cotton et al., 1996; R. Kilner & Johnstone, 1997), therefore, parents can assess the aspect of 'need' of their offspring and respond to it. Both empirical (Henderson, 1975) and theoretical (Godfray and Parker, 1992) studies showed that begging behaviour of the young is an important factor in the proximate control of parental feeding intensity. My results support this idea that in general, begging intensity of the young ravens is an indicator to get fed from its parents. However, I also showed that female and male offspring are following different strategies on who to beg and how much to beg.

I found that light females beg more among the offspring, and, since ravens are sexually dimorphic, they are also the lightest ones among the siblings. This suggest that light females may show honest signalling indicating their hunger. That was an expected result as many studies showed that lighter chicks beg more (Cotton et al., 1996). I also found that light females

beg more to their father and heavy females beg more to their mother. A similar pattern was observed in blue tits where hungry chicks tended to move towards the father in the nest (Dickens et al., 2008). My observation was focused on the period outside the nest showing that hungry chicks selectively beg more to the father after fledging.

Although my data showed that intensive begging increased the chance of getting fed in general, that was not the case for light females. Fathers were less likely to feed lighter females. Therefore, it is safe to say that in this case, light females were not begging more to the fathers because they got more food from them. However, light females might be following a different strategy to respond to a difference between the sexes in parental food allocation rules. In a study on bi-parental care in the great tit, Kolliker et al. (1998) manipulated the hunger of nestlings and recorded their begging behaviour towards the mothers and fathers. Interestingly, the study showed that hungry nestlings moved closer and begged more intensely towards the mothers than to fathers, the reverse of that found in my study. The authors suggest that the pattern in great tits also relates to differences in the allocation rules of the two parents. It appears that great tit fathers feed nestlings more intensely than mothers (Kolliker et al. 1998), which would make begging towards the fathers costly. Because of great tit fathers are already feeding the offspring more than mothers, light offspring do not need to use energy to beg the father more, but instead, light offspring use that energy to solicit food from mother. This could explain why in their experiment, hungry nestlings moved closer to the mothers, and in my study, light offspring beg more to the fathers because in ravens, mothers feed more than fathers.

Even though I showed that intense begging increases offspring chance to be fed by parents, the parents' response to light female and heavy male offspring was different. Light female and heavy male offspring begged more to the fathers than mothers. Fathers responded by providing more food to heavy sons but not to light daughters. The latter were fed more by their mothers instead. This suggest that fathers discriminate the offspring depending on their body size, and mothers equalize their food distribution to the offspring by responding to their begging intensity.

Alternatively, small offspring may have greater long-term need and they will need constant food allocation. However, because of larger offspring has a bigger body size, they also may need more food allocation in the short-term (Lotem 1998; Karasov & Wright 2002). Therefore, larger nestlings may become hungry faster. In my study, heavy males begged more to the

fathers and fathers were responding with providing more food. Several other studies have found that nestlings which are larger and begging more intensely have a higher probability of successfully soliciting food from their parents (Stamps et al. 1987; Westneat et al. 1995; Leonard and Horn 1996; Krebs et al. 1999; Lessells 2002a). Although fathers fed the heavy male offspring more, I did not find an effect of parental investment on chick growth. I expected that the differential feeding of parents towards sons and daughters result in higher growth, but I was not able to detect it most likely due to low sample size.

## **8 Conclusion**

In species where both parents provide more than one form of parental care, the evolution of differential parental investment is well understood. In these species, parents usually show morphological, physiological, or behavioural differences (Lessells 2002a). Numerous studies on different species showed that the amount and form of parental care can vary depending on the sex of the parents (Albores-Barajas et al., 2015; Creelman & Storey, 1991; Gray & Hamer, 2001; Weimerskirch et al., 2016; Gladbach et al., 2009). However, less is known about the complex relationships between parent sex, individual offspring traits and parent-offspring interactions on parental investment and future success of offspring. I showed that parental care in captive common ravens depends on the specific interactions between parents and offspring, and that this species uses behavioural traits to mediate parental investment towards specific offspring. These interactions between parents and offspring eventually determine the condition of each offspring at the time of dispersal from the nest and consequently their future success when competing for their own survival and reproduction.

## 9 Tables

**Table 1.** Shown are individual IDs, sex, status in the family, date of hatch of offspring.

Individual ID	Sex	Status	Estimate Date of Hatch
AS	female	mother	
HO	male	father	
AH1	female	offspring of AS and HO	2016-03-28
AH2	male	offspring of AS and HO	2016-03-28
AH3	female	offspring of AS and HO	2016-03-28
AH4	male	offspring of AS and HO	2016-03-28
HE	female	mother	
TM	male	father	
HT1	female	offspring of HE and TM	2016-03-28
HT2	female	offspring of HE and TM	2016-03-28
HT3	male	offspring of HE and TM	2016-03-28
HT4	female	offspring of HE and TM	2016-03-28
JY	female	mother	
RK	male	father	
JR1	female	offspring of JY and RK	2016-03-28
JR2	female	offspring of JY and RK	2016-03-28
JR3	female	offspring of JY and RK	2016-03-28
JR4	male	offspring of JY and RK	2016-03-28
LE	female	mother	
MA	male	father	
LM1	male	offspring of LE and MA	2016-04-04
LM2	male	offspring of LE and MA	2016-04-04
LM3	male	offspring of LE and MA	2016-04-04 *died on 2017-06-23
LM4	female	offspring of LE and MA	2016-04-04
SO	female	mother	
OR	male	father	
SO1	male	offspring of SO and OR	2016-04-04
SO2	male	offspring of SO and OR	2016-04-04
SO3	female	offspring of SO and OR	2016-04-04
SO4	female	offspring of SO and OR	2016-04-04

**Table 2.** Detailed ethogram of raven behaviours recorded during behavioural observations.

Behaviour	Definition	Direction
Affiliative	Allo-preening: One bird touches (for longer than 2 seconds) the feathers of another bird with its beak	From parent to offspring, and offspring to parent
	Contact sit: Two birds sit next to each other in a reaching distance	
	Touch/hold: One bird touches another one's body with beak or foot	
Agonistic	Peck/kick: One bird pecks/kicks the other bird (with physical contact)	From parent to offspring
Begging	Offspring signal indicates their level of hunger or need. Begging individual uses combination of auditory and visual signals. Auditory signal is Food/Begging "ha" Call. Begging individual display brightly coloured mouths as they solicit food from their parents.	From offspring to parent
Feeding	Parental response to offspring begging signal. Parent brings food in their beak and place it inside of offspring's beak	From parent to offspring

## 10 Supplementary Information

**Table M1.** Upper table: description of the full statistical model and model variables of the binomial GLMM *Feeding*. Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<2 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes;  $\Delta$ AICc = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; SE = standard error of model estimate; Importance = relative importance of each variable;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description		
<i>Fed</i>	<i>Parent</i>	Sex of the parent who fed the offspring		
	<i>Sex</i>	Sex of the offspring		
	<i>Age</i>	Age of the offspring; days since hatch		
	<i>Beg</i>	Intensive begging from offspring to specific parent		
	<i>AffP</i>	Affiliative behaviour from parent to offspring		
	<i>Sex:Parent</i>			
Variable	DF	AICc	$\Delta$ AICc	W
<i>Parent+Age+Beg</i>	6	364.22	0	0.39
<i>Parent+Sex+Age+Beg</i>	7	364.96	0.74	0.27
<i>Age+Beg</i>	5	365.65	1.43	0.19
<i>Parent+Age+Beg+AffP</i>	7	366.01	1.79	0.16
Variable	Estimate	SE	Importance	
<i>Intercept</i>	-3.95	0.002		$R^2_m = 0.00044$
<i>Beg</i>	0.9	0.002	1.00	$R^2_c = 0.00044$
<i>Age</i>	-0.56	0.002	1.00	
<i>ParentMother</i>	0.58	0.002	0.81	

**Table M1a.** Upper table: description of model variables and model output of the binomial GLMM to investigate female fledgling body mass on feeding probability. Lower table: model results based on hypothesis testing; SE = standard error of model estimate; Z = standard deviation; P = P-value;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description			
<i>Fed</i>	<i>Parent</i>	Sex of the parent who fed the offspring			
	<i>Beg</i>	Intensive begging from offspring to specific parent			
	<i>Age</i>	Age of the offspring; days since hatch			
	<i>Mass Fledge</i>	Female offspring fledgling body mass			
	<i>Parent:MassFledge</i>				
Variable	Estimate	SE	Z	P	
<i>(Intercept)</i>	-4.9218	0.7277	-6.763	< 0.001	$R^2_m = 0.002218$
<i>MassFledge</i>	0.9052	0.6522	1.39	0.17	$R^2_c = 0.002412$
<i>ParentMother</i>	1.0264	0.5696	1.80	0.07	
<i>Age</i>	-0.4361	0.3031	-1.44	0.15	
<i>Beg</i>	1.1964	0.2021	5.92	< 0.001	
<i>MassFledge:ParentMother</i>	-1.1585	0.6091	-1.90	0.06	

**Table M1b.** Upper table: description of model variables and model output of the binomial GLMM to investigate male fledgling body mass on feeding probability. Lower table: model results based on hypothesis testing; SE = standard error of model estimate; Z = standard deviation; P = P-value;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description			
<i>Fed</i>	<i>Parent</i>	Sex of the parent who fed the offspring			
	<i>Beg</i>	Intensive begging from offspring to specific parent			
	<i>Age</i>	Age of the offspring; days since hatch			
	<i>Mass Fledge</i>	Male offspring fledgling body mass			
	<i>Parent:MassFledge</i>				
Variable	Estimate	SE	z	P	
<i>Intercept</i>	-3.05	0.43	-7.15	< 0.001	$R^2_m = 0.000733$
<i>MassFledge</i>	0.74	0.39	1.88	0.06	$R^2_c = 0.083706$
<i>ParentMother</i>	0.04	0.38	0.10	0.92	
<i>Age</i>	-0.55	0.20	-2.74	0.01	
<i>Beg</i>	0.79	0.15	5.45	< 0.001	
<i>MassFledge:ParentMother</i>	-0.83	0.41	-2.03	0.04	



**Table M2.1.** Upper table: description of the full statistical model and model variables of the binomial GLMM *BeggingBinom* (step one of the hurdle model). Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<2 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes;  $\Delta$ AICc = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; SE = standard error of model estimate; Importance = relative importance of each variable;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description		
<i>Beg</i>	<i>Parent</i>	Sex of the parent which offspring begged; mother or father		
	<i>Sex</i>	Sex of the offspring; male or female		
	<i>Age</i>	Age of the offspring; days since hatch		
	<i>AffC</i>	Affiliative behaviour from offspring to parent		
	<i>AffP</i>	Affiliative behaviour from parent to offspring		
	<i>Ago</i>	Agonistic behaviour from parent to offspring		
	<i>Sex:Parent</i>			
Variable	DF	AICc	$\Delta$ AICc	W
<i>Age+AffC+Ago</i>	6	966.88	0	0.4
<i>Age+AffC+AffP+Ago</i>	7	967.54	0.66	0.28
<i>Parent+Age+AffC+Ago</i>	7	968.56	1.68	0.17
<i>Sex+Age+AffC+Ago</i>	7	968.83	1.95	0.15
Variable	Estimate	SE	Importance	
<i>Intercept</i>	-1.77	0.28		$R^2_m = 0.131$
<i>Age</i>	-0.60	0.09	1.00	$R^2_c = 0.262$
<i>AffC</i>	0.20	0.07	1.00	
<i>Ago</i>	0.42	0.09	1.00	

**Table M2.2.** Upper table: description of the full statistical model and model variables of the poisson GLMM *BeggingPoisson* (step two of the hurdle model). Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<2 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes;  $\Delta$ AICc = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; SE = standard error of model estimate; Importance = relative importance of each variable;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description		
<i>Beg</i>	<i>Parent</i>	Sex of the parent which offspring begged; mother or father		
	<i>Sex</i>	Sex of the offspring; male or female		
	<i>Sex:Parent</i>	Interaction between sex of the offspring and parent		

Variable	DF	AICc	$\Delta$ AICc	W
<i>Parent+Sex+Parent:Sex</i>	5	755.06	0	0.7
<i>Parent</i>	3	756.77	1.71	0.3

Variable	Estimate	SE	Importance	
<i>Intercept</i>	0.63	0.13		$R^2_m = 0.063$
<i>ParentMother</i>	-0.14	0.15	1.00	$R^2_c = 0.082$
<i>SexMale</i>	0.28	0.13	0.70	
<i>ParentMother:SexMale</i>	-0.44	0.20	0.70	

**Table M2.1a.** Upper table: description of model variables of the binomial GLMM to investigate female fledgling body mass on begging probability. Lower table: model results based on hypothesis testing; SE = standard error of model estimate; Z = standard deviation; P = P-value;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description		
<i>Beg</i>	<i>Age</i>	Age of the offspring; days since hatch		
	<i>AffC</i>	Affiliative behaviour from offspring to parent		
	<i>Ago</i>	Agonistic behaviour from parent to offspring		
	<i>Mass Fledge</i>	Female offspring fledgling body mass		

Variable	Estimate	SE	z	P	
<i>Intercept</i>	-1.90	0.29	-6.60	< 0.001	$R^2_m = 0.2233$
<i>MassFledge</i>	-0.48	0.24	-2.00	0.05	$R^2_c = 0.2870$
<i>Age</i>	-0.67	0.13	-5.18	< 0.001	
<i>Agonistic</i>	0.53	0.11	4.90	< 0.001	
<i>AffC</i>	0.10	0.11	0.90	0.37	

**Table M2.2a.** Upper table: description of model variables of the poisson GLMM to investigate female fledgling body mass on begging frequency. Lower table: model results based on hypothesis testing; SE = standard error of model estimate; Z = standard deviation; P = P-value;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description
<i>Beg</i>	<i>Parent</i>	Sex of the parent who offspring begged
	<i>Mass Fledge</i>	Female offspring fledgling body mass
	<i>Parent:MassFledge</i>	

Variable	Estimate	SE	z	P	
<i>Intercept</i>	0.65	0.10	6.34	< 0.001	$R^2_m = 0.0813$
<i>MassFledge</i>	-0.30	0.09	-3.37	< 0.001	$R^2_c = 0.0813$
<i>ParentMother</i>	-0.15	0.15	-1.01	0.31	
<i>MassFledge:ParentMother</i>	0.45	0.15	3.05	0.00	

**Table M2.1b.** Upper table: description of model variables of the binomial GLMM to investigate male fledgling body mass on begging probability. Lower table: model results based on hypothesis testing; SE = standard error of model estimate; Z = standard deviation; P = P-value;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description
<i>Beg</i>	<i>Age</i>	Age of the offspring; days since hatch
	<i>AffC</i>	Affiliative behaviour from offspring to parent
	<i>Ago</i>	Agonistic behaviour from parent to offspring
	<i>Mass Fledge</i>	Male offspring fledgling body mass

Variable	Estimate	SE	z	P	
<i>Intercept</i>	-1.67	0.29	-5.70	< 0.001	$R^2_m = 0.1305$
<i>MassFledge</i>	0.36	0.29	1.22	0.22	$R^2_c = 0.2634$
<i>Age</i>	-0.56	0.14	-4.01	< 0.001	
<i>Agonistic</i>	0.35	0.12	2.91	0.00	
<i>AffC</i>	0.27	0.11	2.56	0.01	

**Table M2.2b.** Upper table: description of model variables of the poisson GLMM to investigate male fledgling body mass on begging frequency. Lower table: model results based on hypothesis testing; SE = standard error of model estimate; Z = standard deviation; P = P-value;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description			
<i>Beg</i>	<i>Parent</i>	Sex of the parent who offspring begged			
	<i>Mass Fledge Parent:MassFledge</i>	Male offspring fledgling body mass			
Variable	Estimate	SE	z	P	
<i>Intercept</i>	0.88	0.14	6.12	< 0.001	R <sup>2</sup> <sub>m</sub> = 0.1520
<i>MassFledge</i>	0.22	0.11	2.01	0.04	R <sup>2</sup> <sub>c</sub> = 0.1711
<i>ParentMother</i>	-0.55	0.15	-3.81	< 0.001	
<i>MassFledge:ParentMother</i>	-0.38	0.15	-2.57	0.01	

**Table M3.** Upper table: description of the full statistical model and model variables of the binomial GLMM *Affiliation*. Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<2 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes;  $\Delta$ AICc = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; SE = standard error of model estimate; Importance = relative importance of each variable;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description		
<i>AffP</i>	<i>Parent</i>	Sex of the parent who affiliated with the offspring		
	<i>Sex</i>	Sex of the offspring		
	<i>Age</i>	Age of the offspring; days since hatch		
	<i>AffC</i>	Affiliative behaviour from offspring to parent		
	<i>Ago</i>	Agonistic behaviour from parent to offspring		
	<i>Sex:Parent</i>			
Variable	DF	AICc	$\Delta$ AICc	W
<i>Parent+Sex+Age+AffC+Parent:Sex</i>	8	641.87	0	0.39
<i>Parent+Age+AffC</i>	6	642.74	0.87	0.25
<i>Parent+Sex+Age+AffC+Ago+Parent:Sex</i>	9	643.42	1.55	0.18
<i>Parent+Sex+Age+AffC</i>	7	643.49	1.62	0.17
Variable	Estimate	SE	Importance	
<i>Intercept</i>	-3.35	0.32		$R^2_m = 0.099$
<i>ParentMother</i>	1.16	0.35	1.00	$R^2_c = 0.099$
<i>Age</i>	-0.43	0.12	1.00	
<i>AffC</i>	0.48	0.08	1.00	
<i>SexMale</i>	0.86	0.40	0.75	
<i>ParentMother:SexMale</i>	-0.87	0.46	0.57	

**Table M3a.** Upper table: description of model variables and model output of the binomial GLMM to investigate female fledgling body mass on affiliation probability Lower table: model results based on hypothesis testing; SE = standard error of model estimate; Z = standard deviation; P = P-value;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description			
<i>AffP</i>	<i>Parent</i>	Sex of the parent who affiliated with the offspring			
	<i>Mass Fledge</i>	Female offspring fledgling body mass			
	<i>Age</i>	Age of the offspring; days since hatch			
	<i>AffC</i>	Affiliative behaviour from offspring to parent			
	<i>Parent:MassFledge</i>				

Variable	Estimate	SE	z	P	
<i>Intercept</i>	-3.48	0.33	-10.49	< 0.001	$R^2_m = 0.0008$
<i>ParentMother</i>	1.24	0.36	3.39	< 0.001	$R^2_c = 0.0049$
<i>Age</i>	-0.64	0.18	-3.64	< 0.001	
<i>MassFledge</i>	-0.32	0.30	-1.09	0.28	
<i>AffC</i>	0.43	0.12	3.68	< 0.001	
<i>ParentMother:MassFledge</i>	0.21	0.34	0.60	0.55	

**Table M3b.** Upper table: description of model variables of the binomial GLMM to investigate male fledgling body mass on affiliation probability. Lower table: model results based on hypothesis testing; SE = standard error of model estimate; Z = standard deviation; P = P-value;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description			
<i>AffP</i>	<i>Parent</i>	Sex of the parent who affiliated with the offspring			
	<i>Mass Fledge</i>	Female offspring fledgling body mass			
	<i>Age</i>	Age of the offspring; days since hatch			
	<i>AffC</i>	Affiliative behaviour from offspring to parent			
	<i>Parent:MassFledge</i>				

Variable	Estimate	SE	z	P	
<i>Intercept</i>	-2.51	0.34	-7.49	< 0.001	$R^2_m = 0.0008$
<i>ParentMother</i>	0.30	0.33	0.92	0.36	$R^2_c = 0.0049$
<i>Age</i>	-0.27	0.17	-1.62	0.10	
<i>MassFledge</i>	0.52	0.27	1.92	0.06	
<i>AffC</i>	0.54	0.11	4.69	< 0.001	
<i>ParentMother:MassFledge</i>	-0.84	0.31	-2.73	0.01	

**Table M4.** Upper table: description of the full statistical model and model variables of the binomial GLMM *Agonistic*. Middle table: results from model selection based on Akaike's information criterion (models from subset =  $\Delta AICc < 2$  are shown); DF = degrees of freedom; AICc = AIC for small sample sizes;  $\Delta AICc$  = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; SE = standard error of model estimate; Importance = relative importance of each variable;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description		
<i>Ago</i>	<i>Parent</i>	Sex of the parent who agonise the offspring		
	<i>Sex</i>	Sex of the offspring		
	<i>Age</i>	Age of the offspring; days since hatch		
	<i>Sex:Parent</i>			

Variable	DF	AICc	$\Delta AICc$	W
<i>Parent</i>	4	797.06	0	0.53
<i>Parent+Sex</i>	5	798.61	1.55	0.24
<i>Parent+Age</i>	5	798.78	1.71	0.23

Variable	Estimate	SE	Importance	
<i>Intercept</i>	-1.80	0.16		$R^2_m = 4.443$
<i>ParentMother</i>	-0.63	0.19	1.00	$R^2_c = 4.443$

**Table M4a.** Upper table: description of model variables of the binomial GLMM to investigate female fledgling body mass on agonistic probability. Lower table: model results based on hypothesis testing; SE = standard error of model estimate; Z = standard deviation; P = P-value;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description			
<i>Ago</i>	<i>Parent</i>	Sex of the parent who agonise the offspring			
	<i>Mass Fledge</i>	Female offspring fledgling body mass			
	<i>Parent:MassFledge</i>				

Variable	Estimate	SE	z	P	
<i>Intercept</i>	-1.84	0.19	-9.86	< 0.001	$R^2_m = 0.0000$
<i>ParentMother</i>	-0.72	0.28	-2.59	0.01	$R^2_c = 0.0000$
<i>MassFledge</i>	0.16	0.18	0.87	0.38	
<i>ParentMother:MassFledge</i>	0.08	0.27	0.29	0.77	

**Table M4b.** Upper table: description of model variables of the binomial GLMM to investigate male fledgling body mass on agonistic probability. Lower table: model results based on hypothesis testing; SE = standard error of model estimate; Z = standard deviation; P = P-value;  $R^2_m$  = marginal R squared; conditional  $R^2_c$  = conditional R squared.

Response	Explanatory	Variable description
<i>Ago</i>	<i>Parent</i>	Sex of the parent who agonise the offspring
	<i>Mass Fledge</i>	Female offspring fledgling body mass
	<i>Parent:MassFledge</i>	

Variable	Estimate	SE	z	P	
<i>Intercept</i>	-1.75	0.20	-8.85	< 0.001	$R^2_m = 0.0000$
<i>ParentMother</i>	-0.55	0.28	-1.98	0.05	$R^2_c = 0.0000$
<i>MassFledge</i>	0.13	0.18	0.70	0.49	
<i>ParentMother:MassFledge</i>	-0.22	0.28	-0.78	0.44	

**Table M5.** Upper table: description of the full statistical model and model variables of the LMM *Growth*. Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<2 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes;  $\Delta AICc$  = difference to best statistical model based on AICc; W = Akaike weights.

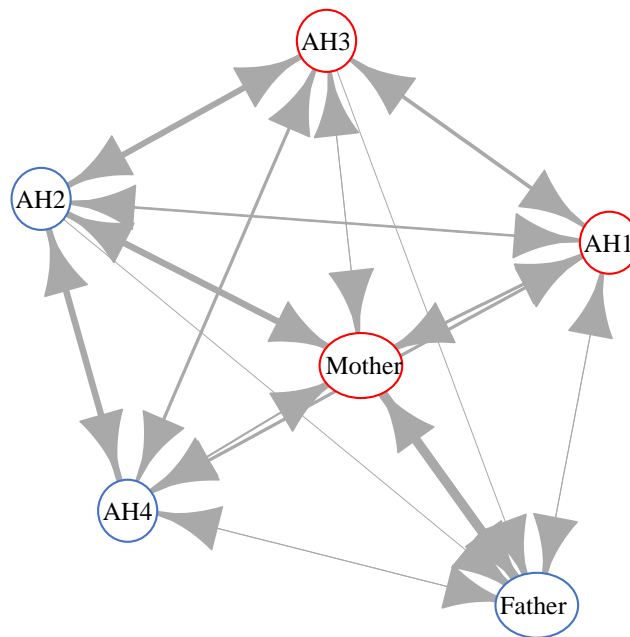
Response	Explanatory	Variable description
<i>Growth</i>	<i>Fed.Father</i>	Mean of feeding by Father
	<i>Fed.Mother</i>	Mean of feeding by Mother
	<i>Sex</i>	Sex of the offspring
	<i>Sex:Fed.Mother</i>	
	<i>Sex:Fed.Father</i>	

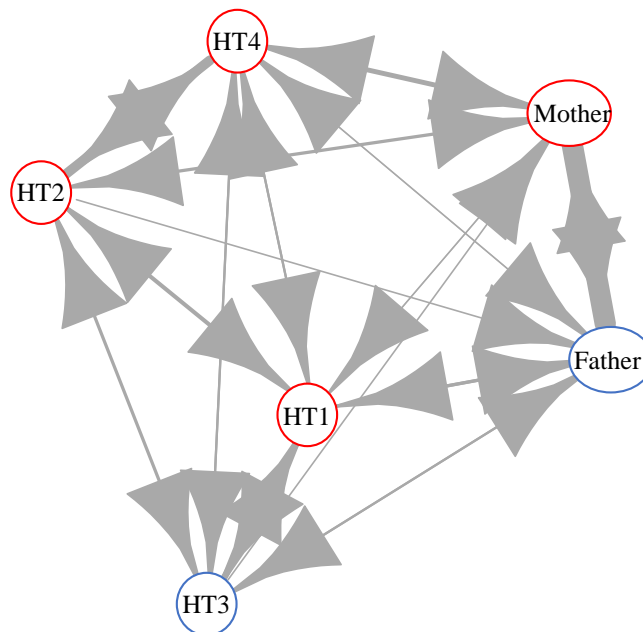
Variable	DF	AICc	$\Delta AICc$	W
<i>Null</i>	3	-235.44	0	0.42
<i>Sex</i>	4	-234.79	0.65	0.3
<i>Fed.Father</i>	4	-233.39	2.05	0.15
<i>Fed.Mother</i>	4	-233.04	2.41	0.13



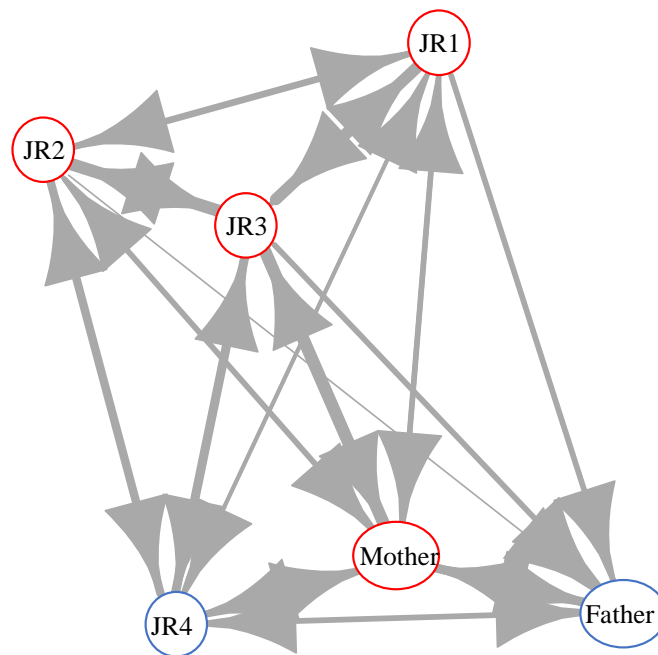
**Figure 11.** Affiliation network on Astrid-Horst family. Red circles indicate females, blue circles indicate males. The lines between individuals show the weight of the interaction calculated by Social Network Analysis (Farine, 2017).



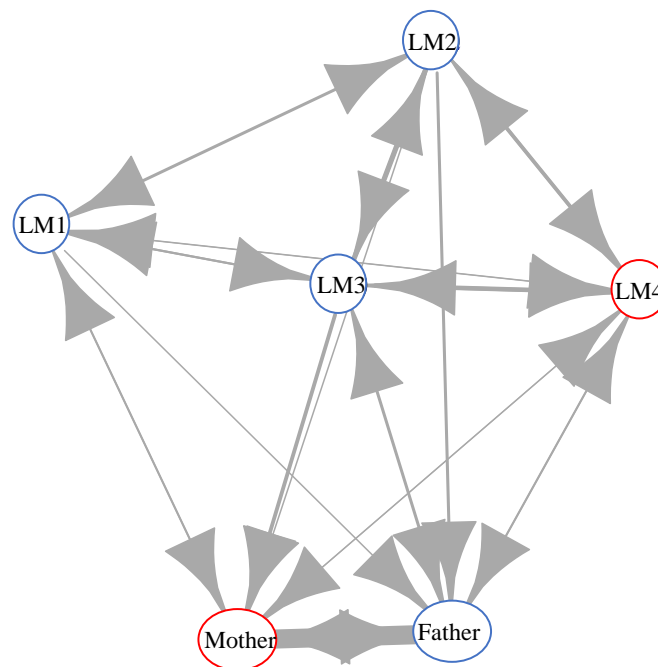
**Figure 12.** Affiliation network on Heidi-Tom family. Red circles indicate females, blue circles indicate males. The lines between individuals show the weight of the interaction calculated by Social Network Analysis (Farine, 2017).



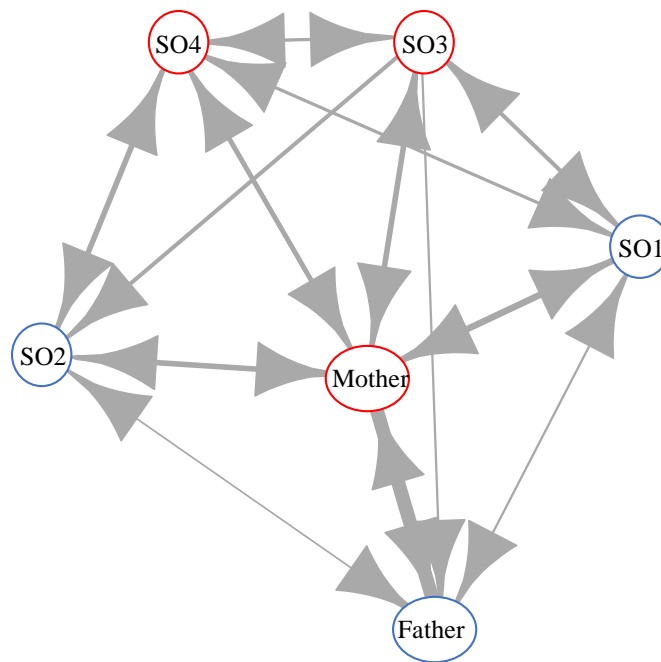
**Figure 13.** Affiliation network on Joey-Rocky family. Red circles indicate females, blue circles indicate males. The lines between individuals show the weight of the interaction calculated by Social Network Analysis (Farine, 2017).



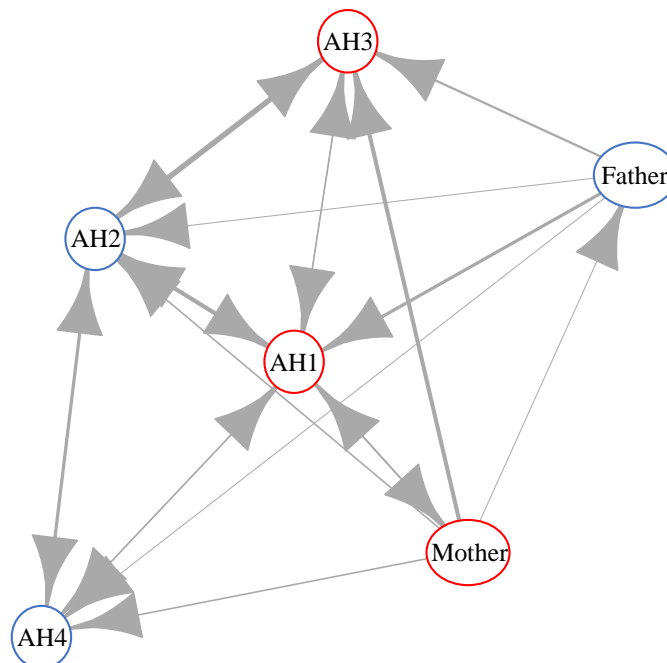
**Figure 14.** Affiliation network on Matte-Lellan family. Red circles indicate females, blue circles indicate males. The lines between individuals show the weight of the interaction calculated by Social Network Analysis (Farine, 2017).



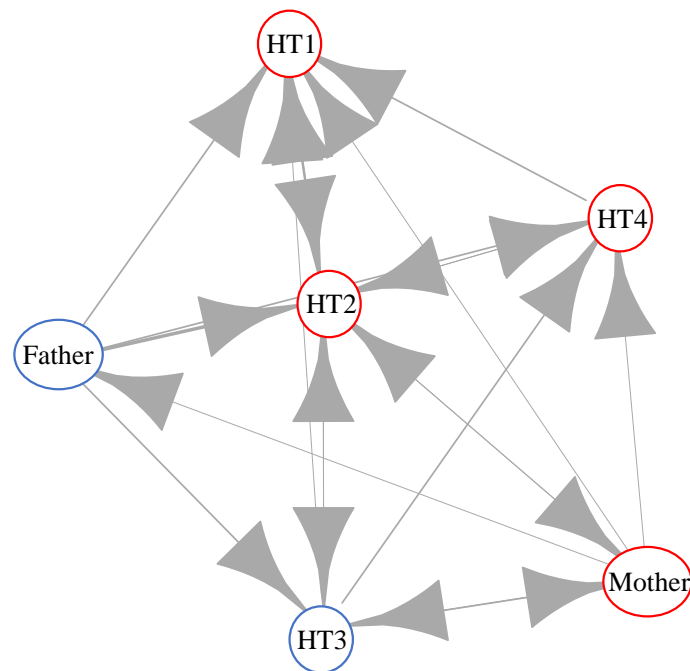
**Figure 15.** Affiliation network on Sophie-Orm family. Red circles indicate females, blue circles indicate males. The lines between individuals show the weight of the interaction calculated by Social Network Analysis (Farine, 2017).



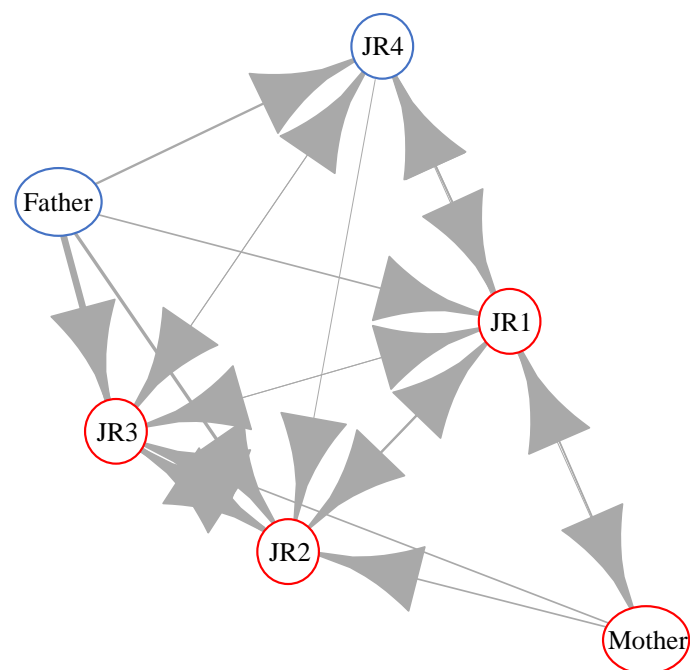
**Figure 16.** Agonistic network on Astrid-Horst family. Red circles indicate females, blue circles indicate males. The lines between individuals show the weight of the interaction calculated by Social Network Analysis (Farine, 2017).



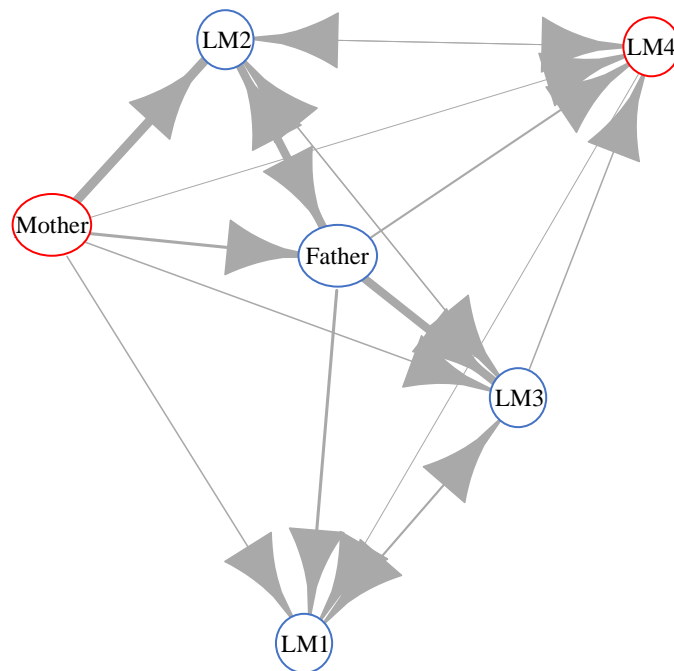
**Figure 17.** Agonistic network on Heidi-Tom family. Red circles indicate females, blue circles indicate males. The lines between individuals show the weight of the interaction calculated by Social Network Analysis (Farine, 2017).



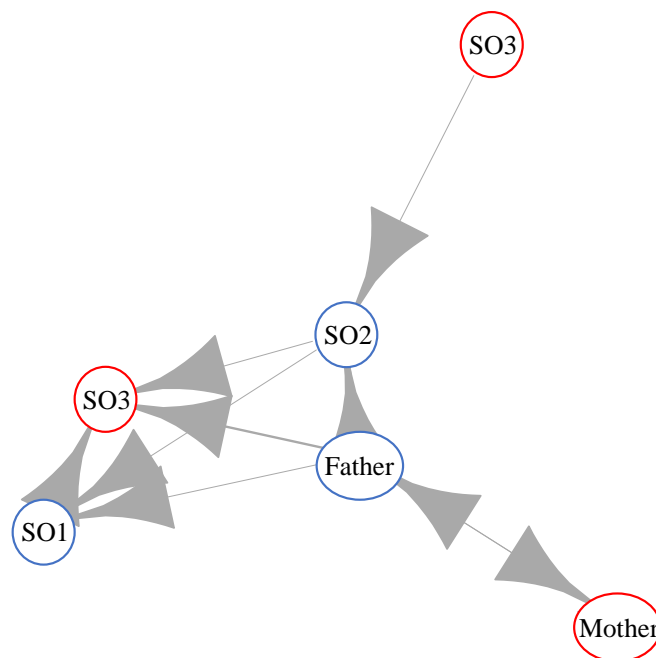
**Figure 17.** Agonistic network on Joey-Rocky family. Red circles indicate females, blue circles indicate males. The lines between individuals show the weight of the interaction calculated by Social Network Analysis (Farine, 2017).



**Figure 18.** Agonistic network on Matte-Lellan family. Red circles indicate females, blue circles indicate males. The lines between individuals show the weight of the interaction calculated by Social Network Analysis (Farine, 2017).



**Figure 19.** Agonistic network on Sophie-Orm family. Red circles indicate females, blue circles indicate males. The lines between individuals show the weight of the interaction calculated by Social Network Analysis (Farine, 2017).



## 11 References

- Ah-King, M. (2013).** On anisogamy and the evolution of “sex roles.” *Trends in Ecology & Evolution*, 28, 1–2. <https://doi.org/10.1016/j.tree.2012.04.004>.
- Ah-King, M., Kvarnemo, C. & Tullberg, B.S. (2005).** The influence of territoriality and mating system on the evolution of male care: a phylogenetic study on fish. *Journal of Evolutionary Biology*, 18: 371–382.
- Albores-Barajas, Y. V., Massa, B., Tagliavia, M., & Soldatini, C. (2015).** Parental care and chick growth rate in the Mediterranean Storm-petrel *Hydrobates pelagicus melitensis*. *Avocetta*, 39(1), 29–35.
- Aureli, F., Preston, S.D. & deWaal, F. B. M. (1999).** Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. *Journal of Comparative Psychology*, 113, 59–65. <https://doi.org/10.1037/0735-7036.113.1.59>
- Barrios-Miller, N. L., & Siefferman, L. (2013).** Evidence that fathers, but not mothers, respond to mate and offspring coloration by favouring high-quality offspring. *Animal Behaviour*, 85(6), 1377–1383. <https://doi.org/10.1016/j.anbehav.2013.03.029>
- Bartoń, K. (2016).** MuMIn: Multi-Model Inference.
- Bates, D. & Sarkar, D. (2007).** lme4: Linear Mixed-Effects Models Using Eigen and S4. R package version 0.9975-12. <http://cran.r-project.org/>.
- Beck, C.W. (1998).** Mode of fertilization and parental care in anurans. *Animal Behaviour*, 55: 439–449.
- Berg, R. (1999).** "Corvus corax" (On-line), Animal Diversity Web. Accessed July 05, 2017 at [http://animaldiversity.org/accounts/Corvus\\_corax/](http://animaldiversity.org/accounts/Corvus_corax/)
- Birkhead, T. R., & Moller, A. P. (1993).** Sexual selection and the temporal separation of reproductive events: sperm storage data from reptiles, birds and mammals. *Biological Journal of the Linnean Society*, 50, 295–31.
- Boarman, W. & Heinrich, B. (1999).** Common raven. In: *The Birds of North America* No. 476 (Ed. by A. Poole & F. Gill). Philadelphia: The Birds of North America, Inc.
- Boncoraglio, G., Martinelli, R., Saino, N. (2008a).** Sex-related asymmetry in competitive ability of sexually monomorphic barn swallow nestlings. *Behavioral Ecology Sociobiology*, 62:729–738
- Boncoraglio, G., Saino, N., Garamszegi, L.Z. (2008b).** Begging and cowbirds: brood parasites make hosts scream louder. *Behavioral Ecology*, 20:215–221

- Braun, A., & Bugnyar, T. (2012).** Social bonds and rank acquisition in raven nonbreeder aggregations. *Animal Behaviour*, 84, 1507–1515.
- Bugnyar, T. (2013).** Social cognition in ravens. *Comparative Cognition & Behavior Reviews*, 8, 1–12. <https://doi.org/10.3819/ccbr.2013.80001>
- Bugnyar, T. & Heinrich, B. (2005).** Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proceedings Royal Society London Series B*, 272, 1641–1646. <https://doi.org/10.1098/rspb.2005.3144>
- Bugnyar, T. & Kotrschal, K. (2002).** Scrounging tactics in free-ranging ravens. *Ethology*, 108, 993–1009 <https://doi.org/10.1046/j.1439-0310.2002.00832.x>
- Buitron, D. (1988).** Female and Male Specialization in Parental Care and Its Consequences in Black-Billed Magpies. *The Condor*, 90, 29–39. <https://doi.org/10.2307/1368429>
- Clayton, N. S., & Krebs, J. R. (1994).** Hippocampal growth and attrition in birds affected by experience. *Proceedings of the National Academy of Sciences of the United States of America*, 91(16), 7410–7414. <https://doi.org/10.1073/pnas.91.16.7410>
- Clutton-Brock, T.H. (1991).** *The Evolution of Parental Care*. Princeton, NJ: Princeton U. Press. pg. 9
- Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1981).** Parental investment in male and female offspring in polygynous mammals. *Nature*, 289.
- Cockburn, A. (2006)** Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society London B Biological Sciences*, 273:1375–1383. <https://doi.org/10.1098/rspb.2005.3458>
- Cotton, P. A., Kacelnik, A., & Wright, J. (1996).** Chick begging as a signal: are nestlings honest? *Behavioral Ecology Behav Ecol*, 7(7).
- Cornioley, T., Jenouvrier S, Borger L., Weimerskirch, H., Ozgul, A. (2017).** Fathers matter: male body mass affects life-history traits in a size-dimorphic seabird. *Proc. R. Soc. B* 284: 20170397. <http://dx.doi.org/10.1098/rspb.2017.0397>
- Creelman, E., & Storey, A. E. (1991).** Sex Differences in Reproductive Behavior of Atlantic Puffins. *Condor*, 93(2), 390–398. <https://doi.org/10.2307/1368955>
- Dickens, M., Berridge, D., & Hartley, I. R. (2008).** Biparental care and offspring begging strategies: hungry nestling blue tits move towards the father. *Animal Behaviour*, 75(1), 167–174. <https://doi.org/10.1016/j.anbehav.2007.04.024>
- Dickens, M., & Hartley, I. R. (2007).** Differences in parental food allocation rules: Evidence for sexual conflict in the blue tit? *Behavioral Ecology*, 18(4), 674–679. <https://doi.org/10.1093/beheco/arm029>

- Farine, D. R. (2017).** A guide to null models for animal social network analysis. *Methods in Ecology and Evolution*. <https://doi.org/10.1111/2041-210X.12772>
- Fischer, B., Taborsky, B., & Kokko, H. (2011).** How to balance the offspring quality-quantity tradeoff when environmental cues are unreliable. *Oikos*, 120(2), 258–270. <https://doi.org/10.1111/j.1600-0706.2010.18642.x>
- Fraser, O. N., & Bugnyar, T. (2010a).** Do ravens show consolation? responses to distressed others. *PLoS ONE*, 5(5). <https://doi.org/10.1371/journal.pone.0010605>
- Fraser, O. N., & Bugnyar, T. (2010b).** The quality of social relationships in ravens. *Animal Behaviour*, 79(4), 927–933. <https://doi.org/10.1016/j.anbehav.2010.01.008>
- Fraser, O. N., & Bugnyar, T. (2011).** Ravens reconcile after aggressive conflicts with valuable partners. *PLoS ONE*, 6(3), 1–5. <https://doi.org/10.1371/journal.pone.0018118>
- Fraser, O. N., & Bugnyar, T. (2012).** Reciprocity of agonistic support in ravens. *Animal Behaviour*, 83(1), 171–177. <https://doi.org/10.1016/j.anbehav.2011.10.023>
- Gill, S. A. (2012).** Strategic use of allopreening in family-living wrens. *Behavioral Ecology and Sociobiology*, 66(5), 757–763. <https://doi.org/10.1007/s00265-012-1323-6>
- Ginther, A. J., & Snowdon, C. T. (2009).** Expectant parents groom adult sons according to previous alloparenting in a biparental cooperatively breeding primate. *Animal Behaviour*, 78(2), 287–297. <https://doi.org/10.1016/j.anbehav.2009.04.020>
- Gladbach, A., Braun, C., Nordt, A., Peter, H.U., & Quillfeldt, P. (2009).** Chick provisioning and nest attendance of male and female Wilson’s storm petrels *Oceanites oceanicus*. *Polar Biol*, 32, 1315–1321. <https://doi.org/10.1007/s00300-009-0628-z>
- Godfray, H. C. J. & Parker, G. A. (1992).** Sibling competition, parent–offspring conflict and clutch size. *Animal Behaviour*, 43, 473–490.
- Gonzalez-Voyer, A., & Kolm, N. (2010).** Parental Care and Investment. *eLS*, 1–7. <https://doi.org/10.1002/9780470015902.a0021907.pub2>
- Gottlander, K. (1987).** Parental feeding behaviour and sibling competition in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica*, 18(4), 269–276.
- Gowaty, P. A. & Droge, D. L. (1991).** Sex ratio conflict and the evolution of sex-biased provisioning in birds. *Proceedings of the 20th International Ornithological Congress*, 932–945.
- Gowaty, P. A., & Hubbell, S. P. (2005).** Chance, time allocation, and the evolution of adaptively flexible sex role behaviour. *Integrative and Comparative Biology*, 45(5), 931–944. <https://doi.org/10.1093/icb/45.5.931>
- Gray, C. M., & Hamer, K. C. (2001).** Food-provisioning behaviour of male and female



- Manx shearwaters, *Puffinus puffinus*. *Animal Behaviour*, 62, 117–121.  
<https://doi.org/10.1006>
- Griggio, M., Morosinotto, C. & Pilastro, A. (2009).** Nestlings' carotenoid feather ornament affects parental allocation strategy and reduces maternal survival. *Journal of Evolutionary Biology*, 22, 2077e2085.
- Güntürkün, O., & Bugnyar, T. (2016).** Cognition without cortex. *Trends in Cognitive Sciences*, 20(4), 291–303.
- Haring, E. (2007).** Phylogeographic patterns in widespread corvid birds, 45, 840–862.  
<https://doi.org/10.1016/j.ympev.2007.06.016>
- Harlow, H. (1958).** The Nature of Love. *American Psychologist*, 13, 573–685.
- Harper, A. B. (1986).** The Evolution of Begging : Sibling Competition and Parent-Offspring Conflict. *The American Naturalist*, 128(1), 99–114.
- Henderson, B. (1975).** Role of the chick's begging behavior in the regulation of parental feeding behavior of *Larus glaucescens*. *Condor*, 77:488–492.
- Hinde, C. A., Johnstone, R. A., & Kilner, R. M. (2010).** Parent-Offspring Conflict and Coadaptation. *Science*, 327(5971), 1373–1376. <https://doi.org/10.1126/science.1186056>
- Houston, A.I. & Davies, N.B. (1985).** The evolution of cooperation and life history in the dunnock *Prunella modularis*. *Behavioural Ecology* (eds R.M. Sibyl & R.H. Smith), pp. 471–487. Blackwell Scientific. Oxford.
- Johnstone, R. A., & Hinde, C. A. (2006).** Negotiation over offspring care - How should parents respond to each other's efforts? *Behavioral Ecology*, 17(5), 818–827.  
<https://doi.org/10.1093/beheco/arl009>
- Karasov, W. H. & Wright, J. (2002).** Nestling digestive physiology and begging. In: The Evolution of Begging. *Competition, Cooperation and Communication* (Ed. by J. Wright & M. L. Leonard), pp. 199–220. Dordrecht: Kluwer Academic.
- Keverne, E. B., Martenz, N. D. & Tuite, B. (1989).** Betaendorphin concentration in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology* 14, 155–161. [https://doi.org/10.1016/0306-4530\(89\)90065-6](https://doi.org/10.1016/0306-4530(89)90065-6)
- Kijne, M., & Kotrschal, K. (2002).** Neophobia affects choice of food-item size in group-foraging common ravens (*Corvus corax*). *Acta Ethologica*.  
<https://doi.org/10.1007/s10211-002-0061-6>
- Kilner, R.M. (2002a).** Parent-offspring and sibling conflict. *Encyclopedia of Life Sciences*.
- Kilner, R. M. (2002b).** Sex differences in canary (*Serinus canaria*) provisioning rules. *Behav Ecol Sociobiol*, 52, 400–407. <https://doi.org/10.1007/s00265-002-0533-8>

- Kilner, R., & Johnstone, R. A. (1997).** Begging the question: Are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution*.  
[https://doi.org/10.1016/S0169-5347\(96\)10061-6](https://doi.org/10.1016/S0169-5347(96)10061-6)
- Kilner, R. M., Noble, D. G., & Davies, N. B. (1999).** Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature*, 397(25).
- Krebs, E. A., Cunningham, R. B. & Donnelly, C. F. (1999).** Complex patterns of food allocation in asynchronously hatching broods of crimson rosellas. *Animal Behaviour*, 57, 753e763.
- Kokko, H., & Jennions, M. D. (2008).** Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, 21(4), 919–948. <https://doi.org/10.1111/j.1420-9101.2008.01540.x>
- Kolliker, M., Richner, H., Werner, I., & Heeb, P. (1998).** Begging signals and biparental care: nestling choice between parental feeding locations. *Animal Behaviour*, 55, 215–22. <https://doi.org/10.1006/anbe.1997.0571>
- Kuijper, B., & Johnstone, R. A. (2017).** How Sex-Biased Dispersal Affects Sexual Conflict over Care. *The American Naturalist*, 189(5), 000–000. <https://doi.org/10.1086/691330>
- Kutsukake, N., & Clutton-Brock, T. H. (2006).** Social functions of allogrooming in cooperatively breeding meerkats. *Animal Behaviour*, 72(5), 1059–1068. <https://doi.org/10.1016/j.anbehav.2006.02.016>
- Kvarnemo, C. (2006).** Evolution and maintenance of male care: is increased paternity a neglected benefit of care? *Behavioral Ecology*. 17: 144–148.
- Labocha, M. K., & Hayes, J. P. (2012).** Morphometric indices of body condition in birds: A review. *Journal of Ornithology*, 153(1), 1–22. <https://doi.org/10.1007/s10336-011-0706-1>
- Lack, D. (1968).** Ecological adaptations for breeding in birds. Methuen & Co., London.
- Lazaro-Perea, C., De Arruda, M. F., & Snowdon, C. T. (2004).** Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour*, 67(4), 627–636. <https://doi.org/10.1016/j.anbehav.2003.06.004>
- Leonard, M. & Horn, A. (1996).** Provisioning rules in tree swallows. *Behavioral Ecology and Sociobiology*, 38, 341–347.
- Leonard, M. L., Teather, K. L., Horn, A. G., Koenig, W. D. & Dickinson, J. L. (1994).** Provisioning in western bluebirds is not related to offspring sex. *Behavioral Ecology*, 5, 455e559.
- Lessells, C. (1998).** A theoretical framework for sex-biased parental care. *Animal Behaviour*,

- 56(2), 395–407. <https://doi.org/10.1006/anbe.1998.0764>
- Lessells, C. M. (2002a).** Parentally biased favouritism: why should parents specialize in caring for different offspring? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 357(1419), 381–403.  
<https://doi.org/10.1098/rstb.2001.0928>
- Lessells, C.M. (2002b).** Parental investment in relation to offspring sex. In: Wright J, Leonard ML (eds) *The evolution of begging: competition, cooperation and communication*. Kluwer Academic, Dordrecht, pp 65–85
- Levréro, F., Blanc, A., & Mathevon, N. (2012).** Response to begging calls by Zebra Finch parents: “First come, first served” rule may overcome a parental preference between chicks. *Comptes Rendus - Biologies*, 335(2), 135–141.  
<https://doi.org/10.1016/j.crvi.2011.11.007>
- Ligon, R. a., & Hill, G. E. (2010a).** Sex-biased parental investment is correlated with mate ornamentation in eastern bluebirds. *Animal Behaviour*, 79(3), 727–734.  
<https://doi.org/10.1016/j.anbehav.2009.12.028>
- Ligon, R. A. & Hill, G. E. (2010b).** Feeding decisions of eastern bluebirds are situationally influenced by fledgling plumage color. *Behavioral Ecology*, 21, 456e464.
- Liu, D., Diorio, J., Day, J. C., Francis, D. D., & Meaney, M. J. (2000).** Maternal care, hippocampal synaptogenesis and cognitive development in rats. *Nature Neuroscience*, 3(8), 799–806. <https://doi.org/10.1038/77702>
- Loretto, M. C., Fraser, O. N., & Bugnyar, T. (2012).** Ontogeny of Social Relations and Coalition Formation in Common Ravens (*Corvus corax*). *International Journal of Comparative Psychology*, 25(3), 180–194. <https://doi.org/10.5811/westjem.2011.5.6700>
- Lotem, A. (1998).** Differences in begging behaviour between barn swallow, *Hirundo rustica*, nestlings. *Animal Behaviour*, 55, 809e 818.
- Maestripieri, D. (1998).** Social and Demographic Influences on Mothering Style in Pigtail Macaques. *Ethology*, 104(5), 379–385.
- Magrath, R.D. (1991).** Nestling Weight and Juvenile Survival in the Blackbird , *Turdus merula*. *Journal of Animal Ecology* , Vol . 60 , No . 1 ( Feb ., 1991 ), pp . 335-351.
- Massen, J. J. M., Pašukonis, A., Schmidt, J., & Bugnyar, T. (2014).** Ravens notice dominance reversals among conspecifics within and outside their social group. *Nature Communications*, 5, 3679. <https://doi.org/10.1038/ncomms4679>
- Mainwaring, M. C., Lucy, D., & Hartley, I. R. (2011).** Parentally biased favouritism in relation to offspring sex in zebra finches. *Behavioral Ecology and Sociobiology*, 65(12),

- 2261–2268. <https://doi.org/10.1007/s00265-011-1235-x>
- Michler, S. P. M., Bleeker, M., van der Velde, M., Both, C., Komdeur, J. & Tinbergen, J. M. (2010).** Parental provisioning in relation to offspring sex and sex ratio in the great tit (*Parus major*). *Behaviour*, 147, 1355–1378.
- Missakian, E. A. (1974).** Mother-Offspring Grooming Relations in Rhesus Monkeys. *Archives of Sexual Behavior*, 3(2).
- Newton, I. (1978).** Feeding and development of Sparrowhawk *Accipiter nisus* nestlings. *Journal of Zoology*, 184: 465–487. <https://doi.org/10.1111/j.1469-7998.1978.tb03302>.
- Parker, G. A. (1985).** Models of parent–offspring conflict. V. Effects of the behaviour of the two parents. *Animal Behaviour*, 33, 519–533.
- Parker, K. J., & Maestripieri, D. (2011).** Identifying key features of early stressful experiences that produce stress vulnerability and resilience in primates. *Neuroscience and Biobehavioral Reviews*, 35(7), 1466–1483.  
<https://doi.org/10.1016/j.neubiorev.2010.09.003>
- R Core Team. (2014).** R: A language and environment for statistical computing.  
<http://www.R-project.org/>.
- Reynolds, J.D. & Jones, J.C. (1999).** Female preference for preferred males is reversed under low oxygen conditions in the common goby (*Pomatoschistus microps*). *Behavioral Ecology*. 10: 149–154.
- Reynolds J.D., Goodwin N.B. & Freckleton R.P. (2002).** Evolutionary transitions in parental care and live bearing in vertebrates. *Philosophical Transactions of the Royal Society B* 357: 269–281.
- Slagsvold, T., Amundsen, T. & Dale, S. (1994).** Selection by sexual conflict for evenly spaced offspring in blue tits. *Nature*, 370, 136–138.
- Sasvari, L. (1990).** Feeding response of mate and windowed bid parent to fledging: an experimental study. *Ornis Scandinavica*, 21, 287–292.
- Shaw, P. (1985).** Brood reduction in the Blue-eyed Shag (*Phalacrocorax atriceps*). *Ibis*. 127: 476–494
- Sherman, P. W. (2010).** *Journal of Zoology*, 280, 103–155. <https://doi.org/10.1111/j.1469-7998.2009.00671.x>
- Stamps, J. A. (1990).** When should avian parents differentially provision sons and daughters? *American Naturalist*, 135, 671–685.
- Stamps, J., Clark, A. B., Arrowood, P. & Kus, B. (1985).** Parent-offspring conflict in budgerigars. *Behaviour*, 94, 1–40.

- Stamps, J. A., Clark, A., Kus, B. & Arrowood, P. (1987).** The effects of parent and offspring gender on food allocation in budgerigars. *Behaviour*, 101, 177e199.
- Stone Sade, D. (1963).** Some Aspects of Parent-off spring and Sibling Relations in a Group of Rhesus Monkeys. *American Journal of Physical Anthropology*, 23:1-18.
- Tanner, M., Kolliker, M. & Richner, H. (2007).** Parental influence on sibling rivalry in great tit, *Parus major*, nests. *Animal Behaviour*, 74, 977e983.
- Teather, K. L. (1992).** An experimental study of competition between male and female nestlings of the red-winged blackbird. *Behavioral Ecology and Sociobiology*, 31,81e87.
- Thogerson, C. M., Brady, C. M., Howard, R. D., Mason, G. J., Pajor, E. A., Vicino, G. A., & Garner, J. P. (2013).** Winning the Genetic Lottery: Biasing Birth Sex Ratio Results in More Grandchildren. *PLoS ONE*, 8(7).  
<https://doi.org/10.1371/journal.pone.0067867>
- Trivers, R.L. (1972).** Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man*, 1871-1971 (pp. 136–179). Chicago, IL: Aldine. ISBN 0-435-62157-2.
- Trivers, R.L., Willard, D.E. (1973).** Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179:90–92.
- Trivers, R. L. (1974).** Parent-offspring conflict. In: *Readings in Sociobiology* (Ed. by T. H. Clutton-Brock & P. H. Harvey), pp. 233e257. Reading: W. H. Freeman.
- Weimerskirch, H., Barbraud, C., & Lys, P. (2000).** Sex Differences in Parental Investment and Chick Growth in Wandering Albatrosses: Fitness Consequences. *Ecology*, 81(2), 309–318.
- Zeh, D.W. & Smith, R.L. (1985).** Paternal investment by terrestrial arthropods. *American Zoologist*. 25: 785–805.