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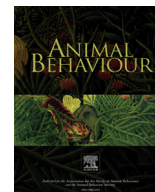
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Sex-specific parental care during postfledging in common ravens

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Parents face a trade-off when allocating limited resources to reproduction and self-maintenance, and this can result in differential investment in individual offspring when rearing multiple offspring simultaneously. In birds with biparental care, it is not well understood how each parent allocates its resources to different chicks of the same brood. Theory suggests that parental investment depends on offspring quality and brood size, but empirical quantification of parent–offspring interactions during the post-fledging stage is often difficult. We worked with captive common ravens, *Corvus corax*, a slightly dimorphic songbird with extended periods of biparental care, to investigate the effects of offspring sex, body mass, brood age and brood size on the feeding probability by both parents. We further investigated the influence of the same factors on offspring begging behaviour and affiliative interactions between parent and offspring. Mothers were more likely to feed and affiliate with their offspring than fathers. Fathers were more likely to feed and affiliate with sons than daughters, whereas mothers showed no preference. When more than one son was present, fathers were more likely to feed and affiliate with heavier sons than light sons. Brood size increased the begging probability of chicks, but decreased their probability of being fed. Our results suggest that biparental care in ravens is skewed towards the mother and that paternal care is selective. Selective paternal investment in the heaviest son may be adaptive in a system where heaviest males better compete for resources during dispersal.

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Parental care requires resources that cannot be invested in an individual's own growth, survival and future reproduction. Therefore, parents face a trade-off when allocating limited resources to their offspring (Trivers, 1972). In long-lived species, where parents attempt multiple breeding events throughout their lives, parents may thus reduce offspring care if it threatens their own survival and future reproductive attempts (Sterns, 1992). This can lead to a conflict between parents and their offspring, where offspring demand more resources than parents can provide (Trivers, 1974). When rearing multiple offspring simultaneously, parents may therefore selectively invest in some of their offspring and less in others (Lessells, 2002b). How resources are allocated to different offspring will likely depend on offspring traits and, in species with biparental care, may vary between fathers and mothers (Lessells, 1998; Ratnieks, 1996; Winkler, 1987). Differential parental

investment has been studied in various species (Lavery & Keenleyside, 1990; Zeveloff & Boyce, 1980) but particularly in birds that show more biparental care than other species (Cockburn, 2006). While it has been shown that factors such as brood (or clutch) size can affect parental investment (Coleman et al., 1985; Godfray & Parker, 1992; Lack, 1947; Lazarus & Inglis, 1986), less is known about sex-specific parental investment in birds with biparental care and how it relates to parent–offspring interactions and offspring traits.

In many bird species, natural selection maximizes the number of offspring through increased brood size, but large broods limit the equity of care provisioning (Lack, 1947; Nur, 1984). When the number of offspring increases, competition between chicks increases. Hierarchies among siblings are often defined by individuals' body mass and larger chicks may use higher begging intensity to receive more food from their parents (Cotton et al., 1996). Indeed, when multiple offspring are present, allocation of parental care (e.g. feeding and/or affiliative behaviours) can vary with offspring quality such as begging intensity or body mass

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(Budden & Wright, 2001a; Gottlander, 1987). There is considerable evidence that chicks' begging intensity influences their probability of getting fed (Budden & Wright, 2001b; Cotton et al., 1996; Kilner et al., 1999; Kilner & Johnstone, 1997; Kölliker et al., 1998) and it is generally assumed that hierarchies among siblings are mediated by selective feeding through the parents (Gottlander, 1987).

In species with biparental care, provisioning by both parents is often necessary to guarantee successful offspring rearing, but males and females may differ in their investment (Barrios-Miller & Siefferman, 2013; Kilner, 2002; Lessells, 1998; Michler, 2010). In such systems, females are often found to invest more in their offspring than males (e.g. Mediterranean storm-petrel, *Hydrobates pelagicus melitensis*, Albores-Barajas et al., 2015; great tit, *Parus major*, Kölliker et al., 1998). Female-biased care is thought to have evolved in response to the cost of egg production compared to sperm production, females standing more to lose than males if they do not invest in offspring survival (Lessells, 2002a; Trivers, 1972). Alternatively, male care could be less favoured because of the uncertainty of paternity (Smith, 1977; Trivers, 1972; Xia, 1992). Unlike females, males can never be certain of paternity and hence, for fathers, the risk of caring for someone else's offspring increases the cost of caring (Ah-King, 2013; Kvarnemo, 2005). Consequently, mothers are more likely to invest in all their offspring, whereas fathers could benefit from allocating an overall smaller amount of care in a few selected offspring. On top of sex effects on the patterns of care allocation, males and females are likely to change their respective allocations over time, following offspring development.

As chicks get older and approach nutritional independence, parental care gradually decreases (Bye, 1990; Davis et al., 2019). This might explain why most studies on the influence of chick quality on food provisioning have been carried out at the nestling stage, and, in general, studies on parental investment in the post-fledging period are rare (but see Slagsvold et al., 1994; Wheelwright et al., 2003). This is also likely to be due to difficulties of monitoring such fine-grain social interactions in mobile animals, in particular in free-flying birds (Tarwater & Brawn, 2010; Wheelwright et al., 2003). In species with sexual size dimorphism, however, differences in care allocation between offspring sexes become most obvious during the postfledging stage (Barrios-Miller & Siefferman, 2013).

Sons and daughters may differ in their need for parental care due to asymmetries between the sexes in growth, maturation, competition and survival (Droge et al., 1991; Lessells, 1998; Stamps, 1990) and each parent may follow a different investment strategy depending on the offspring's sex (Krist, 2006; Lessells, 2002b). However, it is not always clear how the parents are able to discriminate the sex of individual offspring before these attain adult plumage (Stamps et al., 1987). In species with sexual size dimorphism, the size of chicks may be used as a cue to identify the offspring with the highest need (larger offspring require more energy) and indirectly to select the larger sex (Stamps, 1990). In systems with biparental care and male-biased size dimorphism, fathers tend to favour larger offspring while mothers are less likely to discriminate between offspring (Budden & Beissinger, 2009; Ryser et al., 2016; Slagsvold, 1997). In doing so, fathers are likely to select male offspring with the highest chances of survival (Cornioley et al., 2017) and of finding a mate (Jones & Ratterman, 2009). The latter applies in particular to systems where males compete for breeding opportunities and females select males based on qualities such as body size or plumage (Clutton-Brock, 1991). To produce at least one competitive son, parental investment in male offspring may therefore be more selective than in female offspring

and fathers may invest their limited care in the single most promising son.

Among birds, common ravens, *Corvus corax*, are good candidates to study sex-specific parental care at different stages of offspring development. They are songbirds with biparental care, which display slight sexual size dimorphism (i.e. males are slightly larger than females; Boarman & Heinrich, 1999; Ratcliffe, 1997). Ravens form long-term monogamous pair bonds and breeding pairs defend a large territory. Raven parents care for their offspring for extended periods after fledging, and even after offspring become nutritionally independent (Boarman & Heinrich, 1999). In the first months after fledging, juveniles interact almost exclusively with their parents and siblings but after about 10 weeks, start exploring outside the family territory (Ratcliffe, 1997). Once they have dispersed from their family, juvenile ravens join nonbreeder groups where they are exposed to strong competition at feeding sites (Braun & Bugnyar, 2012; Bugnyar et al., 2007). Access to food or reproduction is regulated through dominance relationships, with the heaviest males getting facilitated access to resources, breeding partners and territories (Boarman & Heinrich, 1999; Stöwe et al., 2006). Hence, the quality of parental care received at an early age is likely to affect juveniles' future fitness (e.g. through body mass), with a stronger effect for males than females. While previous studies investigated the early development of hand-raised ravens on social relations (Boucherie et al., 2019; Loretto et al., 2012), less is known about the parental care and development of young ravens in family groups.

In this study, we investigated sex-specific interactions between parents and their offspring in eight captive raven family groups with experimentally manipulated brood sizes (i.e. two or four chicks), during the postfledging period. We analysed the effect of offspring sex, body mass, brood age, brood size and parent sex on patterns of feeding, begging and affiliative interactions. We expected that (1) mothers would show more parental care (i.e. feeding and affiliation) than fathers; and if true, that (2) chicks would beg more to their mother than father; (3) mothers would equally care for all chicks, while fathers would be more selective towards heavier offspring, i.e. their sons; and finally, that (4) parental care per chick would decrease with increasing brood size and age.

METHODS

Study Sites and Animals

The study was conducted from May to July in 2016 and 2018. We collected data at the Haidlhof research station in Bad Vöslau (47°58'07.6"N, 16°08'34.9"E) and the Konrad Lorenz research station in Grünau (47°48'27.4"N, 13°56'52.4"E), Austria. All studied families were housed in separate aviaries of similar size (50–80 m², 5–7 m high). All aviaries were located outdoors and contained trees, dead trunks, rocks and shallow pools for bathing. Food and water were provided two to three times a day in both years, where food included a mix of meat, milk products, vegetables and fruits. Owing to this feeding schedule and because ravens cache food, food availability should not have limited parental care. All ravens were marked with colour rings for individual identification and a blood sample from the brachial vein was collected for molecular determination of the sex (Fridolfsson and Ellegren, 1999).

We collected data from six different raven pairs and their chicks. Two of those pairs were observed in 2016 and 2018, forming a different family each year with their respective yearly chicks. In

2018, we reduced the number of eggs to test for the effect of smaller brood size on parent–offspring interactions (see below). We therefore worked with a total of eight families and 26 raven chicks: in 2016, five families with four chicks, totalling 20 chicks (11 females and nine males); in 2018, three families with two chicks, totalling six chicks (three females and three males). In 2016, the chicks' sex ratios (male–female) were 3–1 (one family), 2–2 (two families) and 1–3 (two families); in 2018, the sex ratios were 1–1 in all three families. Details of family compositions are provided in [Appendix Table A1](#).

For the first few years of their lives, all parent ravens were kept in nonbreeder groups of 8–12 individuals. When they became sexually mature, they freely chose a partner from these groups. The newly formed pairs were then moved to separate aviaries where they were allowed to breed. Pairs start breeding and laying eggs between mid-February and late March, and females incubate for approximately 22 days. Eggs usually hatch on consecutive days; we therefore used the median hatch date to calculate the age of all chicks. Hence, age was the same for all chicks of the same brood; we called this 'brood age' and only used it to test for age-dependent parental care over time, but not between chicks (see analysis below). Chicks fledged after a mean nestling period of 37 days ($SE \pm 0.66$ days). In both years, four to six eggs were laid per nest, of which only four hatched in all 2016 families, and only two were kept in 2018 families (after brood size reduction). Note that the brood size reduction in 2018 was performed after eggs had hatched, and hatchlings removed from their family were hand-raised. In both years, chicks stayed with their parents for a mean period of 73 days ($SE \pm 0.69$ days, until dispersal age) after fledging, until mid-July, when they were transferred to captive nonbreeder groups for an additional 8 weeks, before being released into the wild. Note that this timeline corresponds to the temporal dynamic of chicks' development and dispersal under natural conditions ([Webb et al., 2009](#)).

All chicks were captured and fitted with coloured leg rings in week 6 posthatch when the birds started fledging, and before the observations started. During ringing, all chicks were also weighed, and blood samples collected for molecular sexing.

Ethical Note

All necessary permits to breed ravens in captivity, blood-sample and tag ravens, and study them in free-flight were granted by the Austrian Ministry for Science (permit numbers BMWF-66.006/0009-II/3b/2012 and BMBWF-66.006/0015-V/3b/2018) and the Bezirkshauptmannschaft Gmunden (BHGMM-2018-87893/10-BUT).

Behavioural Data Collection

At both research stations, captive ravens were habituated to visitors and close observations by humans, allowing us to record behaviours with a handheld video camera (Panasonic HC-V808 with 24x optical zoom). To minimize disturbance, observers limited their movements (e.g. no walking, no arm–leg swings) and did not appear to have any effect on the ravens during observations. All observations were conducted between fledging (ca. 37 days old) and dispersal age (ca. 110 days old).

Owing to a switch in the routine observational protocol used to follow all our study birds in our research stations, data were collected using two different methods: ad libitum sampling in 2016 and focal observations in 2018. We switched to a different method in the second year as these data were also used for another study. In both methods, we recorded the behaviours of interest (see below) occurring between a chick and its parents from the chick's

perspective. During ad libitum sampling, we filmed each raven family for 30 min twice a day, in the morning and afternoon. All chicks were therefore observed simultaneously in each session and interactions between chicks and their parents recorded ad libitum. During focal sampling, we filmed each chick (i.e. focal individual) individually for 5 min twice per day, in the morning and afternoon. All chicks were observed one after the other in random order in each focal observation session, and all interactions occurring between the focal chick and its parents recorded. The difference in duration of observation for each method was accounted for in our statistical models (see below). We collected between 24 and 33 ad libitum observations per chick in 2016 (12 h–16 h 30 min per chick) and between 86 and 92 focal observations per chick in 2018 (7 h 10 min–7 h 40 min per chick). More details on sample sizes are provided in [Appendix Table A1](#).

Behaviour Ethogram

Video recordings were scored using CyberTracker in 2016 (CyberTracker, <https://www.cybertracker.org>) and Loopy behavioural coding tool in 2018 (Loopy Loopbio, <http://loopbio.com/loopy/>) to record the following behaviours ([Appendix Table A2](#)): (1) feeding from parents to offspring, defined by one individual directly transferring food from its beak to another individual's beak; (2) begging from offspring to parents, defined by a combination of auditory (short 'chii' calls) and visual (flapping of wings) signals directed from the sender towards the receiver; and (3) affiliative behaviour from parents to offspring, which included touching (e.g. with beak, for less than 2 s), allopreening (touching/cleaning feathers with beak, for longer than 2 s) and contact sitting (within reaching distance). During each observation session, we separately recorded behaviours occurring between a chick and its father (chick–father dyad) and between a chick and its mother (chick–mother dyad). We then summarized each behaviour per session and dyad. In the statistical models, we accounted for the dependency of chick–father and chick–mother dyads collected in the same session (see below).

Statistical Analysis

Offspring sex and brood size

We first investigated how chick sex, brood age, brood size and parent sex affected parent–offspring interactions: feeding and affiliation (from parents to chicks) and begging (from chicks to parents). To do so, we ran three generalized mixed-effects models (GLMM) with a binomial error distribution and a logit link function in R ([R Core Team., 2013](#)) library lme4 ([Bates et al., 2015](#)). Initially, we used behaviour counts per dyad and session for our three response variables, using a hurdle model to account for zero inflation (first step binomial, second step Poisson error distribution). However, the Poisson part did not return reliable model convergence because most behaviours did not occur more than once per session (see histograms [Appendix Fig. A1](#)). We thus decided to dichotomize the response variables (i.e. the behaviour occurred at least once per session, or not) and fitted our models using a binomial error distribution. In all three models, we included an interaction effect between parent sex and offspring sex to account for sex-specific parental investment in sons and daughters. To control for repeated individual sampling and repeated sampling of the same family across years, we used chick identity nested in family identity and year as random terms. To control for the occurrence of two dyads per session (i.e. chick–father and chick–mother), we used session identity as a random term and nested in year. By accounting for the year effect, we also controlled for potential effects caused by the two different observation

methods (2016 = ad libitum, 2018 = focal). In addition, to control for different observation times in 2016 and 2018 we included observation time per dyad and session (30 min or 5 min) as an offset in all models (McCullagh & Nelder, 1989).

Offspring body mass

We then investigated the effect of the interaction between chicks' body mass and sex on parent–offspring interactions (feeding, affiliation and begging). To do so, we had to work with a reduced data set comprising only families with brood size of four chicks (2016 data), i.e. composed of multiple chicks of the same sex. In four-chick families, parents could decide to invest differently in chicks of the same sex, depending on their weight (e.g. invest more in heavy sons). This trade-off could not be observed in two-chick families (i.e. all composed of one son and one daughter). In addition, because offspring sex and body mass were highly correlated (i.e. collinear), we ran separate models for daughters and sons.

As a result, we ran six binomial GLMMs (three for each chick sex) to test for the effects of offspring body mass, brood age and parent sex on the three response variables (feeding, affiliation and begging). Brood age was again included in the model because it is an important covariate that explains a large part of the variance (i.e. reducing the error term). Parent sex was again included to test the interaction between parent sex and chick body mass. Here, we only included chick identity nested in family identity and session identity as random terms. We removed the year effect because we only used data from 2016.

For all nine models, we used the hypothesis testing approach with significance (i.e. *P* values) based on Wald statistics (Bates et al., 2015). We standardized all continuous explanatory variables by subtracting their mean and dividing by their standard deviation. To ensure that predictors were not correlated with each other, we calculated variance inflation factors for model coefficients (Belsley et al., 2005).

RESULTS

Offspring Sex and Brood Size

Mothers invested significantly more in their offspring than fathers did irrespective of the offspring's sex (feeding and affiliation; Table 1). Following this, chicks begged significantly more towards their mother than their father (Table 1). Overall, sons received significantly more food than daughters (Table 1). Fathers fed their sons significantly more than their daughters (Table 1, Fig. 1a). Accordingly, daughters begged significantly less to their father than sons (Table 1). In four-chick families, chicks were fed (Fig. 1b) and received affiliative behaviour significantly less than in two-chick families (Table 1). The probability of begging, being fed and receiving affiliative behaviour from their parents decreased significantly with brood age (Table 1).

Table 1
Effect of chick sex, brood age, brood size and parent sex on feeding, begging and affiliation

Variable	Feeding Estimate	SE	<i>P</i>	Begging Estimate	SE	<i>P</i>	Affiliation Estimate	SE	<i>P</i>
Intercept	−7.59	0.45	<0.001	−5.62	1.25	<0.001	−6.42	0.28	<0.001
Brood age	−0.77	0.14	<0.001	−0.59	0.11	<0.001	−0.41	0.11	<0.001
Brood size	−0.71	0.21	<0.001	1.36	0.70	0.053	−0.48	0.12	<0.001
Sex:Male	1.50	0.45	<0.001	0.53	0.33	0.109	0.82	0.33	0.014
Parent:Mother	1.27	0.37	<0.001	0.57	0.20	0.004	1.09	0.30	<0.001
Sex:Male*Parent:Mother	−1.57	0.46	<0.001	−0.91	0.28	0.001	−0.76	0.39	0.053

Feeding (parent to chick), begging (chick to parent) and affiliation (parent to chick) interactions between parents and chicks in ravens. Significance (*P*) is based on Wald statistics. Broods contained two (*N* = 3) or four chicks (*N* = 5).

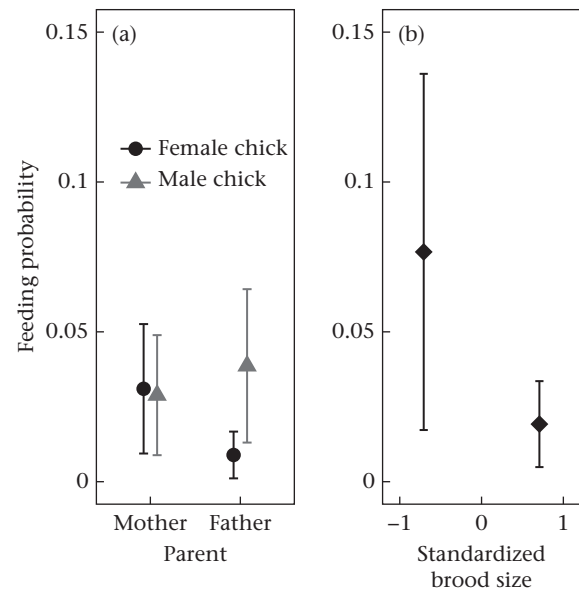


Figure 1. Feeding probabilities of raven parents towards female and male chicks depending on (a) parent sex and (b) brood size. Probabilities and 95% confidence intervals are predicted by a GLMM with binomial error distribution. In (b) points capture the change in feeding probability for a 1 SD increase in brood size.

Offspring Body Mass

At the time of dispersal, the mean body mass of male chicks (1200 ± 3.19 g) was higher than that of female chicks (1050 ± 2.7 g). Fathers invested significantly more in heavy sons than light sons whereas mothers invested in all sons equally (feeding and affiliation; Table 2, Fig. 2). Investment in daughters did not depend on body mass (Table 2).

DISCUSSION

We compared maternal and paternal investment and parent–offspring interactions postfledging in eight families of captive ravens of different sizes (two and four chicks). We found that, overall, mothers invested more in and interacted more with their chicks than fathers did (feeding and affiliation). In addition, mothers invested similarly in all chicks irrespective of chicks' sex or body mass. Fathers, in contrast, invested more and interacted more with their sons than daughters, and if they had more than one son, they did so with the heaviest son. Accordingly, sons received significantly more food than daughters, and chicks begged more towards the parent from whom they got more food. Increased brood size decreased parents' feeding and affiliation probability. Here, we discuss possible causes of female-biased parental care in

Table 2

Effects of chick body mass, brood age and parent sex on feeding, begging and affiliation between parents and their female or male chicks, respectively

Variable		Feeding Estimate	SE	P	Begging Estimate	SE	P	Affiliation Estimate	SE	P
Male chicks	Intercept	−3.46	0.43	<0.001	−2.33	0.38	<0.001	−2.69	0.34	<0.001
	Brood age	−0.68	0.26	0.009	−0.80	0.23	0.000	−0.21	0.17	0.227
	Mass	0.78	0.41	0.056	0.79	0.37	0.033	0.62	0.28	0.024
	ParentMother	0.03	0.41	0.948	0.04	0.27	0.874	0.52	0.33	0.110
	Mass*ParentMother	−0.88	0.44	0.047	−0.65	0.29	0.023	−0.89	0.31	0.004
Female chicks	Intercept	−8.39	1.39	<0.001	−2.18	0.31	<0.001	−4.12	0.40	<0.001
	Brood age	−0.57	1.50	0.703	−0.71	0.17	<0.001	−0.79	0.24	0.001
	Mass	−0.09	0.88	0.915	−0.33	0.25	0.191	−0.21	0.36	0.560
	ParentMother	0.71	0.55	0.194	0.12	0.24	0.628	1.47	0.41	<0.001
	Mass*ParentMother	−0.36	0.58	0.534	−0.17	0.23	0.454	0.24	0.39	0.536

Feeding (parent to chick), begging (chick to parent) and affiliation (parent to chick) interactions between parents and chicks in ravens. Significance (*P*) is based on Wald statistics. Only broods containing four chicks were used (*N* = 5).

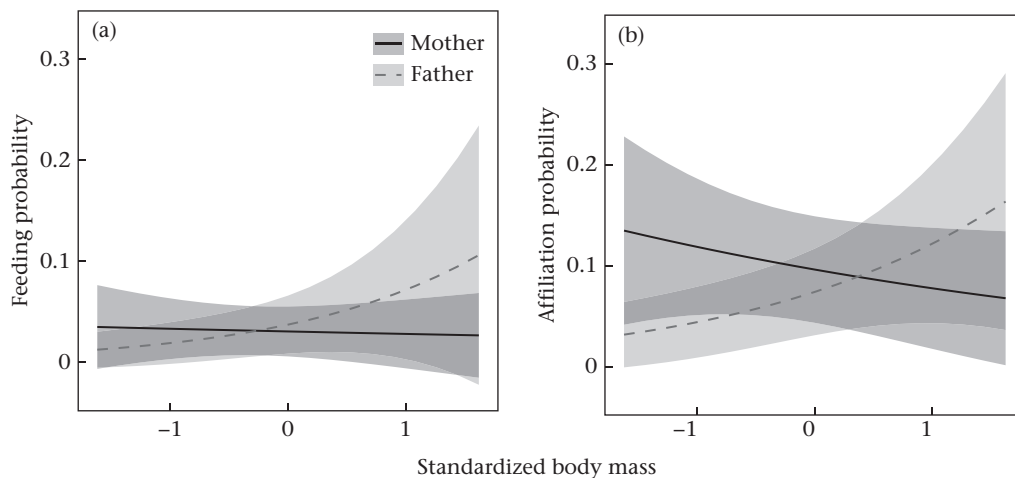


Figure 2. (a) Feeding and (b) affiliation probabilities of raven parents towards male chicks depending on chick body mass. Probabilities and 95% confidence intervals are predicted by a GLMM with binomial error distribution. Slopes capture the change in behaviour probabilities for a 1 SD increase in body mass.

ravens and the selective care of raven fathers based on offspring sex and quality.

The observed female-biased parental care concurs with [Trivers's \(1972\)](#) hypothesis, which suggests that females should invest more in parental care than fathers due to the high energetic demands of producing eggs. In ravens, as in many other avian species, 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 ca. 50% of nestling care ([Lessells, 2002a](#); [Trivers, 1972](#)). When conditions allow, it is therefore conceivable that mothers invest equally in all offspring postfledging. This pattern is common in birds with biparental care such as blue tits, *Cyanistes caeruleus* ([Dickens & Hartley, 2007](#); [Slagsvold et al., 1994](#)) and black redstarts *Phoenicurus ochruros* ([Draganoiu et al., 2005](#)). Raven fathers, on the other hand, invested more in their sons than daughters. Selective investment in sons could be adaptive for raven fathers in a system where males compete for resources during dispersal, i.e. in nonbreeder groups. Ravens face a challenging social environment in nonbreeder groups, which are characterized by fission–fusion dynamics ([Braun & Bugnyar, 2012](#); [Loretto et al., 2017](#)) and high competition for access to food and breeding territories ([Heinrich, 1988](#); [Webb et al., 2011, 2012](#)). Male and female ravens differ in how they deal with these challenges, young males engaging in agonistic conflicts more often than females; they do so irrespective of group composition in nonbreeder groups in captivity ([Fraser and](#)

[Bugnyar, 2012](#); [Loretto et al., 2012](#); [Boucherie et al., 2020](#)) and especially in the first few months after joining nonbreeder groups under field conditions ([Boucherie et al., 2021](#)). We therefore speculate that the selective paternal care towards sons may increase their competitive abilities in nonbreeder groups.

When more than one male offspring was present in the family, fathers invested more in the heavier sons. Selective investment in the heaviest offspring is observed in several dimorphic species, for example blue tits ([Garcia-Navas et al., 2014](#)). In the size-dimorphic wandering albatross, *Diomedea exulans*, selective investment in the heaviest chicks increased their survival as juveniles ([Cornioley et al., 2017](#)). Body mass increases male juvenile ravens' competitive ability during male–male competition in nonbreeder groups and secures their position in the hierarchy ([Braun & Bugnyar, 2012](#); [Heinrich, 1994](#)). Heavier males should have a better chance of accessing food and be more likely to find a mate and establish a territory for reproduction than lighter males. We therefore speculate that selective paternal care and increased body mass at dispersal increase fitness of males later in life. Female juvenile ravens, on the other hand, tend to experience less competition in the nonbreeder group ([Fraser and Bugnyar, 2012](#); [Boucherie et al., 2021](#)). Thus, body mass may not be as crucial for females as it is for males during the first few years after dispersal. Females may benefit from increased body mass when they start breeding, heavy females commonly showing higher reproductive success ([Peters,](#)

1983). However, ravens do not form breeding pairs and thus start reproducing before 3 years old (based on field monitoring of marked wild ravens over more than a decade, Bugnyar, 2021). Body mass mediated by parents' care is therefore unlikely to affect breeding success years later. This could explain why females were not favoured by either their mothers or their fathers. Future studies should focus on long-term following of individuals, throughout the nonbreeder stage and until the first breeding season, to understand fitness consequences of parental care.

Since all families were studied in captivity, receiving ad libitum food and experiencing no competition from other peers or predation, we can assume that all the ravens were facing favourable environmental conditions. Our observations of mothers being more likely to invest equally in all offspring and fathers being more likely to invest selectively are consistent with studies of other species conducted under favourable conditions (Barrios-Miller & Siefferman, 2013; Marshall et al., 2006), and with mathematical models (Fischer et al., 2011; McGinley et al., 1987). Under such favourable conditions, by combining their efforts and respective investments, male and female breeding ravens certainly both contribute to a sustainable reproductive strategy. While mothers ensure basic needs for survival of all chicks, fathers more specifically favour heavy sons, further securing the reproductive component of their offsprings' (and their own) inclusive fitness. Numerous intrinsic (e.g. brood size, pair bond quality, number of past reproduction events) and extrinsic factors (e.g. environmental conditions such as food availability) certainly affect the quality and distribution of parental care (Byholm et al., 2011; Whittingham & Robertson, 1994). Illustrating this, we showed that parental care decreased with increasing brood size. We can thus hypothesize that under less optimal conditions, females may be forced to invest decreasing resources in fewer offspring while males might cease care entirely. Future research should thus aim to investigate further how intrinsic and extrinsic factors might eventually lead to adjustments in the balance of investments between the two parents, as well as patterns of negotiation around parental care, in particular over repeated breeding attempts.

Finally, concerning chicks' begging behaviour, our results support previous studies showing that begging intensity is an indicator of the chicks' nutritional need that parents can assess and respond to (Cotton et al., 1996; Kilner & Johnstone, 1997). Both empirical (Henderson, 1975) and theoretical (Godfray & Parker, 1992) studies show that begging behaviour of the young is an important factor in the proximate control of parental feeding intensity. Following this, we found that offspring begging behaviour was in line with parents' feeding behaviour, the amount of food being unequally allocated depending on the chicks' begging efforts: individuals that were more likely to beg were more likely to be fed (i.e. male offspring). In addition, raven chicks were most likely to beg to the parent from which they were most likely to receive food.

Our study highlights the importance of investigating the complex interactions between parent sex and offspring traits to fully understand patterns of parental care and their later effect on offspring fitness. We showed that postfledgling parental care in captive common ravens is strongly skewed towards mothers which tend to invest in all chicks irrespectively, while fathers selectively invest in heavier sons, using behavioural traits to mediate their parental investment towards those offspring that are likely to face high competition after leaving the parents. These interactions between parents and offspring eventually determine the condition of each offspring at the time of dispersal from the family and consequently their future success.

Author Contributions

S.E. and T. Bugnyar designed the study, S.E., P.H.B. and T. Boehly collected the data, S.E., N.M. and P.H.B. analysed the data, and S.E. drafted the manuscript with substantial contributions from all other authors.

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Appendix

Table A1
Details of all raven offspring studied during 2016 (ad libitum observations) and 2018 (focal observations)

Year	Station	Family	Chick ID	Chick sex	Median brood date of birth	Chick mass (g)	Total no. of observations	
							Ad libitum	Focal
2016	Haidlhof	Astrid–Horst	AH1	F	28 March 2016	1040	30	NA
			AH2	M	28 March 2016	1180	30	NA
			AH3	F	28 March 2016	1040	30	NA
			AH4	M	28 March 2016	1200	30	NA
2016	Haidlhof	Joey–Rocky	JR1	F	28 March 2016	1160	28	NA
			JR2	F	28 March 2016	1100	28	NA
			JR3	F	28 March 2016	1200	28	NA
			JR4	M	28 March 2016	1340	28	NA
2016	Konrad Lorenz	Matte–Lellan	LM1	M	4 April 2016	1260	24	NA
			LM2	M	4 April 2016	1160	33	NA
			LM3	M	4 April 2016	1300	33	NA
			LM4	F	4 April 2016	980	33	NA
2016	Konrad Lorenz	Sophie–Orm	SO1	M	4 April 2016	1195	27	NA
			SO2	M	4 April 2016	1180	27	NA
			SO3	F	4 April 2016	1070	27	NA
			SO4	F	4 April 2016	1090	27	NA
2016	Haidlhof	Heidi–Tom	HT1	F	28 March 2016	1140	25	NA
			HT2	F	28 March 2016	1140	25	NA
			HT3	M	28 March 2016	1300	25	NA
			HT4	F	28 March 2016	1120	25	NA
2018	Haidlhof	Joey–Rocky	Jolly	M	30 March 2018	1260	NA	90
			Twinkle	F	30 March 2018	920	NA	86
2018	Haidlhof	Heidi–Tom	Apollo	F	2 April 2018	NA	NA	91
			Arthemis	M	2 April 2018	NA	NA	92
2018	Haidlhof	Rufus–Munia	Gusgus	M	6 April 2018	1040	NA	86
			Mufasa	F	6 April 2018	1020	NA	86

In 2016, raven families contained four chicks and in 2018 two chicks. In all families, we observed parent–offspring interactions from fledging age (ca. 37 days) until dispersal age (ca. 110 days). The individual highlighted in bold (Chick ID = LM3) died at the age of 79 days. F: female; M: male; NA: not applicable.

Table A2
Ethogram of recorded behaviours during ad libitum and focal observations

Behaviour	Definition	Direction
Feeding	Parent brings food in its beak and places it inside offspring's beak	From parent to offspring
Begging	Offspring signal indicates its level of hunger or need. Begging individual uses combination of auditory (short 'chii' calls) and visual (flapping of wings and displays brightly coloured mouth to solicit food) signals	From offspring to parent
Affiliation	Preening: parent touches or cleans feathers of the offspring with beak, for longer than 2 s Contact sit: two birds sit next to each other in reaching distance Touch: parent touches the offspring's body with beak for less than 2 s	From parent to offspring

When none of the behaviours in the ethogram occurred, birds were considered idle.

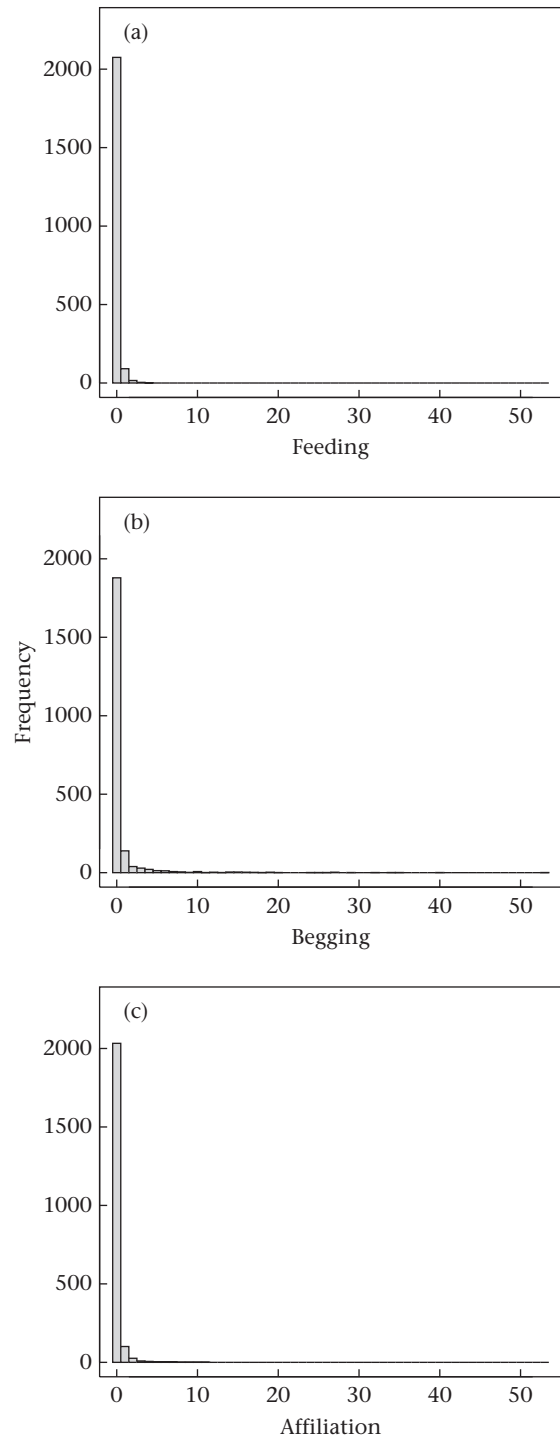


Figure A1. Histograms of behaviour counts per observation session: (a) feeding, (b) begging and (c) affiliation. Most behaviours were usually not observed more than once per session and we therefore used binary response variables for the analysis of all behaviours (i.e. 0 = behaviour was not observed, 1 = behaviour was observed at least once). We originally conducted hurdle models (first step = binomial, second step = Poisson without zeros) to accommodate zero-inflated count data. However, because counts > 1 were so few, the models did not converge.