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FEATURED STUDENT RESEARCH PAPER

# Brood sex ratio modulates the effects of extra food on parental effort and sibling competition in a sexually dimorphic raptor

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## Abstract

Conflicts are inherent to family systems and may occur at three levels. First, each parent benefits if its mate takes the greater share of parental investment. Second, offspring try to manipulate their parents into devolving more resources than it is optimal for them. Third, siblings compete for resources. Food availability can affect the dynamics of each level of interaction. By means of a food supplementation experiment, we assessed how the initial availability of extra food during breeding affects later parental effort, sibling competition, and parent-offspring interactions in a small dimorphic raptor, the lesser kestrel (*Falco naumanni*). Being the larger sex, female nestlings are likely to have higher energy requirements. Female-biased broods had a higher rate of aggressive interactions and were fed more frequently in control nests. Food was not shared evenly among broodmates, and daughters tended to receive more feedings than sons. In young broods, parents controlled food allocation by entering the nest, whereas in older broods, offspring controlled food allocation by monopolizing the nest site entrance. Extra food induced male parents to reduce the rate of feedings delivered by entering the nest. Additionally, extra food improved nestling growth in male-biased broods, leading to an increase in the frequency of parental feedings and aggressive interactions, likely due to faster growth rates. These findings reveal a key effect of brood sex ratio in determining family interactions in a species with reverse sexual size dimorphism and suggest that all levels of conflict between family members should be considered simultaneously when investigating the evolution of parental care.

## Significance statement

Breeding poses energetic costs on parents, and environmental resources are usually limited. To successfully breed, parents coordinate their efforts and manage the allocation of resources to offspring, while offspring communicate their needs. Conflict can arise among family members: each parent benefits if the other takes on most of the workload, offspring ask for more care than what parents can provide, and siblings compete for food. Food availability affects these interaction levels separately, but they have rarely been integrated. By providing extra food to lesser kestrel (*Falco naumanni*) nests, we show that parental provisioning behaviour and sibling competition are *simultaneously* affected by initial resource availability during breeding. Although lesser kestrel nestlings show only moderate sex differences in body size (and therefore energy requirements), the effect of extra food on family interactions primarily depended on the sex ratio of the brood.

**Keywords** Parental care · Food supplementation · Favouritism · Sex ratio · Aggressive interactions

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## Introduction

In animals, family is the most common social unit. However, we are still far from completely understanding the selection pressures acting within families and how they determine patterns of parental care (Royle et al. 2016). Family dynamics are shaped by cooperation and conflict. Three types of conflict of interest exist between family members: sexual conflict between parents, conflict between siblings, and conflict between parents and offspring (Mock and Parker 1998; Parker et al. 2002; Royle et al. 2004).

First, parents may cooperate to raise offspring, for example, by taking turns or synchronizing nest visits (Bebbington and Hatchwell 2015; Baldan and Griggio 2019; Siefferman and Burdick 2020). However, each parent benefits from letting its partner sustain the greater share of parental care, up to complete brood desertion by one parent (e.g. Griggio and Pilastro 2007). Hence, sexual conflict between parents arises (Trivers 1972; Houston et al. 2005). The second type of conflict is sibling competition for resources, which is composed of all behavioural interactions between siblings that increase the fitness of an individual offspring at the expense of the fitness of its siblings (Roulin and Dreiss 2012). Competition with broodmates often takes the form of begging scrambles (e.g. Fresneau et al. 2018) or aggressive interactions (e.g. Müller et al. 2014). Third, parents have to trade off the investment directed to any given offspring against other current (intra-brood conflict) or future (inter-brood conflict) offspring (Kilner and Hinde 2012). As a consequence, the amount of care that is optimal for a parent is usually suboptimal for an offspring (Trivers 1974; Godfray 1995; Hinde et al. 2010). Selection favours the evolution of signals that communicate offspring need to the parent, such as begging. However, signals will not necessarily be honest, because selection on offspring will favour exaggerated signals that induce parents to devolve a greater investment (Trivers 1974; Kilner and Hinde 2008). In the context of parent-offspring interactions, we observe parental favouritism: when offspring in a brood differ in phenotypic quality, parents may invest more resources in those who grant the maximum fitness returns. Parents can use a number of cues to identify offspring with higher chances of surviving and recruiting into the breeding population, such as plumage coloration or nestling body size (e.g. Parejo et al. 2010; Avilés et al. 2011; Romano et al. 2016). When males and females have different size and energy requirements, parents may differentially feed nestlings according to their sex. For example, in the brown falcon (*Falco berigora*), a species with reverse sexual dimorphism in size, parents allocate less food to last-hatched females because raising a small female has low fitness returns as only large females are recruited into the breeding population (McDonald et al. 2005).

Behavioural interactions among family members can be heavily affected by resource availability (e.g. Botterill-James et al. 2017). For example, the probability that a female Tengmalm's owl (*Aegolius funerus*) deserts its brood, leaving the entire workload to the male, depends on prey density and the partner's body condition (Eldegard and Sonerud 2009). Ecological conditions also shape parent-offspring signalling: at the interspecific level, resource availability and predictability are the main drivers of differences in parental responsiveness to offspring begging signals (Caro et al. 2016). In addition, parental favouritism for offspring with different phenotypic quality has been found to vary as the breeding season progresses, with parents switching from feeding smaller to larger offspring as food availability declines (Bize et al. 2006). Low food availability leads to both parent-offspring competition for resources, which can directly reduce offspring survival (Meunier and Kölliker 2012), and increased sibling competition. For example, in meerkats (*Suricata suricatta*), the rate of aggressive interactions between littermates is negatively predicted by the amount of food available (Hodge et al. 2009).

Providing extra food, adding to what is naturally available, is a way to experimentally manipulate general ecological conditions. Most food supplementation experiments report positive effects of extra food on reproductive parameters, including advanced laying date and improved offspring growth and breeding success (Ruffino et al. 2014; Grüebler et al. 2018; Bowers et al. 2019). In raptor species, extra food supplied during brood rearing led to asymmetric decreases in feeding effort by the two parents, with one sex benefiting more than the other from the reduced workload in terms of body condition and survival (Wiehn and Korpimäki 1997; Dawson and Bortolotti 2002; Karell et al. 2008; Eldegard and Sonerud 2010; Santangeli et al. 2012). Supplying extra food may also affect sibling interactions. In black-legged kittiwakes (*Rissa tridactyla*), broodmate aggression decreased when extra food was provided throughout the breeding season (White et al. 2010). However, despite each level of interaction within a family being intrinsically dependent on the others, studies manipulating food availability have rarely examined parental investment, sibling competition, and parent-offspring interactions simultaneously.

In lesser kestrels (*Falco naumanni*), breeding decisions and breeding output are strongly influenced by environmental resources (Bonal and Aparicio 2008; Catry et al. 2012, 2016; Marcelino et al. 2020). In previous experiments, providing extra food significantly advanced laying date (Aparicio and Bonal 2002), increased egg mass, improved nestling growth, decreased the chances of brood desertion for females in poor body condition (Podofillini et al. 2019), and increased fledging success (Gal et al. 2019). In addition, asynchronous hatching in this species produces a size hierarchy that penalizes younger offspring, leading to frequent brood reduction, with nearly 90% of mortality attributable to nestlings starvation (Negro et al. 1993). Hence, there is substantial scope for parent-offspring conflict over resource allocation. As pointed out by Rodríguez et al. (2008), the high mortality rate of nestlings should select for parental control over food allocation in order to maximize breeding output. At the same time, nestlings may jostle for positioning near the nest site entrance, and parents may be forced to accept the outcome of sibling competition (e.g. Whittingham et al. 2003).

By means of a food supplementation experiment carried out from egg laying to early nestling rearing, we studied how the initial availability of extra food affects simultaneously parental provisioning effort, sibling competition and parent-offspring interactions in the middle-late nestling rearing stage. We recorded behavioural interactions immediately after the end of the food supplementation period in order to measure natural behaviours rather than the direct response to the extra food placed in the nests. Indeed, during extra food provisioning, behavioural interactions between nestlings are likely to be reduced due to an immediate satiation effect (e.g. Cook et al. 2000; Roulin 2001), and, in the same way, parental feeding rate might be reduced as a direct response to nestlings' satiation (e.g. Watson and Ritchison 2018). We examined how extra food was allocated to parental condition and nestling growth in a parallel study (Podofillini et al. 2019). Extra food supplied during egg laying and incubation allowed food-supplemented females to produce heavier last-laid eggs and increased moult investment for both parents, but it did not affect clutch size or sex allocation (Podofillini et al. 2019). Extra food supplied during early nestling rearing improved nestling growth; nestlings in food-supplemented nests had a 10% greater body mass increase compared with nestlings in control nests and grew longer feathers at 16 days of age (Podofillini et al. 2019). Based on this evidence, we made three predictions on how parental effort, sibling competition, and parent-offspring interactions should respond to the initial increased food availability during the breeding attempt.

First, parents may either increase their provisioning rate, given the enhanced survival probability of the current brood (scenario A); or decrease their provisioning rate to preserve energy for future breeding attempts (scenario B) (e.g. Dawson and Bortolotti 2002; Santangeli et al. 2012). In scenario A, parents respond to cues of nestlings' growth rate, and improved growth of food-supplemented nestlings may trigger increased provisioning rates (e.g. in Eurasian kestrels (*Falco tinnunculus*) provisioning rates increase with nestling growth to peak at 15–17 days of age; Steen et al. 2012). In scenario B, parents compensate for the perceived increase in the partner's provisioning rate (represented by extra food) by decreasing their own provisioning rate and maintain this compensation even when extra food is not present, due to a temporal delay in adjusting to the perceived partner's provisioning rate (e.g. Schwagmeyer et al. 2002). In the latter scenario, males may decrease parental effort more than females. Indeed, females generally spend more time at the nest, whereas males engage in most of the hunting effort during incubation and the early nestling rearing (Hernández-Pliego et al. 2017).

Second, extra food may aid nestling growth (Podofillini et al. 2019) and reduce the level of competitive asymmetry between older and younger siblings (Gill et al. 2002; Saino et al. 2010), increasing sibling competition. We hence expected a higher frequency of aggressive interactions in food-supplemented broods (Cook et al. 2000). We also expected an increase of begging in food-supplemented broods because, after the end of extra food provisioning, nestlings compete over limited food resources, and improved early rearing conditions may allow food-supplemented nestlings to invest more in costly begging behaviour (Morales and Velando 2018; Bowers et al. 2019).

Third, considering the high mortality rate characterizing lesser kestrel nestlings (Podofillini et al. 2019), we predicted parental favouritism towards older and larger nestlings as the strategy by which parents minimize feeding effort waste (Jeon 2008). We expected favouritism to be less pronounced in food-supplemented broods because extra food may decrease the asymmetry between broodmates (Saino et al. 2010).

## Materials and methods

### Study species and field procedures

The lesser kestrel is a small (ca. 120 g) diurnal raptor showing sexual dimorphism in both colouration (Cade and Digby 1982) and size (females are ca. 15% heavier than males, Podofillini et al. 2019). Females lay one clutch of 2–6 eggs per breeding season, incubated by both parents for ca. 30 days (Cramp 1998). Chicks fledge at 35–40 days, but, if the nest site allows, after 16 days, they start to get out of the nest and wait for parental feedings in its immediate vicinity (Podofillini et al. 2018). Lesser kestrels forage in the countryside surrounding the colony (Cecere et al. 2020), feeding mainly on invertebrates, lizards, and small mammals (Rodríguez et al. 2010).

The present study was carried out in April–July 2016 at the breeding colony of the city of Matera (Southern Italy; 40° 67′ N, 16° 60′ E), where many pairs breed in nestboxes (details in Podofillini et al. 2018). Nestboxes were regularly inspected (2–3 times/week) in order to record breeding activities. The data were collected within the framework of a food supplementation experiment involving 100 nestboxes (Podofillini et al. 2019); starting from the laying of the first egg(s) of each clutch, we simulated high food availability by placing dead laboratory mice (*Mus musculus*, ca. 20 g each) inside nestboxes three times a week. Food was regularly supplied to lesser kestrel nests until the early nestling rearing stage, i.e. 8-day-old broods: three mice were provided during egg laying and early nestling rearing, while one mouse was provided during incubation (for details see Podofillini et al. 2019). We found white fur in regurgitated pellets inside food-supplemented nestboxes between consecutive visits, which confirms that the mice were regularly eaten. During egg laying and incubation, extra food was most likely eaten by the female parent, as female lesser kestrels spend more time at the nest and are fed by the male during these breeding stages (Donázar et al. 1992; Cramp 1998). During early nestling rearing, we have evidence from a pilot video-recording that mice were dismembered and fed to the nestlings. Control nestboxes were monitored with the same schedule as food-supplemented ones to homogenize disturbance between treatments; we inserted our hands into the nestboxes, but no food was provided. At hatching, we attributed to each nestling a rank based on hatching order. The first hatched nestling was assigned the highest rank (i.e. rank 1), while subsequent nestlings were assigned lower ranks (i.e. 2 to 5). When we found two or more nestlings hatched on the same visit to the colony, rank was assigned based on body mass (larger nestlings were assigned higher rank) (Podofillini et al. 2019). When broods were 8–10 days old, we weighed each nestling on a precision balance (to the nearest 0.1 g), measured tarsus length and collected a blood sample (ca. 200 μl) for molecular sexing (see Costanzo et al. 2020). Body mass was recorded again when nestlings were 15–16 days old.

After the period of extra food provisioning, we randomly selected a subsample of 15 food-supplemented and 13 control nestboxes in which we deployed digital cameras to record the behaviour of family members (see Fig. 1 for a diagram of the experimental plan). We video-recorded each brood once between 8 and 22 days post-hatching (mean brood age 13.2 ± 4.2 SD days). At each visit to the colony, we installed two video cameras (Kodak PlayFull waterproof videocamera, 720p HD) powered by portable powerbanks (4400 mAh) in one food-supplemented nest and one control nest to record for 7 hours, which was the maximum duration allowed by battery life. However, due to heat exposure (temperature loggers on rooftops where the nestboxes are placed recorded up to 52 °C during daytime), we experienced occasional battery failure due to overheating; hence, the mean video-recording duration per brood was 262 ± 148 SD min. Video-recording duration did not differ between treatments (Mann-Whitney test: $Z = -0.12$, $p = 0.91$). Video recording occurred in the range 08:00–17:00 for both food-supplemented and control nests with no time difference between treatments (Mann-Whitney test: $Z = 0.47$, $p = 0.64$). Nestlings were marked with a unique combination of black dots on the head using a non-toxic black marker for identification on footage. Nestlings never left the nestbox during video-recordings.

Brood traits of food-supplemented and control nests did not differ significantly (see Supplementary Table S1). Out of 106 nestlings in 28 broods, 17 died before the time of behavioural measurements (16%). Mortality rate did not differ between treatments (Supplementary Table S1). There was no overall effect of nestling mortality on brood sex ratio; brood sex ratio at the time of behavioural measurements was highly correlated with brood sex ratio at hatching in both control (Pearson's $r = 0.93$) and food-supplemented broods ($r = 0.98$). Indeed, nestling mortality was not sex-biased in the study population (Podofillini et al. 2019). In the present dataset, nestlings from food-supplemented broods were not heavier than those from control broods at 8 days post-hatching, although they tended to be heavier at 16 days (Supplementary Table S1). Data from the entire sample of nestboxes involved in the food supplementation experiment ($n = 85$ broods, deserted nests excluded) showed that extra food provisioning significantly improved early nestling growth (Podofillini et al. 2019).

## Behavioural variables

Since video cameras were positioned inside the nestbox, we were able to identify the sex of the parent bringing food only when it entered the nestbox. Hence, we separated feeding events into two categories: internal feedings, whenever the parent was inside the nestbox when delivering prey ($n =$

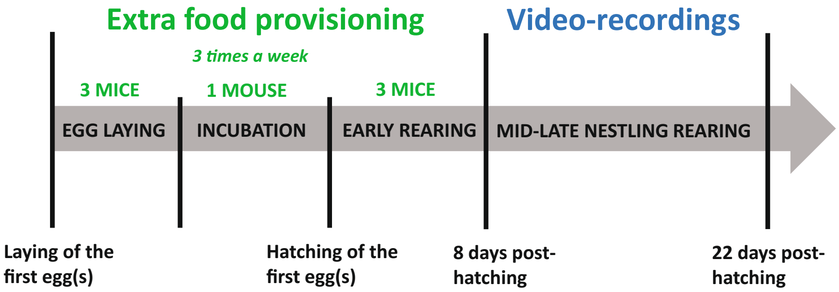

**Fig. 1** Schematic representation of the extra food provisioning experiment and of the behavioural sampling design. The arrow indicates time while black bars separate different reproductive stages, i.e. egg laying, incubation, and early (day 0 to 8 post-hatching) and middle-late nestling rearing (day 8 to 22). Nestboxes were visited three times a week. Extra food provisioning (different number of supplied food items per visit in green) began with egg laying and ended at the fourth visit at the nestbox since hatching, i.e. 8 days post-hatching. Video-recordings (blue heading) for behavioural sampling were performed soon after extra food provisioning, during the middle-late nestling rearing stage (8–22 days post hatching). Each brood was video recorded once

152, mean duration: 38 ± 98 SD s; mean number of occurrences: 10.8 ± 8.4 SD in 8 control nests and 8.3 ± 6.7 SD in 8 food-supplemented nests), and external feedings, whenever the parent left prey at the nest site entrance ($n$ = 153, mean duration: 3 ± 4 SD s; mean number of occurrences: 5.3 ± 3.4 SD in 10 control nests and 9.1 ± 8.7 SD in 11 food-supplemented nests). For each feeding event, we scored the proximity of each nestling to the parent for internal feedings and to the nest site entrance for external feedings. Indeed, when examining how feedings are allocated within a brood, nestling proximity allows to account for the positioning of each nestling during feedings, which can be an indication of both the outcome of nestling competition and active parental choice. To obtain a measure of proximity that was independent of brood size (2–4 nestlings), we assigned a proximity score of 1 to the closest nestling, 2 to the nestlings in between, and 3 to the furthest nestling; this means that for broods of two nestlings, we assigned 1 to the closest nestling and 3 to the furthest, whereas for broods of four nestlings, the two nestling with intermediate proximity were assigned a score of 2 (Fargallo et al. 2003). The brood size of video-recorded nests did not differ between treatments (Supplementary Table S1).

According to scramble models of competition between offspring, nestlings compete for parental feedings by jostling for position: if the parent leaves a prey item at the nest-entrance, nestling jostling for position is likely to be the main determinant of within-brood food allocation patterns. On the contrary, if the parent enters the nest to deliver a prey item, the parent has the potential to exert control over food allocation. To determine whether a nestling's proximity to the parent was the outcome of competition between siblings or of parental feeding decisions during internal feedings, we scored the proximity of a nestling both to the parent and to the nest site entrance, where proximity to the nest site entrance was assessed when the parent's head first appeared at the nest-entrance hole. Proximity to the nest site entrance exclusively reflects offspring jostling for position.

We also computed a favouritism index for each brood as the ratio between the maximum number of feedings received by a nestling and the total number of feedings provided to the brood during the recording period.

Aggressive interactions among siblings consisted of food-stealing attempts and food thefts. Indeed, prey items took time to be eaten, leaving room for food stealing attempts (Roulin et al. 2008). We defined a stealing attempt as an active motion of a nestling's head, with open beak, towards a sibling holding a prey, and a theft as a nestling effectively taking a prey item from a sibling's bill, feet, or their immediate proximity (Roulin et al. 2008, 2012, 2016). To determine the rate of aggressive interactions for each nestling, we summed all food stealing attempts and food thefts initiated by the nestling and divided this number by total video-recording duration for a given brood.

Begging was observed during feeding events and during aggressive interactions. In the latter case, nestlings begged even in the absence of a parent, likely to negotiate over the prey item (Romano et al. 2015; Watson and Ritchinson 2018). Indeed, food stealing attempts can be accompanied by vocal communication between siblings (Roulin et al. 2008). We used begging persistency, i.e. the proportion of time a nestling emitted begging calls throughout either the feeding event or the aggressive interaction, as a proxy of begging intensity (Fargallo et al. 2003). To avoid observer error in attributing simultaneous vocalizations to different nestlings, we computed begging time for each nestling with the following protocol: any time a single nestling begged, seconds were counted only for that individual; when two or more nestlings were vocalizing, seconds were added to all nestlings in the brood; pauses were considered when they lasted at least two seconds. The sum of seconds for each nestling was then divided by the duration of the feeding event (seconds elapsed from the appearance of the parent at the nest-entrance to prey delivery) or the aggressive interaction (seconds elapsed from when the attacking nestling began to stare at its sibling until when the siblings did not look at each other for 5 s, as staring at a siblings' head while it is holding a prey item constitutes a weak competitive interaction (Roulin et al. 2008)). To compare begging behaviours in food-supplemented vs. control broods, we used mean begging persistency of each nestling during either feeding events or aggressive interactions. All behaviours were scored by a single observer (CS) blind of treatment.

## Statistical analysis

### General approach

The effects of extra food provisioning on parental feeding rate, frequency of sibling aggressive interactions, and begging persistency were analysed by generalized linear models (GLMs) or linear mixed models (LMMs) with food supplementation (0 = control; 1 = food-supplemented), brood size, mean brood age, and brood sex ratio (proportion of males in a brood) at the time of behavioural measurements as fixed effects. The two-way interactions between food supplementation and other covariates were also included as fixed effects in the initial models. Non-significant interaction terms were dropped from initial models in a single step. Brood identity was included as a random effect in LMMs. We mean-centred sex ratio, brood size, and age in all models. Models had a normal error distribution unless otherwise stated. When the assumption of normality was not met (Shapiro-Wilk test), the dependent variables were transformed using a Yeo-

Johnson transformation (Yeo and Johnson 2000). Data from one control brood were omitted due to missing sex ratio (no sexing was possible). The final sample size was thus 15 food-supplemented vs. 12 control broods.

Statistical analyses were performed using R 3.6.0 (R Core Team 2019) and LMMs were fitted using the *lmerTest* package (Kuznetsova et al. 2017). We checked the normality of residuals, dispersion, and presence of outliers with the *DHARMa* package (Hartig 2020). Interaction effects were plotted using the *visreg* package (Breheny and Burchett 2017). Means and model estimates are reported with their associated standard error (± SE), unless otherwise stated. Details of specific analyses conducted to assess the extent of conflict between parents, sibling competition, and parent-offspring conflict are provided below.

### Conflict between parents

To assess the effect of extra food provisioning on parental feeding effort, we first ran a GLM with hourly feeding rate per nestling (i.e. hourly feeding rate divided by brood size, including both internal and external feedings) as the dependent variable.

We then checked for any difference between control and food-supplemented broods in (1) the rate of internal feedings, (2) the rate of external feedings, and (3) the proportion of internal to external feedings, by three separate GLMs with (1) hourly internal feeding rate per nestling, (2) hourly external feeding rate per nestling, and (3) the proportion of internal to external feedings as dependent variables. We used a normal error distribution in (1) and (2) and a binomial error distribution (controlling for overdispersion; dispersion parameter = 6.83) in (3). Since the sex of the parent was known only for internal feedings, we then compared feeding rates by each parent in the subset of broods for which we recorded internal feeding events ($n$ = 30 internal feeding rates from 7 control and 8 food-supplemented broods). For this analysis, we set the hourly internal feeding rate per nestling by each parent as the dependent variable in a LMM with sex of the parent (0= female, 1= male), food supplementation, brood size. and brood sex ratio at the time of behavioural measurements (and the two-way interactions between food supplementation and these variables) as fixed effects. We did not include mean brood age as a predictor in this model because age and sex ratio were strongly correlated in this subsample of 15 broods (Pearson's $r$ = 0.72), despite this not being the case in the entire sample of 27 broods (Pearson's $r$ = 0.20). The model including sex ratio as a predictor provided a better fit than the model including brood age according to the corrected Akaike Information Criterion (AICc) (AICc = 11.02 vs. 13.78, respectively).

### Sibling competition

The effect of extra food provisioning on aggressive interactions between siblings and on begging persistency was modelled using three distinct LMMs with the following dependent variables: (1) hourly rate of aggressive interactions per nestling ($n$ = 38 control nestlings from 12 broods; $n$ = 46 food-supplemented nestlings from 14 broods), (2) begging persistency during aggressive interactions (sample size as above), (3) begging persistency during feeding events ($n$ = 38 control nestlings from 12 broods and $n$ = 50 food-supplemented nestlings from 15 broods). The lower sample size in (1) and (2) was due to limited visibility preventing individual identification during an aggressive interaction in one food-supplemented brood, which was then excluded from these analyses.

Brood sex ratio emerged as a determinant of the rate of aggressive interactions per nestling in (1). Hence, we a posteriori decided to perform additional analyses to investigate how brood sex ratio affected (a) nestling growth and (b) competitive asymmetry in the two treatments.

To investigate (a), we ran two LMMs with either nestling tarsus length or nestling body mass at 8–10 days post-hatching as dependent variables. Brood sex ratio at hatching, food supplementation, nestling age, maximum brood size, and the interaction between each of these variables and brood sex ratio were entered as fixed effects ($n$ = 31 control nestlings from 10 broods and $n$ = 43 food-supplemented nestlings from 13 broods). Nestling sex was not included in the model because it was strongly correlated with brood sex ratio at hatching (Pearson's $r$ = 0.59), and the models including sex as a predictor did not provide a better fit than the models including sex ratio (sex as predictor—body mass model AICc = 558.34, tarsus length model AICc = 622.59; sex ratio as predictor—body mass model AICc = 558.04, tarsus length model AICc = 602.69).

To investigate (b), we ran a GLM with mean body mass difference (mean of the absolute value of pairwise differences in body mass; body mass asymmetry hereafter) between nestlings within a brood at 8–10 days post-hatching ($n$ = 12 control broods and $n$ = 15 food-supplemented broods) as the dependent variable. Food supplementation, brood size, and sex ratio at 8–10 days post-hatching, and the two-way interaction terms between food supplementation and these variables were included as fixed effects.

Finally, we checked for sex differences in body mass and tarsus length at 8–10 days post-hatching by means of two LMMs with either body mass or tarsus length as dependent variable ($n$ = 38 control nestlings from 12 broods and $n$ = 50 food-supplemented nestlings from 15 broods). Food supplementation, brood size, nestling sex (male = 1, female = 0), and age, as well as the two-way interactions between sex and the other variables, were entered as fixed effects. We also examined whether there was a sex-bias among first-hatched and last-hatched nestlings (category senior = rank 1–3 vs. category junior = rank 4–5) by means of a GLMM with binomial error distribution, brood identity as random factor, and sex as the dependent variable. Junior/senior, food supplementation, and the two-way interaction between these variables were included as fixed terms.

### Parent-offspring conflict

We compared the favouritism index between food-supplemented and control broods by using a GLM with a binomial error distribution. We then investigated the proximate factors determining food allocation among nestlings within a brood ($n$ = 38 control nestlings from 12 broods and $n$ = 50 food-supplemented nestlings from 15 broods). To this end, we ran an LMM with hourly feeding rate per individual nestling as the dependent variable, while including food supplementation, nestling age, sex, mean begging persistency, and its mean proximity score during feeding events as fixed effects. Two-way interactions between food supplementation and these variables were also included in the initial model.

To assess the relevance of nestlings' control vs. parental control in determining within-brood food allocation during internal feedings, we compared the AICc of two LMMs with internal hourly feeding rate per individual nestling as the dependent variable, and nestling sex and age as fixed effects, along with either (a) mean proximity to the parent or (b) mean proximity to the nest site entrance across all feeding events. This analysis was performed on broods receiving at least one internal feeding in which both proximity scores were determined for all nestlings in the brood ($n$ = 24 control nestlings from 7 broods and $n$ = 25 food-supplemented nestlings from 8 broods).

## Results

### Effect of extra food provisioning on parental conflict

Parental feeding rate per nestling did not differ between control and food-supplemented broods, but it was affected by brood sex ratio differently in the two treatments (significant food supplementation × sex ratio interaction, Table 1); in food-supplemented broods, the feeding rate increased with increasing proportion of male nestlings, whereas control broods showed an opposite trend (Fig. 2a). The same interaction effect of brood sex ratio and food supplementation was

**Table 1** Effects of extra food provisioning on total feeding rate per nestling (generalized linear model, GLM) and internal feeding rate per nestling by each parent (linear mixed model, LMM). Coefficient estimates ± SE and $F$-statistic are given for each fixed term in the model. The initial model included all two-way interactions between food supplementation and other variables, and non-significant interaction terms were removed from the final model. For significant interactions, we report group means (for categorical predictors) or coefficient estimates and relative $t$-statistic of regression lines (continuous predictors). In the LMM, degrees of freedom (df) were estimated according to Kenward-Roger's approximation

| Predictors | Estimate ± SE | $t$ | $F$ | df | $p$ |
|---|---|---|---|---|---|
| Feedings/h per nestling ($n$ = 27 broods) | | | | | |
| Food supplementation | 0.08 ± 0.11 | | 0.57 | 1, 21 | 0.46 |
| Sex ratio[a] | − 0.44 ± 0.30 | | 2.14 | 1, 21 | 0.16 |
| Brood size[a] | − 0.10 ± 0.06 | | 3.50 | 1, 21 | 0.07 |
| Mean age[a] | − 0.08 ± 0.06 | | 1.97 | 1, 21 | 0.18 |
| Food supplementation × sex ratio | | | 6.24 | 1, 21 | 0.021 |
| Control broods | − 0.47 ± 0.30 | − 1.59 | | 22 | 0.13 |
| Food-supplemented broods | 0.49 ± 0.24 | 2.09 | | 22 | 0.049 |
| Internal feedings/h per nestling by each parent ($n$ = 30 feeding rates, 15 broods) | | | | | |
| Food supplementation | 0.04 ± 0.08 | | 0.27 | 1, 20 | 0.61 |
| Sex ratio[a] | − 0.26 ± 0.10 | | 7.18 | 1, 11 | 0.021 |
| Brood size[a] | − 0.10 ± 0.04 | | 0.04 | 1, 11 | 0.85 |
| Sex of the parent | 0.01 ± 0.07 | | 0.02 | 1, 13 | 0.88 |
| Food supplementation × sex of the parent | | | 5.74 | 1, 13 | 0.032 |
| Female control | 0.29 ± 0.06 | | | | |
| Male control | 0.30 ± 0.06 | | | | |
| Female supplemented | 0.33 ± 0.06 | | | | |
| Male supplemented | 0.12 ± 0.06 | | | | |

[a] Estimate for mean-centred covariate

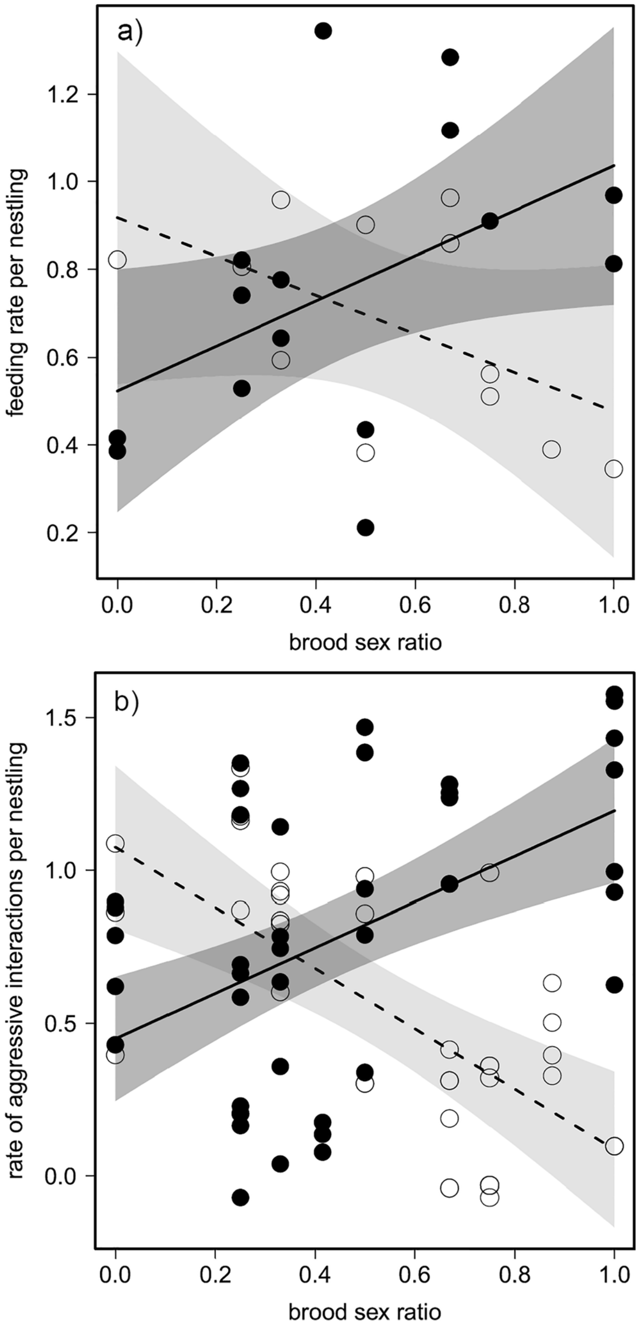

**Fig. 2** Relationship between brood sex ratio (proportion of males) and **a** total feeding rate (feedings/h) per nestling and **b** the rate of aggressive interactions (Yeo-Johnson transformed aggressive interactions/h) per nestling, according to treatment (solid line, filled dots: food-supplemented nests; dashed line, empty dots: control nests). The fitted lines (with 95% confidence bands) are derived from the corresponding models reported in Table 1 (**a**) and Table 2 (**b**)

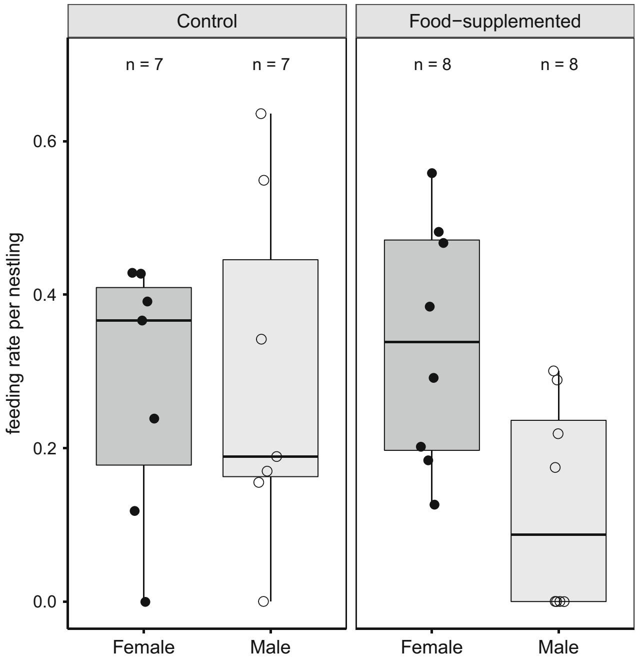

**Fig. 3** Boxplot showing the effect of extra food provisioning on male and female feeding rate per nestling (feedings delivered inside the nest only). Sample sizes (number of feeding rates) are given above each box. Each box shows the group median and interquartile range. Whiskers represent the highest and lowest values and extend to a maximum of 1.5 times the interquartile range. Filled dots indicate female feeding rates and empty dots indicate male feeding rates

found when analysing external feedings only (Supplementary Table S2).

The proportion of internal over external feedings did not differ between treatments and varied according to brood age, decreasing in older broods (Supplementary Table S2). Indeed, external feeding rate per nestling increased with brood age (Supplementary Table S2). At the same time, internal feeding rate per nestling decreased with brood age, with no internal feedings recorded after 17 days of age, independently of food supplementation (Supplementary Table S2).

Focusing only on the middle nestling rearing phase (8-17 days), when parents still enter the nestbox to feed their offspring (15 broods for which internal feeding events were recorded), we found that male parents significantly decreased their internal feeding rate in food-supplemented nests (Table 1; Fig. 3). In addition, the internal feeding rate was higher in broods with a higher proportion of female nestlings for both male and female parents, independently of treatment (non-significant interactions sex of the parent × brood sex ratio and food supplementation × brood sex ratio; see Table 1).

## Effect of extra food provisioning on sibling competition

The rate of aggressive interactions per nestling depended on the interaction between food supplementation and sex ratio (Table 2); it decreased with increasing proportion of male nestlings in control broods while the reverse was the case in food-supplemented broods (Table 2, Fig. 2b). In addition, the rate of aggressive interactions decreased with increasing nestling age (Table 2). The rate of aggressive interactions was not simply the consequence of parental feeding rate (non-

**Table 2** Effects of extra food provisioning on the rate of aggressive interactions per nestling and mean nestling begging persistency during feedings and during aggressive interactions (linear mixed models, LMMs). Coefficient estimates ± SE and *F*-statistic are given for each fixed term in the model. The initial model included all two-way interactions between food supplementation and other variables, and non-significant interaction terms were removed from the final model. For significant interactions, we report group means (for categorical predictors) or coefficient estimates and relative *t*-statistic of regression lines (continuous predictors). Degrees of freedom (df) were estimated according to Kenward-Roger's approximation

| Predictors | Estimate ± SE | *t* | *F* | df | *p* |
|---|---|---|---|---|---|
| Aggressive interactions/h[b] (*n* = 84 nestlings, 26 broods) | | | | | |
| Food supplementation | 0.25 ± 0.14 | | 3.00 | 1, 20 | 0.10 |
| Sex ratio[a] | −0.87 ± 0.39 | | 5.09 | 1, 21 | 0.035 |
| Brood size[a] | −0.11 ± 0.12 | | 0.96 | 1, 22 | 0.34 |
| Mean age[a] | −0.05 ± 0.01 | | 13.85 | 1, 54 | < 0.001 |
| Food supplementation × sex ratio | | | 9.78 | 1, 21 | 0.005 |
| Control nests | −0.97 ± 0.40 | −2.42 | | 22 | 0.024 |
| Food-supplemented nests | 0.63 ± 0.33 | 1.90 | | 21 | 0.071 |
| Begging persistency during feeding events[b] (*n* = 88 nestlings, 27 broods) | | | | | |
| Food supplementation | −0.22 ± 0.34 | | 0.42 | 1, 22 | 0.53 |
| Sex ratio[a] | −0.83 ± 0.59 | | 2.03 | 1, 22 | 0.17 |
| Brood size[a] | 0.04 ± 0.27 | | 0.03 | 1, 23 | 0.87 |
| Mean age[a] | −0.01 ± 0.04 | | 0.09 | 1, 36 | 0.76 |
| Begging persistency during aggressive interactions[b] (*n* = 84 nestlings, 26 broods) | | | | | |
| Food supplementation | 0.03 ± 0.08 | | 0.16 | 1, 21 | 0.69 |
| Sex ratio[a] | −0.08 ± 0.13 | | 0.40 | 1, 21 | 0.53 |
| Brood size[a] | −0.01 ± 0.06 | | 0.01 | 1, 23 | 0.93 |
| Mean age[a] | −0.02 ± 0.01 | | 8.85 | 1, 67 | 0.004 |

[a] Estimate for mean-centred covariate

[b] Yeo-Johnson transformed

significant hourly feeding rate per nestling when added as a predictor in the model displayed in Table 2).

Food supplementation had no effect on mean begging persistency during feeding events and aggressive interactions (Table 2). No significant predictor of mean begging persistency during feeding events emerged, whereas mean begging persistency during aggressive interactions decreased significantly with nestling age (Table 2).

We found no significant effect of food supplementation and brood sex ratio at hatching on nestling body mass at 8–10 days post-hatching (see Supplementary Table S3). However, tarsus length at 8–10 days post-hatching depended on two interaction effects. First, nestlings belonging to male-biased broods had longer tarsi but only among large broods (significant interaction brood sex ratio × maximum brood size, see Supplementary Table S3; Supplementary Fig. S1a). Second, nestlings belonging to male-biased broods had longer tarsi but only among food-supplemented nests (significant interaction brood sex ratio × food supplementation, Supplementary Table S3; Supplementary Fig. S1b).

Food supplementation, sex ratio, and their interaction did not significantly predict body mass asymmetry within a brood at 8–10 days post-hatching (Supplementary Table S4). Finally, female nestlings were not significantly heavier than males at 8–10 days post-hatching (sex − 1.48 (± 2.90 SE), $t_{83.00} = -0.51$, $p = 0.61$; food supplementation 4.57 (± 3.28

**Table 3** Effects of extra food provisioning on favouritism (generalized linear model, GLM) and determinants of within-brood food allocation (linear mixed model, LMM). Coefficient estimates ± SE and *F*-statistic are given for each fixed term in the model. The initial model included all two-way interactions between food supplementation and other variables, and non-significant interaction terms were removed from the final model. In the LMM, degrees of freedom (df) were estimated according to Kenward-Roger's approximation

| Predictors | Estimate ± SE | *F* | df | *p* |
|---|---|---|---|---|
| Feedings/h[b] (*n* = 88 nestlings, 27 broods) | | | | |
| Food supplementation | −0.06 ± 0.08 | 0.48 | 1, 23 | 0.50 |
| Sex | −0.11 ± 0.05 | 3.61 | 1, 73 | 0.061 |
| Age[a] | −0.04 ± 0.01 | 19.65 | 1, 32 | < 0.001 |
| Proximity[a] | −0.40 ± 0.06 | 51.92 | 1, 68 | < 0.001 |
| Begging persistency[a] | 0.01 ± 0.17 | 0.00 | 1, 76 | 0.95 |
| Favouritism index (*n* = 27 broods) | | | | |
| Food supplementation | −0.01 ± 0.18 | 0.00 | 1, 22 | 0.98 |
| Sex ratio[a] | −0.17 ± 0.34 | 0.16 | 1, 22 | 0.69 |
| Brood size[a] | −0.15 ± 0.13 | 0.85 | 1, 22 | 0.37 |
| Mean age[a] | −0.57 ± 0.17 | 8.42 | 1, 22 | 0.008 |

[a] Estimate for mean-centred covariate

[b] Yeo-Johnson transformed

SE), $t_{24.36} = 1.39$, $p = 0.18$; age: 9.24 (± 1.36), $t_{56.06} = 6.81$, $p < 0.001$; brood size − 4.41 (± 2.43 SE), $t_{25.07} = -1.81$, $p = 0.08$; non-significant interactions were removed from the model) nor had significantly longer tarsi (sex 3.50 (± 4.44 SE), $t_{81.63} = 0.79$, $p = 0.43$; food supplementation 2.71 (± 5.58 SE), $t_{26.97} = 0.49$, $p = 0.63$; age 17.32 (± 2.17), $t_{66.36} = 7.98$, $p < 0.001$; brood size 1.42 (± 4.13 SE), $t_{27.74} = 0.35$, $p = 0.73$; non-significant interactions were removed from the model). However, we found that last-hatched nestlings were more often males (junior vs. senior − 1.47 (± 0.74 SE), $Z = -1.99$, $p = 0.047$; food supplementation: − 0.39 (± 0.50 SE), $Z = -0.78$, $p = 0.44$; the interaction was non-significant and was removed from the model).

### Effect of extra food provisioning on parent-offspring conflict

Female nestlings tended to receive more feedings than males (Table 3). In addition, younger nestlings were fed more frequently (Table 3), and this was not due to a correlation between sex and age (Pearson's $r = -0.11$). The average proximity of a nestling either to the parent (internal feedings) or to the nest site entrance (external feedings) was also a significant predictor of its feeding rate (Table 3). When considering only internal feedings, average proximity to the parent was a better predictor of feeding rate per individual nestling compared with average proximity to the nest site entrance (AICc of LMMs with proximity to the parent as predictor = 63.48; with proximity to the nest site entrance = 72.39; ΔAICc = 8.91).

The favouritism index did not differ between control (0.63 ± 0.25) and food-supplemented broods (0.64 ± 0.26), while it increased with mean brood age (Table 3).

## Discussion

Following extra food provisioning, parents modified their provisioning behaviour in relation to brood sex ratio: total feeding rate was higher in food-supplemented broods with a higher proportion of male nestlings, while the opposite was the case in control broods. Male parents also reduced the rate of feedings delivered by entering the nest in the middle rearing stage (8–17 days-post-hatching) while female parents did not. Similarly, extra food provided during early rearing altered the dynamics of sibling competition in relation to brood sex ratio in the middle-late rearing stage; the rate of aggressive interactions tended to be higher in food-supplemented broods with a higher proportion of male nestlings, while the opposite was the case in control broods. Hence, brood sex ratio mediated the effect of extra food on both parental feeding rates and offspring aggressive interactions. In addition, food was not distributed evenly within the brood; female nestlings tended to receive more feedings compared with males, despite moderate reverse sexual dimorphism in size among lesser kestrel nestlings. Below we discuss potential explanations for these findings with a focus on the three levels of conflict within a family: parental conflict, sibling competition, and parent-offspring conflict.

### Parental conflict

Male parents responded to extra food (supplied until 8–10 days post-hatching) by reducing the rate of prey provisioned by entering the nest in the middle nestling rearing stage (8–17 days), while this was not the case among females. This may indicate a decreased parental effort by fathers, as predicted by scenario B. Indeed, lesser kestrel mothers not only bear the costs of egg production (Nilsson and Råberg 2001; Vézina and Williams 2005; Vézina and Salvante 2010). but they also engage in a larger share of incubation and brooding of newly hatched nestlings (Hernández-Pliego et al. 2017). Hence, females may have lower survival prospects and remating opportunities in comparison with males (Dijkstra et al. 1990; Korpimäki and Rita 1996) and prioritize investment in the current breeding attempt (Podofillini et al. 2019). A reduction of paternal investment in response to extra food has been found in previous studies of raptor and passerine species (Santangeli et al. 2012; Cleasby et al. 2013). However, these studies performed behavioural observations during the period of extra food provisioning, whereas we measured feeding rates after extra food provisioning, in both the middle (8–17 days) and late (18–22 days) nestling rearing stage. In our study, total feeding rate during the middle and late nestling rearing stage did not differ between food-supplemented and control broods. This suggests that male parents from food-supplemented nests compensated for the reduction in the rate of internal feedings by increasing the number of external feedings, rather than decreasing their total effort. Interestingly, we observed 15 instances in which the male transferred the prey to the female inside the nestbox; this happened 4 times in 3 control broods (1326 min of footage) and 11 times in 3 food-supplemented broods (964 min of footage). Feedings are often announced by vocalizations outside the nestbox, and we could unambiguously determine the sex of the parent vocalizing in 37 instances: 33 times it was the male, and 4 times, the female (in 4 food-supplemented nests and 2 control nests). This behaviour, in which the male vocalizes outside the nestbox and transfers prey to the female inside, has been previously observed in the Eurasian kestrel (Sonerud et al. 2013, 2014). Recent evidence demonstrates that partners can vocally negotiate over parental effort, for example, when coordinating their incubation shifts (Mariette 2019). In lesser kestrels, the male might vocalize before prey delivery to check if the female is already inside the nest or if the nestlings approach the entrance to receive the prey (when they are older). The latter instance might provide a simple mechanism guiding the passage from internal to external feedings towards the late nestling rearing stage. These observations suggest that male parents responded to the initial availability of extra food by changing their offspring provisioning behaviour: improved growth of food-supplemented broods might induce males to enter the nest less often to deliver prey. A second, non-mutually exclusive explanation is that early food abundance caused shifts in male and female provisioning roles (e.g. Wieringa et al. 2019). The change in male provisioning behaviour may be the outcome of sexual conflict, i.e. benefiting the male to the detriment of female fitness, or cooperation, i.e. benefiting the fitness of both parents. Future studies on the relationship between the timing of male and female foraging trips, the use of vocal negotiation over parental effort, and parental fitness will help to clarify the extent of cooperation in this species.

## Sibling competition

Contrary to our predictions, providing extra food to the broods during early nestling rearing did not increase the frequency of aggressive interactions or begging persistency during the middle-late nestling rearing stage. However, extra food provisioning altered sibling competition in relation to the sex ratio of the brood. Indeed, the rate of aggressive interactions was higher in female-biased broods among control nests and tended to be higher in male-biased broods among food-supplemented nests (Fig. 2b). Despite females not being significantly heavier or larger than males at 8–10 days post-hatching in our sample, a previous study showed that female lesser kestrel nestlings have a higher maximum growth rate and reach a higher body mass at 20 days post-hatching compared to males (Braziotis et al. 2017). Hence, females are expected to have higher energy requirements (Anderson et al. 1993b; Riedstra et al. 1998; Kalmbach et al. 2009). For example, female nestlings of the European sparrowhawk (*Accipiter nisus*) have a total metabolised energy equal to 1.4 times that of males (Vedder et al. 2005). Therefore, competition for resources is likely to be more severe in female-biased broods (Uller 2006), causing more frequent aggressive interactions. When extra food is provided to these broods, female nestlings may acquire the additional resources to the detriment of male siblings (competitive advantage hypothesis, e.g. Anderson et al. 1993a; Arroyo 2002; Nicolaus et al. 2009). In this regard, we note that last-hatched nestlings were more often males (see Results and Podofillini et al. 2019), and thus, male nestlings further suffer from a size disadvantage due to hatching delay. In male-biased broods, extra food may be shared more evenly and promote nestling growth, because each male nestling requires a lower share of resources to grow. In line with this prediction, food-supplemented nestlings in our study grew longer tarsi by 8–10 days of age if they belonged to male-biased broods (Supplementary Table S3; Supplementary Fig. S1b). However, contrary to our predictions, we did not find evidence of lower body mass asymmetry in food-supplemented broods at the end of the period of extra food provisioning, irrespective of brood sex ratio (see Supplementary Table S4). Hence, the observed tendency of aggressive interactions to become more frequent in male-biased food-supplemented broods is not due to reduced competitive asymmetry between nestlings leading to repeated thefts of the same prey among siblings. The most likely explanation for the higher rate of aggressive interactions in male-biased food-supplemented broods is that nestlings in these broods were hungrier (e.g. Machmer and Ydenberg 1998). Indeed, given that extra food supply supported nestling growth in male-biased broods more than in female-biased broods, male-biased broods may have reached their maximum growth rate earlier than female-biased broods.

Finally, during food stealing attempts, younger nestlings has higher begging persistency than older nestlings in both food-supplemented and control broods. Begging in this case is likely to be a signal of need and willingness to compete for a prey item. As found for barn owls (*Tyto alba*), younger nestlings might vocalize more to deter their older siblings from stealing a prey item, as they have a competitive disadvantage (Roulin et al. 2008).

## Parent-offspring conflict

In line with the higher energy requirements expected for female-biased broods (Vedder et al. 2005; Kalmbach et al. 2009), female-biased control broods were provisioned more often. However, in nests that received extra food, total parental feeding rate increased with the proportion of male nestlings (Fig. 2a). If male-biased broods reached their maximum growth rate earlier than female-biased broods in food-supplemented nests, this may have required an increase in parental feeding effort. More prey delivered means also there is more prey to fight over; hence, higher provisioning rates could have directly caused the increase in aggressive interactions found for male-biased food-supplemented broods. This explanation is unlikely, however, as total parental feeding rate did not significantly predict the rate of aggressive interactions per nestling (see Results). Finally, while external feeding rate increased with the proportion of male nestlings in food-supplemented broods, as did total feeding rate, when we analysed internal feedings only, we found that both parents were provisioning more often female-biased broods irrespective of food supplementation. This inconsistency is likely due to the fact that internal feedings occurred only during the middle nestling rearing stage (8–17 days), whereas external feedings were observed throughout the middle-late rearing stage (recorded from 9 days post-hatching up to 22 days post-hatching). In addition, in the subsample of 15 nests in which we observed internal feedings, female-biased broods were also younger (correlation between sex ratio and mean brood age, Pearson's $r = 0.72$), and internal feeding rates are higher for young broods (see Supplementary Table S2).

The index of parental favouritism (ratio between the maximum number of feedings received by a nestling in the brood and total number of feedings received by the brood) did not decrease in food-supplemented broods, contrary to our prediction. Indeed, nestlings in food-supplemented broods did not have a reduced body mass asymmetry at the end of the period of extra food provisioning. However, food was not shared equally among broodmates in both food-supplemented and control broods; broods. In our sample, mean brood size was 3 nestlings; hence, if all members of the brood were fed equally, the index would be 0.33, whereas all broods exceeded this value and the mean favouritism index value was 0.64. Female nestlings tended to receive a larger share of feedings compared to males, as observed in Eurasian kestrel broods (Fargallo et al. 2003). The fact that the mean proximity to the parent was a better predictor of a nestling's feeding rate compared with mean proximity to the nest site entrance may suggest active parental choice, i.e. potential parental favouritism for female nestlings. This would be in line with previous findings on biased parental food allocation in relation to offspring sex in species showing sexual dimorphism in size (Magrath et al. 2004, 2007; McDonald et al. 2005). The favouritism index increased with brood age, controlling for brood size (see Table 3); feedings became highly skewed at 18–20 days post-hatching. At this age parents almost never enter the nest to deliver prey items (Podofillini et al. 2018; see also Supplementary Table S2), so this skew in within-brood food allocation likely depends on sibling competition rather than parental favouritism, and it may result from the firm establishment of a dominance hierarchy among siblings (Drummond 2006). In line with this hypothesis, aggressive interactions also decreased in frequency with increasing nestling age. Therefore, as previously suggested for the northern goshawk (*Accipiter gentilis*) (Byholm et al. 2011), both parental and offspring control of resources may take place at different time points during nestling rearing. Finally, we did not find evidence of parental favouritism towards older nestlings. On the contrary, feeding rate was higher for younger nestlings, independently of food supplementation. It is unlikely that this finding reflects active parental allocation to younger nestlings, considering the frequent brood reduction occurring in this species, normally at the expense of younger nestlings (Podofillini et al. 2019). A more likely explanation may be that after 15–17 days post-hatching nestling growth rate and energy intake decrease and parents adjust feeding rate accordingly, as observed in Eurasian kestrel broods (Steen et al. 2012).

## Concluding remarks

The present study provides novel insights into how food availability shapes parental care behaviours by integrating the three levels of interaction within a family. We demonstrate that initial food availability during breeding affects at the same time both parental provisioning behaviour and sibling competition. The response to extra food was likely mediated by sex differences in energy requirements and growth rates. Indeed, female nestlings (i.e. the larger sex) tended to receive more feedings compared with males. In addition, female-biased broods showed higher sibling competition (rate of aggressive interactions) and parents fed these broods more frequently (total parental feeding rate) in controls. Extra food promoted nestling growth in male-biased broods, thus inducing higher parental feeding effort and sibling competition, likely due to earlier maximum growth rates. Therefore, we here provide evidence for the often implicit assumption that behavioural interactions among family members are intrinsically interdependent and respond simultaneously to changes in resource availability. In addition, brood sex ratio emerged as a key determinant of parental effort, sibling competition, and parent-offspring interactions even in a species with moderate reverse sexual dimorphism in size among offspring.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00265-021-02970-0.

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**Data availability** The dataset analysed in this study is available in Figshare, DOI: https://doi.org/10.6084/m9.figshare.13502553

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interests.

**Ethics approval** Handling of wild birds was performed by the Italian Institute for Environmental Protection and Research (ISPRA) under the authorization of Law 157/1992 [Art. 4 (1) and Art. 7 (5)]. No bird was injured by the handling procedure. All applicable international, national, and/or institutional guidelines for the use of animals were followed.

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