



Sex-specific food provisioning patterns by parents in the asynchronously hatching European hoopoe



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Hatching asynchrony is common among bird species. It results from starting incubation before clutch completion and is often accompanied by brood reduction, an adaptive strategy of the parents to selectively starve the younger chicks in times of food scarcity. The different developmental stages of nestlings are expected to affect their competitive abilities, their hunger state and thereby parental food allocation patterns. Here we used the combination of a correlative and an experimental field study to investigate sex-specific feeding patterns in the hoopoe, *Upupa epops*, in relation to a chick's rank and hunger state. Male parents showed a strong bias in their feeding pattern towards larger chicks, while females' feeding pattern was significantly more even. Only females were responsive to experimentally altered chicks' hunger state, especially so with small chicks at the lower end of the size hierarchy. This differential food allocation pattern mainly resulted from females mostly entering the nestbox to feed the chicks, while males more often delivered prey from the nestbox entrance hole without entering the cavity. Hence, when entering the nestbox, females can exert some parental control over food allocation, whereas competition among chicks to access the entrance hole mainly rules food allocation when the parents feed from the nestbox entrance hole. Similar sex-specific feeding patterns might be widespread in cavity breeders and it remains to be investigated to what extent variation in these male and female feeding patterns can affect nestling mortality and ultimately breeding success.

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Hatching asynchrony is common among bird species and implies the start of incubation before clutch completion, resulting in chicks hatching on different days. This leads to chicks of different ages within a brood, i.e. a size hierarchy among the nestlings that varies strongly among species (Stenning, 1996). There are several hypotheses explaining this incubation or breeding pattern, most seen as a female strategy to maximize reproductive success (Lack, 1968; Mock & Forbes, 1995). A popular hypothesis for species showing extreme hatching asynchrony is the so-called brood reduction hypothesis that states that hatching asynchrony is an adaptation to uncertainties in food availability. In years of scarce food supply, the youngest and smallest chicks will die without endangering the development of the older chicks. In synchronous broods in which all chicks have the same age, there would be stronger competition, which would result in all nestlings being in poorer condition (Valkama, Korpimäki, Holm, & Hakkarainen,

2002). Therefore, it may pay to produce fewer chicks of good quality rather than many chicks in poorer condition (Szollosi, Rosivall, & Torok, 2007).

A consequence of strong hatching asynchrony is that male and female parents face the task of allocating food to their nestlings that vary not only in hunger state but also in age, size and competitive abilities. What allocation rules parents should use when feeding their dependent offspring under such conditions is not trivial and has been the focus of theoretical research (Lessells, 2002). Models indicate that whenever nestlings within a brood vary considerably in competitiveness or the degree of required care, selection is expected to favour division of labour among parents (Lessells, 2002). This form of parental care where males and females specialize on specific tasks, thereby making it impossible for single dominant offspring to simultaneously solicit food from both parents and so reducing parent–offspring conflict, is a form of cooperation among both parents that can result in sex-specific feeding patterns also known as parentally biased favouritism (Lessells, 2002).

Indeed, there is good correlative and experimental evidence that males and females feed different subsets of chicks within a brood. Even in species showing a small degree of hatching asynchrony, males

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often feed the loudest chicks or those closest to them, which are, by competition among the nestlings, often the older and bigger ones (blue tit, *Cyanistes caeruleus*: Dickens, Berridge, & Hartley, 2008; great tit, *Parus major*: Kölliker, Richner, Werner, & Heeb, 1998; tree swallow, *Tachycineta bicolor*: Leonard & Horn, 1996). Females, on the other hand, rather feed smaller nestlings, thus ensuring their survival, possibly to compensate for the feeding behaviour of the male which feeds stronger chicks (tree swallow: Leonard & Horn, 1996; pied flycatcher, *Ficedula hypoleuca*: Gottlander, 1987). Stamps, Clark, Arrowood, and Kus (1985) found that in budgerigars, *Melopsittacus undulatus*, a species showing high hatching asynchrony but low chick mortality, females devalued begging according to age and size of the nestling, so that food was allocated without advantages for the bigger chicks. Males, on the other hand, only responded to the begging of the offspring, feeding the stronger beggars more, regardless of their size. Finally, Budden and Beissinger (2009) found that male green-rumped parrotlets, *Forpus passerinus*, another species with high hatching asynchrony and low chick mortality, biased their feeding towards the older nestlings, while females fed late-hatched chicks more in large broods. This intriguing sex-specific feeding pattern appears when chicks are still in the nest (Kölliker et al., 1998) and seems to be widespread after fledging (reviewed in Lessells, 2002; Slagsvold, 1997a), while the underlying mechanisms are not well understood yet.

Few studies indicate that parents try to reduce offspring competition by adjusting their feeding positions to each other. In great tits, parents fed from consistent, and different, positions within the nestbox (Kölliker et al., 1998; Lessells, 2002), thereby probably reducing the degree of chick competition and ultimately also parent–offspring conflict. Whether different feeding positions can affect the allocation patterns in relation to chick characteristics remains untested. It is suggested that certain feeding positions might favour large and dominant offspring and lead to the starvation of young nestlings under adverse environmental conditions, especially so in species showing hatching asynchrony (Lessells, 1998; Mock & Forbes, 1995).

Hoopoe, *Upupa epops*, broods have strong hatching asynchrony. Incubation starts with the laying of the first up to the third egg; females typically lay 5–10 eggs (mean clutch size: 6.89 ± 1.92 eggs in our study population). During incubation and for the first 8–10 days following hatching of the first chick, only the male provides food while the female stays inside the nest and covers the young until they can regulate their body temperature (Cramp, 1985; Kristin, 2001). Food items are then mainly transferred from the male to the female, which then directly feeds the chicks. Nestling mortality in this species mainly occurs within the first 8–10 days (Kubik, 1960; Martin-Vivaldi, Palomino, Soler, & Soler, 1999); the last nestling in the hierarchy has the highest probability of dying and only the female allocates the food among the chicks (Martin-Vivaldi et al., 1999). Previous data indicate that nestling mortality often occurs within the first few days after hatching and that mortality is generally high, ranging from 20% (Arlettaz, Schaad, Reichlin, & Schaub, 2010a) to almost 50% of the chicks within a brood (Kubik, 1960). These results suggest that hoopoes adopt a brood reduction strategy. Once the female leaves the nest, she helps in providing food to the offspring during the remaining 12–18 days until fledging, although to a lesser extent than the male (Cramp, 1985; Kristin, 2001). The present correlative and experimental study investigated fine-scaled variation of male and female feeding patterns in relation to a chick's age and state of need. For this purpose we monitored food provisioning and allocation by parents when both adults were feeding (Arlettaz et al., 2010a; Guillod, Arlettaz, & Jacot, 2016) and when food demand by chicks was highest (maximum growth rate, Arlettaz et al., 2010a). The largest part of brood reduction may already have happened at this brood

stage but chick mortality can still occur at this time and later on (Martin-Vivaldi et al., 1999). We examined whether males and females feed different subsets of nestlings within a brood, with respect to age/size of the nestlings and their own feeding position. In an experimental approach we further investigated how males and females react to different states of need of small and large chicks within the size hierarchy. Again, we examined whether male and female feeding patterns differ with respect to chick age/size and chick hunger level. This study provides insights into the fine-scaled feeding patterns of male and female Hoopoes and the mechanisms underlying variation in feeding patterns.

METHODS

General Methods

This study was conducted in a hoopoe population breeding in nestboxes in the upper Rhône valley in Valais in 2011. Further specifications about the study area are described in detail in Arlettaz et al. (2010b). Nestboxes were checked regularly for start of egg laying and hatching. In Valais, molecrickets, *Gryllotalpa gryllotalpa*, are the most profitable prey of hoopoes, making up most of the biomass provided to chicks (Arlettaz et al., 2010a, 2010b; Fournier & Arlettaz, 2001; Guillod et al., 2016). Molecrickets have a life cycle of 2 years and all three age classes are available during the breeding season of the hoopoe (Thorens & Nadig, 1997). Adult molecrickets are large and cannot readily be swallowed by young chicks until around the age of 5 days (own observations; Slagsvold & Wiebe, 2007).

Correlative Field Study: Sex-Specific Feeding Patterns

By filming the nestboxes from the inside, we observed how often and what prey males and females fed to their offspring. The recording system consisted of small infrared cameras (Conrad CMOS B/W camera with IR-LED light; lens 3.6 mm, Germany) connected to a solid-state recorder (Lupus AEON-MDVR Mini Security Recorder, Germany) and powered by two batteries (Panasonic 6V Rechargeable Sealed Lead-Acid Battery, Japan). When the oldest chick was around 12 days old (range 11–15 days), the brood was filmed during 15 h (0530–2000 hours). Day 12 was selected because both parents provide food and provisioning activity is high due to a high energy demand by chicks at this brood stage (Arlettaz et al., 2010a). Nestlings at this stage engage in physical competition (i.e. gaping, neck stretching, standing, wing flapping) and use vocal cues when begging for food; the degree of begging intensity most likely reflects a chick's state of need (Kilner & Johnstone, 1997). Nestling mortality of our focal broods, calculated as the difference between clutch size and fledging number, ranged between 0 and 83% with a mean nestling mortality of $41.55 \pm 18.45\%$. Most nestling mortality happened within the first 12 days (Poisson generalized linear mixed model, GLMM: -0.46 ± 0.04 , $t = -10.26$, $P < 0.001$), while nestling mortality still occurred until fledging (Poisson GLMM: -0.13 ± 0.05 , $t = -2.59$, $P = 0.01$). A total of 30 nestboxes were analysed: 24 of them were filmed completely and six only partly (range of recorded time 5–11 h).

The day before filming, we measured tarsus length and weight of all nestlings, ranked them according to their body mass (tarsus length was used to distinguish between chicks with very similar weights) and we marked each chick individually on its bill with small spots of light blue acrylic paint. We never observed that parents pecked on the markings of the chick's bill. The parents were caught before the filming (when the oldest chick was about 4 days old), and the female was marked with light blue acrylic paint on the head and bill to distinguish it on the video recording from the male.

For each recorded feeding event, we noted (1) which parent (male/female) was feeding, (2) which chick (rank) was fed, (3) what it was fed (prey category and item size class), (4) time of day and (5) whether the parent entered the nestbox to feed or fed from outside. We distinguished between different prey dry biomass categories (based on three item size classes for molecrickets, and another for Lepidoptera larvae and other small invertebrate prey items) according to Arlettaz and Perrin (1995, see their appendix 2). Big molecrickets have an average dry biomass of 0.68 g, medium molecrickets 0.46 g and small molecrickets 0.36 g. Caterpillars, worms and other insect larvae were attributed an average dry biomass of 0.08 g. Small unknown prey we also assigned a biomass of 0.08 g while to medium unknown prey we assigned a biomass of 0.36 g (Arlettaz et al., 2010a).

Experimental Field Study: Hunger Experiment

A hunger experiment was performed when the oldest chick was 13–15 days old, i.e. a few days after the correlative study was performed. The brood was divided into three size/age categories: junior chicks (smaller chicks, i.e. youngest third of the brood), medium chicks (the middle-aged third of the brood) and senior chicks (the largest, i.e. oldest third of the brood). Brood size ranged from three to eight chicks. Whenever brood size made it impossible to separate chicks into three equal age categories, we preferentially allocated the chicks to the extreme two age categories, e.g. a brood of five chicks resulted in two junior, one middle-aged and two senior chicks. To investigate the effect of hunger status on food allocation patterns in adults, chicks were either exposed to experimental food deprivation for 95 min ('Hungry' treatment; isolated and transferred to dummy nestbox) or they were fed with four or five medium-sized crickets, *Acheta domestica* ('Satiated' treatment; fed in isolation, time span <10 min). The 'Hungry' treatment corresponds to a lack of approximately seven feeding events per brood (Arlettaz et al., 2010a), i.e. one or two feeding events per chick. Treatments were always performed with one randomly selected junior and one senior nestling for each brood and each nestling experienced both hunger treatments (i.e. Senior Satiated and Hungry; Junior Satiated and Hungry) on 2 consecutive days in a randomized order. During one experimental trial only one chick per brood was treated and a maximum of two trials per brood were performed per day. These manipulations were performed on 28 broods (56 chicks in 112 experiments in total). Begging behaviour and parental food allocation were filmed during the 3 h following the experimental treatment, and we focused on the first three feedings to the brood for later analyses.

The begging behaviour of the chicks was recorded with the camera system described above. The following begging measures were taken: (1) begging intensity of the focal chick, (2) begging duration (s) of the focal chick, (3) chick identity that received the food and (4) the sex of the feeding parent. Our index of begging intensity most likely reflects the combination of physical engagement in scramble competition together with vocal begging intensity (Roulin 2001) and was classified using four begging postures: 0 = not begging, 1 = gaping, 2 = gaping and neck stretching, 3 = gaping, neck stretching and standing, 4 = all former three measures plus wing flapping (according to Griffith 2007). Begging duration was not measured when the focal chick received the food, since the feeding event interrupts the begging behaviour.

Analysis

All statistical analyses were done with R, version 3.0.2 (R Development Core Team, 2013). Nestling mortality was analysed using a GLMM with Poisson error distribution, number of offspring

as dependent variable and brood stage (clutch size, number of nestlings at day 12, number of fledglings) as independent variable and nest as random factor. The mean delivered prey biomass in relation to the sex of the parent was analysed using a general linear mixed model (package nlme, Pinheiro, Bates, DebRoy, & Sarkar, 2013) with the body mass of each delivered prey item as dependent variable, sex of the parent as independent variable and box and adult ID as random factors. The number of feedings per day was analysed using a GLMM with Poisson error distribution with the sum of the number of feedings as dependent variable, sex of the parent as independent variable and nestbox as random factor. To analyse the feeding pattern in relation to chick rank and feeding position, we used GLMMs with Poisson error distribution with the number of feedings per chick as dependent variable, sex of the parent and feeding position (entering/not entering the box) as fixed factors, chick rank as continuous covariate and nestbox as random factor. Analyses were still performed with chick rank as continuous variable (1 = oldest chick, 2 = second oldest chick, etc.), but the graphs show the chick classes.

In the experimental study we analysed the following variables for each focal chick: probability of begging, begging intensity, begging time and the probability of being fed. The probability of begging (yes/no) was analysed using a GLMM with binomial error distribution, with the hunger treatment (Hungry/Satiated), chick rank (Junior/Senior) and their interaction as fixed factors and box and chick ID as random terms (glmmPQL, Venables & Ripley, 2002). Nestling begging time was analysed using a GLMM with Gaussian error distribution, with the hunger treatment (Hungry/Satiated), chick rank (Junior/Senior) and their interaction as fixed factors and box and chick ID as random terms. Begging intensity (ordinal response), was analysed with the package 'ordinal' with cumulative link mixed models (clmm), with the same model structure as described in the previous two analyses. Finally, to analyse the treatment effects on the probability of being fed (yes/no) we used a GLMM with a binomial error distribution. The independent variable was the outcome of the first three feedings to the brood for the focal chick, with the first three feedings to the brood after the experimental manipulation entered as dependent variable and again with the hunger treatment (Hungry/Satiated), chick rank (Junior/Senior) and their interaction as fixed factors, brood size as covariate and box and chick ID as random terms. For model simplification, we used a stepwise backward procedure and tested the significance of predictor variables in a hierarchical fashion, retaining lower order effects in the analyses when a higher order term was significant. For each analysis we present the model estimate with its standard error and the test statistics.

Ethical Note

All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed in this study were in accordance with the ethical standards of the Swiss Federal Office for the Environment (FOEN) and the Swiss Ornithological Institute and comply with the Swiss legislation.

RESULTS

Correlative Study: Sex-Specific Feeding Patterns

Males and females differed in their feeding patterns: females fed their offspring more often than males (Poisson GLMM: -0.72 ± 0.04 , $z = -17.43$, $P < 0.001$) and with smaller prey items (GLMM: 0.09 ± 0.03 , $t_{28} = 2.91$, $P < 0.01$). Moreover, the sexes differed in their feeding pattern in relation to chick rank (Poisson

GLMM: chick rank*sex: -0.15 ± 0.03 , $z = -5.59$, $P < 0.001$). A post hoc test revealed that males showed a stronger feeding bias in relation to chick rank (Poisson GLMM: -0.22 ± 0.02 , $z = -9.27$, $P < 0.001$) than females (Poisson GLMM: -0.05 ± 0.02 , $z = -2.92$, $P = 0.004$; Fig. 1): large chicks were fed more than small chicks. This sex-specific food allocation pattern is partly explained through parental differences in entering the box when feeding. Females mostly entered the box to feed (92.33%, 1612/1746 feeding events; paired t test: $t_{29} = 5.69$, $P < 0.001$), while males fed equally from inside (59.87%, 461/770 feeding events) and outside (40.31%, 309/770 feeding events; paired t test: $t_{29} = 1.07$, $P = 0.29$). When analysing the data in relation to feeding position, we found that both sexes preferentially fed larger chicks when feeding from outside (Poisson GLMMs: males: chick rank*position: -0.29 ± 0.05 , $z = -6.2$, $P < 0.01$; females: chick rank*position: -0.12 ± 0.05 , $z = -2.51$, $P = 0.01$). Males' preference for older chicks was stronger when feeding from outside (Poisson GLMM: -0.38 ± 0.04 , $z = -10.65$, $P < 0.001$) and weaker, but still detectable when feeding from inside (Poisson GLMM: -0.08 ± 0.03 , $z = -2.61$, $P = 0.009$). In contrast, females only biased their feeding pattern towards older chicks when feeding from outside (Poisson GLMM: -0.20 ± 0.05 , $z = -4.41$, $P < 0.01$; Fig. 2a, b), while no bias was detected when feeding from inside (Poisson GLMM: -0.009 ± 0.02 , $z = -0.53$, $P = 0.60$; Fig. 2a, b). Additionally, males in comparison to females, always biased their feeding pattern more towards larger chicks when feeding from outside (Poisson GLMM: sex*chick rank: -0.18 ± 0.06 , $z = -3.10$, $P = 0.002$) and when entering the box to feed (Poisson GLMM: sex*chick rank: -0.10 ± 0.03 , $z = -3.03$, $P = 0.002$).

Experimental Study: Hunger Experiment

The hunger experiment affected a chick's probability of begging (binomial GLMM: 1.13 ± 0.27 , $t_{280} = 4.15$, $P < 0.001$): junior chicks were more likely to beg than seniors (binomial GLMM: -0.99 ± 0.46 , $t_{56} = -2.13$, $P = 0.03$) and the treatment effect was independent of age category (binomial GLMM: age category*treatment: -1.08 ± 0.60 , $t_{279} = -1.79$, $P = 0.07$). Both begging intensity (ordinal GLMM: 0.64 ± 0.10 posture index/h,

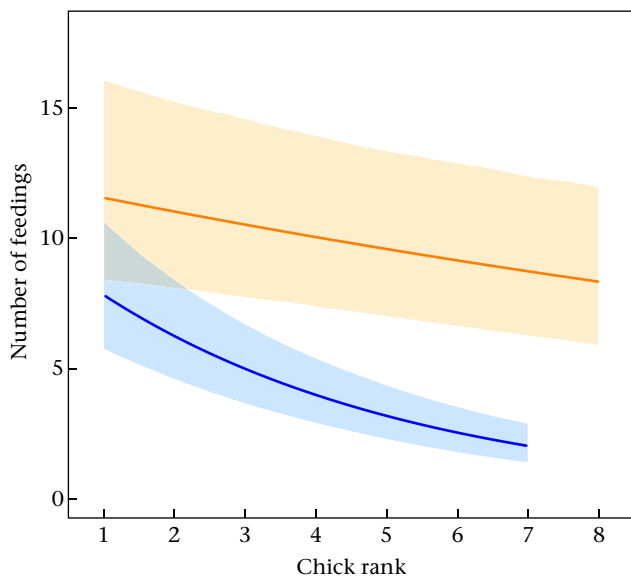


Figure 1. Relationship between chick rank (1 = largest chick) and the number of feedings by females (orange) and males (blue). The 95% CrI (credible intervals) are shown in light orange and light blue within the range of observations.

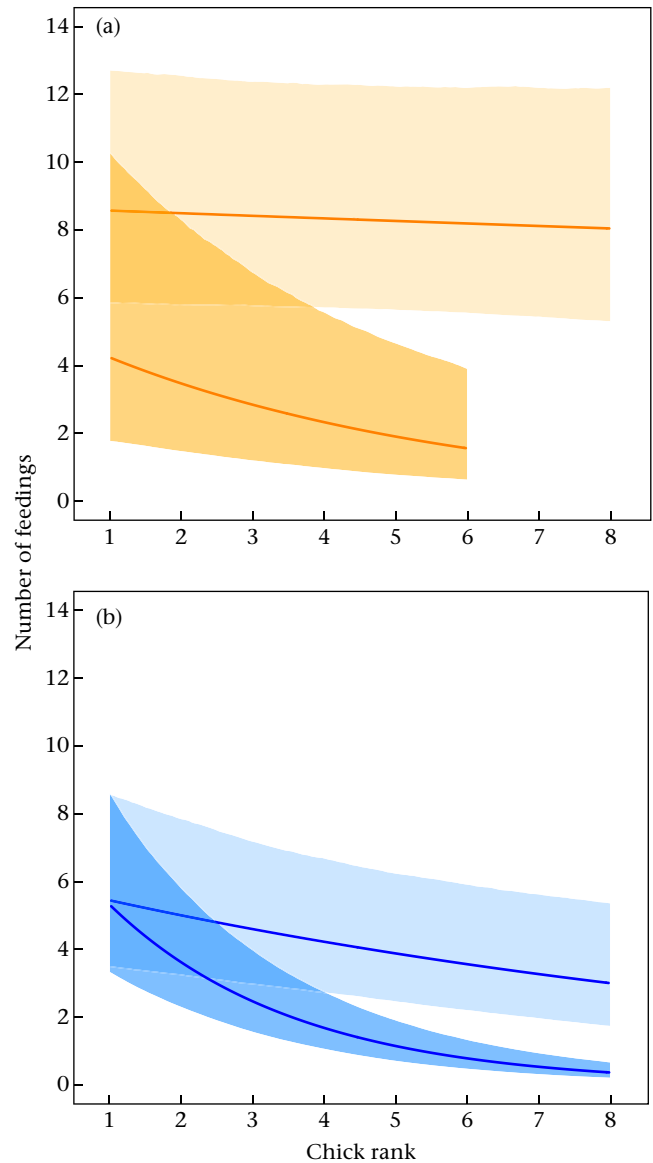


Figure 2. Relationships between chick rank (1 = largest chick) and the number of feedings of (a) females and (b) males in relation to the feeding position. The light colour indicates the 95% CrI (credible intervals) of feedings from inside, while the darker colour indicates those for feedings from outside, always within the range of observations.

$t_{365} = 6.49$, $P < 0.001$) and begging duration (GLMM: 4.18 ± 1.32 s, $t_{365} = 3.16$, $P < 0.01$) were affected by the treatment. Hungry chicks begged at a higher posture and for a longer time. These results demonstrate that the experiment effectively altered the chick's state of need, a prerequisite when investigating sex-specific food allocation patterns.

As the three-way interaction between the sex of the parents, the hunger treatment and the age category was not significant (binomial GLMM: sex*treatment*age category: 0.48 ± 1.09 , $t_{275} = 0.43$, $P = 0.66$) we analysed each group separately. Food allocation was affected by the chicks' nutritional treatment only in female parents. Females were more likely to allocate food to hungry juniors (binomial GLMM: 1.44 ± 0.54 , $t_{57} = 2.62$, $P = 0.01$; brood size: -0.54 ± 0.27 , $t_{22} = -2.02$, $P = 0.06$; Fig. 3), while the effect was weaker and nonsignificant in seniors (binomial GLMM: 0.80 ± 0.52 , $t_{63} = 1.53$, $P = 0.13$; Fig. 3). Males fed junior (binomial

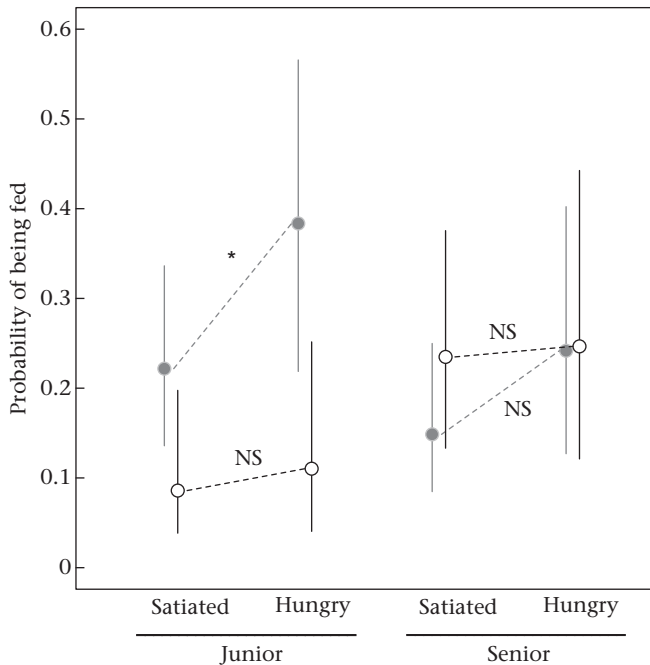


Figure 3. The probability (mean \pm 95% CrI) of being fed according to the feeding treatment. The grey symbols indicate the female's and the white symbols the male's food allocation to the chicks.

GLMM: 0.54 ± 0.50 , $t_{59} = 1.07$, $P = 0.28$) and senior (binomial GLMM: 0.42 ± 0.52 , $t_{53} = 0.81$, $P = 0.42$; brood size: -0.63 ± 0.32 , $t_{24} = -1.97$, $P = 0.06$) chicks irrespective of their state of need (Fig. 3).

DISCUSSION

This field study demonstrates that hoopoes show sex-specific feeding patterns: males allocate more food to older chicks within the size hierarchy than females. This result is partly explained by the sex of the adult birds but additionally by the feeding location (inside versus outside of nestbox). Males fed significantly more often from outside the nestbox where large, dominant chicks got most food. This feeding pattern was less biased when adults entered the cavity, especially so in females. Females mostly entered the nestbox, fed the chicks more evenly when inside the cavity and were more attentive to the nutritional state of chicks, specifically to young, subordinate chicks.

In line with other studies (e.g. Budden & Beissinger, 2009; Leonard & Horn, 1996; Stamps et al., 1985) we found that females fed the chicks more evenly than males, which preferentially fed large and old chicks. It is often argued that the male's feeding pattern reflects the outcome of chick competition, meaning that older chicks are more capable of dominating the feeding event by reaching closer to the feeding parent than smaller chicks (Budden & Beissinger, 2009; Dickens et al., 2008). The proximate mechanism behind the males' behaviour in the present case is best explained by whether the parent enters the nest cavity or not. When entering the box, both male and female hoopoes showed a more even feeding pattern, while they biased their feeding pattern more when feeding from outside. When parents feed from outside, chicks engage in scramble competition: the chick that is reaching highest to the entrance hole, and thus is closest to the feeding parent, is most likely to get the prey item (Dickens et al., 2008). As a result, small, subordinate chicks have a very poor chance of getting food under such a feeding regime. However, when parents feed from inside the box they are probably

better able to distinguish and select the neediest chicks via the intensity of their begging display and thus may exert some parental control over food allocation (Aviles, Parejo, & Rodriguez, 2011). The degree of parental control may differ between males and females, since male hoopoes still showed a strong bias towards large chicks when feeding from inside. Females had an even feeding pattern but, given the higher overall feeding rate, we cannot exclude that fine-scaled preferences in the feeding pattern (see Fig. 1) are somehow masked by a ceiling effect. However, in line with our results in the correlative approach, we found that only females reacted to experimentally food-deprived young chicks, most likely because they often entered the nestbox when feeding, thereby detecting and subsequently feeding the needy chick.

Our results are in line with theoretical models predicting division of labour among parents when chick competition varies within broods (Lessells, 2002). But why are we observing this consistency in sex-specific feeding patterns, i.e. why are the females not feeding from outside? Or in other words, why are males more reluctant to enter the cavity when feeding? Several nonmutually exclusive hypotheses might explain this sex-specific behaviour. First, the consistency of the roles of the two sexes could be a consequence of the investment during the early brood stage, as females are the sex that incubates the clutch and allocates food to the young nestlings. Females may be preadapted and specialized on tasks related to brood care that persist until an advanced brood stage. Second, female hoopoes might have been selected to choose the smallest possible entrance hole of their breeding cavity in order to minimize the risk of predation. Given the sexual dimorphism of this species (ca. 5–10%), larger males may have difficulties entering the cavity and may thus have adopted a strategy to feed from outside. Alternatively, by feeding from outside, males might reduce the risk of being predated, or avoid parasite and pathogen infections (e.g. Heeb, Kölliker, & Richner, 2000), which would affect their residual reproductive success. Females, on the other hand, can only increase their reproductive success by investing in their own brood, except for species that show intraspecific brood parasitism, which is definitely not the case for hoopoes (Berthier, Leippert, Fumagalli, & Arlettaz, 2012). Whatever the ultimate cause of these differential sex-specific tactics, this 'cryptic' division of labour among hoopoe parents seem to balance food allocation among the chicks and may result in the highest individual fitness gains for both sexes. How variation in breeding conditions (e.g. adverse weather, food shortage) can affect preferences for specific feeding positions, where allocation rules are dominated by chick competition that leads to the starvation of the youngest chicks, needs to be further investigated.

Interestingly, several studies on secondary cavity-breeders have similarly found that males preferentially feed the larger and females the smaller chicks (Budden & Beissinger, 2009: green-rumped parrotlets; Stamps et al., 1985: budgerigars; Leonard & Horn, 1996: tree swallows; Gottlander, 1987 and Lifjeld, Breihagen, & Lampe, 1992: pied flycatchers; Krebs & Magrath, 2000: crimson rosellas, *Platycercus elegans*; Sasvari, 1990: great tits). In all these examples, differential food allocation between the sexes might simply be explained by a mechanism similar to that in the hoopoe, with males being more reluctant than females to enter the brood cavity to feed offspring. It is symptomatic in this respect that most studies showing no sex-specific food allocation rules all concerned species breeding in the open (but see Westneat, Clark, & Rambo, 1995), such as the American robin, *Turdus migratorius* (Slagsvold, 1997b; Weatherhead & McRae, 1990), white ibis, *Eudocimus albus* (Frederick, 1987) and the bluethroat, *Luscinia svecica* (Smiseth, Amundsen, & Hansen, 1998, 2003). In this group of birds, the feeding position of parents may play a smaller role in food allocation to chicks, and thus not influence the outcome of chick competition for food acquisition.

Taken together, these results may highlight a mechanism accounting for nestling mortality at a late brood stage. Once both parents are feeding the chicks, at a time when most nestling mortality, i.e. brood reduction, has happened, females may adopt a compensatory behaviour, preferentially feeding the younger and hungry chicks from inside the box to counteract a male's strong feeding bias towards older and dominant chicks. However, any intrinsic or external factors that affects a female's propensity to enter the box when feeding could negatively affect chick survival and lead to reduced breeding success via increased brood reduction. Under these conditions males and females may increase their bias in feeding from outside so that only those chicks that are in good condition will manage to get the food and fledge. Most importantly, the present study reveals that understanding the proximate mechanisms governing male and female parental investment might shed light on the relative importance of feeding location versus the sex of a bird species. The compelling importance of the feeding position for allocation rules requires further studies to investigate the importance of the feeding position in relation to variation in environmental conditions that may affect reproductive success via enhanced chick mortality.

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