Prey delivery strategy at nestbox determines differential food allocation to nestlings by male and female Hoopoe parents

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Abstract

Hatching asynchrony is common among birds: it results from starting incubation before clutch completion. Hatching asynchrony is often linked to brood reduction, an adaptive strategy of the parents to selectively starve the youngest chicks in times of environmental uncertainty such as food scarcity. The different developmental stages of the nestlings further dictate food allocation by parents. In general, the male feeds according to the outcome of chick competition, favouring the larger and more dominant chicks, while the female often compensates for this bias by preferentially feeding the smaller chicks. By filming Hoopoe (*Upupa epops*) broods from inside nestboxes, we first examined if the occurrence of asynchronous hatching, a species' characteristic, resulted in males and females feeding different subsets of chicks. We then tested whether male quality and/or prey quality (i.e. prey item size) influence the female's feeding pattern. Finally, we studied the links between these provisioning strategies and brood reduction. Males preferentially fed larger chicks, while females fed all chicks evenly. This differential food allocation by parents resulted from females mostly entering the nestbox to feed the chicks while males usually delivered prey from the nestbox entrance hole without entering the cavity. Hence, females can exert some parental control over food allocation, whereas competition among chicks to access the nestbox entrance hole rules prey allocation by males. In terms of prey size, males fed bigger prey to older chicks while females fed all chicks evenly, i.e. irrespective of prey item size. This implies some control of the male over prey distribution to nestlings. Finally, we did not find any effect of male or prey quality on the female feeding pattern, while no brood reduction was observed in our sample. These results indicate that the sex-specific pattern observed in food allocation to nestlings is merely due to differences in the way the genders approach a brood within a cavity. This pattern could be more common than usually thought in cavity-breeding birds.

Keywords

Brood reduction; Entering nestbox; Hatching asynchrony; Hoopoe; Prey size; Sex-specific feeding pattern

Introduction

Hatching asynchrony is common among bird species and implies the start of incubation before clutch completion, resulting in chicks hatching at different days. This leads to chicks of different ages within a brood and to a size hierarchy among the nestlings (Stenning 1996). There are several hypotheses explaining this incubation or breeding pattern, most seen as a female strategy that maximizes reproductive success. For all hypotheses about e.g. sexual conflicts or peak load reduction see Nilsson (1993).

One important hypothesis is the brood reduction hypothesis. It says that hatching asynchrony could be an adaptation to uncertainties in food availability. With asynchronous hatching the youngest chick will die in years of scarce food supply without endangering the development of the older chicks. In synchronous broods where all chicks have the same age, there would be more competition, which would result in all nestlings being in poor condition (Valkama *et al.* 2002). Fledging in poor condition reduces the survival of the offspring (Szollosi *et al*. 2007) and therefore it may pay off to produce fewer chicks of good quality rather than many chicks in poor condition. This means in bad years a trade-off between the number and the quality of chicks limits the number of offspring produced (Nager *et al*. 2000), whereas in years of good food supply, all chicks can fledge regardless of the size differences (Szollosi *et al*. 2007).

Nestlings beg to show their need for food, and the begging behaviour normally reflects the state of a chick, with hungrier chicks begging more than less hungry ones (Kilner & Johnstone 1997; Saino *et al.* 2001). In species with asynchronously hatching chicks, the different sizes of the chicks are likely to have an effect on their begging intensity and thus on the amount of food they receive. Price & Ydenberg (1995) showed that hungry chicks of the yellow-headed blackbird begged more and received more food than satiated chicks. But they also found an effect of the size of the chick. Small food-deprived chicks begged more intensely and received more food than before, but still less than their larger siblings. In tree swallows, Leonard & Horn (2001) found that both parents responded to begging calls of food-deprived nestlings, meaning they preferentially fed the hungrier chicks. But only large nestlings increased the amplitude of their begging calls during food deprivation, but small ones did not.

And Saino *et al.* (2000) showed that in barn swallows parents fed chicks according to both their need and their body condition, and that body condition is assessed independently of begging rate. These examples indicate that parents could control to whom they allocate food. But parental control may not always be absolute, because sibling competition may complicate getting food for small chicks. This means larger chicks can have an advantage when there is direct competition between the nestlings, for example when they position themselves closest to the feeding adult or reach higher and thereby outcompete their smaller siblings (Budden & Beissinger 2009). Such a pattern was found for example in the canary (Kilner 2002), where food distribution depended on the height to which nestlings stretched. Similarly, Smiseth *et al.* (1998) found that parents in the bluethroat fed larger nestlings more than smaller ones, potentially due to the outcome of chick competition. And McRae *et al.* (1993) found that American robin chicks were actively moving each other to obtain the central position where they were more likely to acquire food. These examples highlight the complexity of parental feeding patterns that may often combine aspects of chick competition and parental control.

Differences in feeding subsets of chicks could arise because of a different parental behaviour. It is well known that males and females often feed a subset of chicks after fledging (known as brood division) (e.g. Leedman & Magrath 2003). However, it is less well known that in several bird species male and female parents show preferences for different subsets of chicks while they are still in the nest. This could be because parental care implies a high energy expenditure, and it thus trade-offs with investment into future reproduction (Houston *et al*. 2005). Females can only increase their fitness via their brood, while males can invest into extra-pair copulations (EPCs) to increase their reproductive output (Kempenaers & Dhondt 1993). This can entail a different value of the brood to the parents, meaning that the female will be more interested in raising the whole brood than the male, and these different interests could have an effect on feeding behaviour.

This is shown by the fact that males often just feed the loudest chicks or those closest to them, which are, by competition among the nestlings, often the older and bigger ones (Dickens *et al*. 2008). Therefore this pattern is likely under chick control (Rodriguez-Girones *et al*. 1996). This means, on the other hand, females then rather feed the smaller nestlings – most likely to compensate the feeding behaviour of the male and to ensure the survival of the younger chicks (Budden & Beissinger 2009). There are several studies which found this sex-specific feeding pattern. In a study on tree swallows, Leonard & Horn (1996) showed that males preferentially fed larger nestlings and females smaller nestlings, although they did not find significant differences in begging behaviour of the chicks. In another study with pied flycatchers by Gottlander (1987), not only the begging intensity but also the position in the nest was important for the nestlings to obtain food. But there was still a difference in feeding between the parents, with the females having a preference for feeding the lightest nestlings and the males feeding more evenly. Stamps *et al.* (1985) found that budgerigar females devalue begging according to age and size of the nestling, so that food is allocated without advantages for the bigger chicks. Males on the other hand only responded to the begging of the offspring, they fed the stronger beggars more, regardless of the size. And Budden & Beissinger (2009) found that male green-rumped parrotlets biased their feeding towards the older nestlings, while in large broods females fed late-hatched chicks more. But they received less food than would be expected by their begging behaviour, suggesting that the females respond also to other factors. This sex-specific feeding pattern is intriguing and very widespread among different bird species (see Lessells 2002). There are some hypotheses trying to deliver explanations for this phenomenon (reviewed in Slagsvold 1997a), but the ultimate reason behind it is not well understood yet.

Hoopoe broods show a strong hatching asynchrony. Females normally start incubation after the first or second egg is laid. Hatching then happens with an interval of about 24 hours between the eggs (Martin-Vivaldi *et al*. 1999). During incubation and for the first eight to ten days after the chicks hatched, only the male is providing food. The female stays in the nest and covers the young until they can thermoregulate themselves (Arlettaz *et al*. 2010a). After this period both male and female feed the chicks. But females provide the food more frequently, also because they often receive it from the male (Martin-Vivaldi *et al*. 1999). It has been found by Martin-Vivaldi *et al.* (1999) that the number of surviving chicks was correlated with the amount of food provided by the parents,

which suggests that brood size is adjusted after laying according to food availability. They also found that many chicks actually died at a young age when the female was still in the nest distributing the food, which shows that the survival of the chicks at this stage mainly depends on the male’s provisioning efficiency. But we cannot exclude that female food provisioning patterns in relation to chick size may partly explain age-related mortality among chicks.
However, once the female leaves the nest and thus both parents contribute to chick feeding, there could be a different feeding behaviour of the parents, and the causes of chick mortality may differ. Quite often in the early stages of nesting, male Hoopoes pass prey items directly to the female that feeds the nestlings. Later on, males mostly shortly visit the box, deliver the food and leave again, which indicates that they may rather feed the chicks closest to them or the ones with the highest begging intensity. Males often do not even enter the nestbox but just feed from the outside. In contrast, female Hoopoes normally enter the nestbox to feed and thus could be better able to distinguish between the needs of the chicks and feed selectively (unpublished field observations). So through their food-provisioning behaviour females could compensate for the selective feeding behaviour of the male to prevent young chicks from starving.

In this study we wanted to quantify male and female feeding patterns. For this purpose we observed broods at a stage when both parents are feeding and when food demand within the brood is high. We hypothesized that males and females feed different subsets of nestlings within a brood, with males rather feeding the oldest chicks and females the younger ones. Additionally, we looked at daily feeding rhythms to see if parents differ in their activity over the day. If differences in feeding patterns can be confirmed, we wanted to investigate in a second step variation among these patterns, the underlying mechanisms and their influence on breeding success. It is possible that the subset of nestlings being fed by the female depends on the amount of food brought by the male. The assumption is that in broods where the male feeds a lot, he will mostly feed the larger nestlings and the females will focus on the remaining smaller offspring. However, in broods where the male feeds little, he will only feed few large chicks and the female has to shift her feeding to intermediate chicks. This means the very small chicks will not be fed enough and could die of starvation.

The same shifts in feeding patterns could also be expected to be dependent on the quality of the food items. We predicted that, as soon as prey size is small, the competition among the chicks within a brood will increase which could lead to an increase in brood reduction. When males mainly feed smaller prey items, the larger chicks will be hungry again after a short time and "dominate" the next feedings. This is expected to translate into enhanced mortality of the youngest chicks, since the female will shift her feedings to intermediate chicks and the youngest ones don't get the chance of being fed. To see how feeding patterns change when the size of prey varies, we quantified (Arlettaz *et al*. 2010a) what prey (type and size) the parents feed. Additionally we wanted to know whether different prey is fed to different chicks within a brood, that is whether there is any control of the parents over the size of food items given to the chicks. And we wanted to know if there was any variation in the prey brought by both parents over the course of the day.

In summary, this study aimed at giving insights into the fine-scaled feeding patterns of male and female Hoopoes, the mechanisms underlying variation in feeding patterns and the effects on brood reduction.

Material & Methods

Study species

Our study species was the Hoopoe *Upupa epops*. Once widespread, the Hoopoe has become rare in Central and Western Europe (Arlettaz *et al*. 2010a). Possibly due to climatic fluctuations and agricultural intensification, there was a strong decline in these populations in the last century (Bezzel 2006). In Switzerland, the Hoopoe is red-listed and today is mainly restricted to the Valais in the southwest (Arlettaz *et al*. 2010a).

The study took place in the upper Rhône valley in Valais, between Martigny and Sierre, where nestboxes had been installed. During the 1980s, a population decline was recorded in the Valais (Fournier & Arlettaz 2001). It has been found that the lack of suitable nesting sites in the plain, where the birds find most of their food, was the main cause of decline. Hoopoes are hole-nesting birds that use mostly cavities excavated by woodpeckers or holes in walls and rocks. These were only available on the foothills though, which meant a long flight distance to the feeding grounds in the plain and therefore a low provisioning efficiency

(Fournier & Arlettaz 2001). After these findings, more than 700 nestboxes were installed in the plain to provide nesting sites closer to the food sources (Arlettaz *et al*. 2010b). The population increased steadily afterwards with more than 100 broods per year nowadays (Arlettaz *et al*. 2010a). In past years a slight decrease in reproductive success was observed (Arlettaz *et al*. 2010b) which may have resulted from density-dependent effects (Sierro *et al*. 2008), although the exact mechanism is still unclear. Potential mechanisms range from rapid food depletion in high-density areas to enhanced stress through an increase in intraspecific conflicts (Rodenhouse *et al*. 2003).

In Valais, molecrickets (*Gryllotalpa gryllotalpa*) are the most profitable prey, making up most of the biomass provided to chicks (Fournier & Arlettaz 2001). Molecrickets are up to 5 cm long and live most of the time below ground (Bellmann 1985). Because they have a life-cycle of three years, different sizes are available during the breeding season of the Hoopoe (Thorens & Nadig 1997).

Recording system

By filming the nestboxes from the inside, it was observed how often and what prey males and females fed, and which chicks they preferentially fed. To film the chicks in the nestboxes, 10 camera systems were used. These consisted of small infrared cameras (Conrad CMOS B/W camera with microphone and IR-LED light) with wide-angle lenses (Conrad lens 3.6 mm) and recording systems (Lupus AEON-MDVR Mini Security Recorder) with 4 GB SD memory cards. They were linked to two car batteries (Panasonic 6V Rechargeable Sealed Lead-Acid Battery), which were connected to the system with converter cables (MW DC-DC Convertor and Multiplier) so that the voltage could be set separately for the camera and the recorder. The cameras were attached to 10 newly constructed lids in a way that only the lids and not the whole camera systems had to be exchanged for filming different boxes. The nestboxes are made of wood with a basal area of 24 x 25 cm and a height of 35 cm. The lid was also made of wood with the same basal area and a height of 15 cm. The camera was fixed inside at the top and the cables were put through a little hole on the side. The batteries could then be placed on top of the lid. On boxes which were not totally protected from rain, the batteries and recording system were protected with a plastic cover. To test if the image and sharpness is set right and to program the recorder, a portable screen (Sony Digital Video Cassette Recorder GV-D800E PAL) was used which could be connected to the camera system.

Field work

Most of the nestboxes were installed inside huts and farm buildings (Arlettaz *et al*. 2010b). All boxes were checked in March 2011 to determine which ones were suitable for filming (they required enough space on top for the camera system) and to clean them. Starting in April all nestboxes were checked every second week. Occupied nestboxes were additionally controlled about every second day. They were checked through the entrance hole with a small mirror on a flexible stick and a light bulb. The date of first egg laying was recorded and the approximate date of hatching calculated (+17 days (Martin-Vivaldi *et al*. 1999)). Around the expected hatching day the boxes were checked every day to determine the exact hatching date. The goal was to film as many broods as possible, so all broods that were in accessible boxes usable for filming were included.

The day before the filming started, the chicks were weighed and tarsus length was measured to determine their rank within the brood. They were ranked according to their weight, and tarsus length was used to distinguish between chicks with very similar weights. Then they were marked with light blue acrylic paint (which we found to be visible best on the videos) on the bill. Each chick got a different pattern with different amounts of points on different positions. Big chicks normally got more points than small chicks and very small ones didn't get a mark. The parents were also caught before the filming (when the oldest chick was about 4 days old). The female could normally be taken out of the box, since she was still inside warming the chicks. The male was caught with a trap installed at the entrance hole. The female was then marked with blue colour on the head and bill to distinguish it from the male. Where this was not possible, the parents could be distinguished on the video by their individual feather patterns on the head.

When the oldest chick was around 12 days old (range 11-15 days), the box was filmed during 15 hours. Day 12 was selected based on the study of Arlettaz *et al.* (2010a) which showed that at this brood stage both parents provided food and provisioning activity was high. The cameras were installed the day before and the filming started in the morning at 5:30 am, triggered by the timer of the recording system. Then it was filmed until 8:30 pm. After the filming, the nests were checked again regularly and the chicks ringed shortly before fledging.

Analysis of film material

To analyse the film material the videos were watched at 16x speed. This way the feeding events were still detectable and the video was stopped when a parent was feeding. For each feeding event, it was noted (a) which parent (male/female) was feeding, (b) which chick (rank) they were feeding, (c) what they were feeding (prey species and prey size), (d) the daytime and (e) whether they did enter the nestbox to feed or not. According to their biomass, we used three categories of molecrickets and another category for Lepidoptera larvae and other prey (Arlettaz *et al*. 2010a). Big molecrickets have an average dry biomass of 0.68 g, medium molecrickets one of 0.46 g and small molecrickets one of 0.36 g. Caterpillars, worms and insect larvae were all counted as caterpillars with an average dry biomass of 0.08 g. To small unknown prey we also assigned a dry biomass of 0.08 g and to medium unknown prey the dry biomass of small molecrickets, that is 0.36 g.

A total of 30 nestboxes could be analysed, 24 of them were filmed completely and 6 only partly (range of recorded time: 5-11 h) because the recording system sometimes failed. This resulted in 425.5 hours of film material with 2516 feeding events recorded.

Statistical analyses

All analyses were done using the program R version 2.13.1 (The R foundation for statistical computing, 2011). To generate minimum adequate models, we used a stepwise backward procedure in all analyses. We tested the significance of predictor variables in a hierarchical fashion, retaining lower order effects in the analyses in case a higher order term was significant. All models which tested for differences in daily activity, feeding patterns and prey biomass fed, were linear mixed-effects models which required the package nlme (Pinheiro *et al.* 2005). Sex of the parents and behaviour (entering/not entering the box) were taken as fixed factors, chick rank or time of day as continuous variables and nest as random factor. To test for a correlation between the number of feeds and the biomass fed, a linear model was used. And to analyse if the birds are more likely to enter the nestbox to feed or not, paired t-tests were used. Given variation in brood size, chick rank is a relative number, i.e. in small broods rank 3 may indicate the youngest chick while it may indicate a medium chick in large broods. So for visual purposes, chicks were grouped in three groups, 1=old, 2=medium and 3=young chicks according to their rank. Analyses were still done for all chicks and their rank (1=oldest chick, 2=second oldest chick etc.), but the graphs show the chick groups.

To analyse daily feeding rhythms of males and females, for each nest it was counted how often they feed per hourly time interval. The first interval was from 5:30 am until 6:30 am, the second interval from 6:31 am until 7:30 am etc. until 8:30 pm. We also tested for a quadratic relationship, but didn't get better results. For the analysis of the prey biomass fed over the course of the day, the same intervals were used. For each nest, the average biomass fed per hour was calculated. For the analysis of the feeding behaviour, the number of feeds by males and females to the chicks within a nest were always calculated per hour because some nests were only filmed partly. To compare whether the frequency of entering the box to feed changed later on, we compared our data of 17 nests with the data of an experiment that took place in the same nests one and two days after the filming.

To test the hypothesis that the feeding pattern (especially of the female) changes with different feeding activities by males, the males were put in two categories. From all nests, the average number of feeds per hour by the males was calculated and males divided in a group that fed more and one that fed less than average. The nests with the males that fed less than average (now named "bad males") were then analysed separately from the ones where the males fed more than average (now named "good males").

And to analyse whether the feeding pattern (especially of the female) changes with food biomass fed by both males and females, the average biomass fed per nest was calculated. Then two groups were defined, one with the nests where less biomass than average was fed (now named "small prey") and one with the nests where more biomass than average was fed (now named "big prey").

Results

Daily rhythms in feeding behaviour

Males and females showed a different temporal feeding pattern over the day (interaction sex*daytime, estimate±SE= 0.14±0.07, $F_{1,789}$=4.12, p=0.04). When analysing the sexes separately we found that males fed evenly over the day (estimate±SE= -0.02±0.02, $F_{1,380}$=0.35, p=0.55), while females fed more in the morning (estimate±SE= -0.12±0.06, $F_{1,380}$=3.81, p=0.05, Fig. 1). Females also fed more often than males (estimate±SE= -2.36±0.3, $F_{1,790}$=60.32, p<0.001). In a second step we tested whether the biomass fed to the chicks changed over the day. Mean biomass brought to the chicks varied with daytime, but only in males (interaction sex*daytime, estimate±SE= 0.01±0.003, $F_{1,545}$=5.35, p=0.02). Females fed even amounts of biomass over the day (estimate±SE= -0.0004±0.002, $F_{1,298}$=0.16, p=0.69), while males fed less biomass in the morning than later on in the day (estimate±SE= 0.01±0.002, $F_{1,221}$=6.82, p<0.01, Fig. 2). Overall, males fed more biomass, meaning bigger prey items than females (estimate±SE= 0.09±0.01, $F_{1,546}$= 41.02, p<0.001).

Food allocation patterns

In the overall analysis, there was no effect of chick rank on the food distribution pattern (estimate±SE= -0.05±0.03, $F_{1,248}$=40.91, p=0.09), nor any interaction (interaction sex*rank, estimate±SE= -0.05±0.05, $F_{1,247}$=0.80, p=0.37). In a second step we analysed the sexes separately. Males fed the older chicks more often than the younger ones (estimate±SE= -0.08±0.02, $F_{1,109}$=25.58, p<0.001), while the females did not show a preference in relation to chick rank (estimate±SE= -0.02±0.04, $F_{1,109}$=0.32, p=0.57, Fig. 3). As a covariate, brood size was not significant, but when splitting the broods in two groups (small: 2-4 chicks, large: 5-8 chicks) we find that males preferentially fed old chicks in large broods (estimate±SE= -0.09±0.02, $F_{1,72}$=27.64, p<0.001) while there was no effect in small broods (estimate±SE= -0.01±0.03, $F_{1,36}$=0.15, p=0.69). Females never preferentially fed chicks in relation to rank (small broods: estimate±SE= -0.04±0.05, $F_{1,36}$=0.52, p=0.47; large broods: estimate±SE= -0.02±0.05, $F_{1,72}$=0.18, p=0.67).

Prey biomass

With 57.7% (90.3% of the biomass) of all prey items being molecrickets, they were the most abundant prey fed. 32.4% (60.2% of the biomass) were big molecrickets, 19.3% (24.2% of the biomass) medium molecrickets and 6% (5.9% of the biomass) small molecrickets. 16.1% (3.5% of the biomass) of prey items were caterpillars, worms and other insect larvae, and 26.2% (6.2% of the biomass) was unknown prey. Of this, 25.6% (5.6% of the biomass) was small and 0.6% (0.6% of the biomass) was medium unknown prey.

Analysing males and females separately, we found that only males fed chicks differently, with bigger prey being fed to older chicks and smaller prey being fed to younger chicks (estimate±SE= -0.02±0.007, $F_{1,80}$= 7.14, p<0.01), while females didn't feed different amounts of biomass to different chicks (estimate±SE= -0.01±0.01, $F_{1,100}$= 1.54, p=0.22, Fig. 10).

Influence of feeding position at nestbox

Males and females differed in their feeding behaviour. Females mostly entered the box to feed (92.33%, 1612 of 1746 feeding events), while males fed both from inside (59.87%, 461 of 770 feeding events) and outside (40.31%, 309 of 770 feeding events). Females were more likely to enter the nestbox (paired t-test, t_{29}=5.69, p<0.001), while for the males there is no such preference (paired t-test, t_{29}=1.07, p=0.29). The propensity to enter the box changed with chick age. Already one to two days later, both sexes were less likely to enter the box when feeding. A female's probability to enter the box decreased from 95.2% to 59.3% (estimate±SE= 0.36±0.07, $F_{1,16}$=29.62, p<0.001) while a male's probability decreased from 50.6% to 18.6% (estimate±SE= 0.32±0.08, $F_{1,16}$=14.54, p<0.01)

Both adults preferentially fed the larger offspring when feeding from outside (females: estimate±SE= -0.01±0.004, $F_{1,109}$=9.54, p<0.01; males: estimate±SE= -0.06±0.01, $F_{1,109}$=37.8, p<0.001, Fig. 4) while there was no detectable preference when feeding from inside (females: estimate±SE= -0.01±0.04, $F_{1,109}$=0.09, p=0.75; males: estimate±SE= -0.01±0.01, $F_{1,109}$=0.74, p=0.39, Fig. 5).

When entering the nestbox to feed, both parents fed bigger prey items than when they didn't enter the box (female: estimate±SE= -0.13±0.03, $F_{1,116}$=

14.88, $p<0.001$; male: estimate±SE= -0.07±0.03, $F_{1,100}=7.48$, $p<0.01$). Females in both cases didn't feed different amounts of biomass to different chicks (enter: estimate±SE= -0.01±0.01, $F_{1,95}= 2.34$, $p=0.13$; not enter: estimate±SE= -0.001±0.01, $F_{1,14}=0.01$, $p=0.91$, Fig. 11), while males in both cases fed more biomass to older chicks than to younger ones (enter: estimate±SE= -0.02±0.008, $F_{1,48}=6.98$, $p=0.01$; not enter: estimate±SE= -0.03±0.01, $F_{1,42}=7.02$, $p=0.01$, Fig. 12).

The biomass of the provided food correlated with the number of feeds. The lower the biomass fed in a nest was, the more frequently the parents had to feed, and vice versa (estimate±SE= -0.07±0.02, $F_{1,28}=18.11$, $p<0.001$, Fig. 13).

Good vs. bad male

In both subsets of nests (nests where males fed more or less than average), females didn't feed chicks differently ("good male": estimate±SE= 0.0007±0.12, $F_{1,39}<0.001$, $p=0.99$; "bad male": estimate±SE= -0.03±0.02, $F_{1,69}=2.83$, $p=0.09$), while males in both groups fed older chicks more often than younger chicks ("good male": estimate±SE= -0.16±0.08, $F_{1,39}=8.94$, $p<0.01$; "bad male": estimate±SE= -0.08±0.02, $F_{1,69}=28.92$, $p<0.001$, Figs 6 & 7).

Small vs. big prey

Females in both groups (nests where more or less biomass than average was fed) didn't feed chicks differently ("small prey": estimate±SE= -0.07±0.12, $F_{1,38}=0.36$, $p=0.55$; "big prey": estimate±SE= 0.003±0.01, $F_{1,70}=0.07$, $p=0.79$), while males in both groups fed older chicks more often than younger chicks ("small prey": estimate±SE= -0.14±0.04, $F_{1,38}=13.84$, $p<0.001$; "big prey": estimate±SE= -0.05±0.01, $F_{1,70}=16.59$, $p<0.001$, Figs 8 & 9).

Discussion

This field study demonstrates that Hoopoes show a sex-specific feeding pattern. Overall, females fed the chicks more often than males, they fed smaller prey items and they decreased their feeding rate over the day while the male showed a constant temporal feeding rate. Most interestingly females fed all chicks within a brood evenly, while males fed older chicks more often and with bigger prey items than younger ones. Here, I will discuss how these male and female feeding patterns fit the concepts of food allocation in relation to chick competition and parental control.

We found several differences in the feeding behaviour of male and female Hoopoes. Females fed chicks more often than males. This was also observed by Martin-Vivaldi *et al.* (1999) and might partly be because of females often receiving prey from the male outside of the nest and then feeding it to the chicks. Females also fed a bit more often in the morning than later on, while males fed evenly over the day. This might be because chicks are hungry in the morning and therefore need food more urgently. The feeding pattern of females may reflect the plastic response to chick hunger level given that females often enter the nestbox and are better able to perceive differences in chick begging intensity (Leonard & Horn 2001). Males on the other hand may follow a static feeding pattern and not react to short-term changes in chicks' state of need (Nakagawa *et al.* 2007).

Concerning the prey fed, we found that males fed bigger prey (more biomass) than females. This has also been found in the study of Arlettaz *et al.* (2010a) and may reflect a female's feeding strategy or the consequence of sex-specific knowledge of the most profitable feeding grounds. During incubation and the early chick stage, males are responsible for providing all food to the female and the chicks. This way they might know profitable feeding grounds with bigger prey better than females. Alternatively, females could select smaller food items given that they preferentially feed smaller chicks. Or because they are the only ones mothering the chicks they want to return faster to the nest and thus invest less time in foraging (Wiebe & Slagsvold 2009). Males also feed smaller prey (less biomass) in the morning than later on, while females feed even amounts of biomass over the day. It is unlikely that males foraged on less profitable feeding grounds closer to the nest in the morning, because then they would have shown a higher feeding activity in the morning (Tarwater *et al.* 2009). More likely is that males invest in self-maintenance in the morning, meaning they eat the largest prey items themselves and subsequently increase their investment into their progeny.

Sex-specific feeding patterns

Overall, females fed the chicks more evenly compared to the males who preferentially fed large and old chicks. For males, the same pattern could be found in several studies on other bird species (e.g. Budden & Beissinger (2009) with green-rumped parrotlets; Stamps *et al.* (1985) with budgerigars; Leonard & Horn (1996) with tree swallows). It was argued that this feeding pattern might be 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). In the Hoopoe, we found that this feeding pattern of the male is actually only true for large broods (5 to 8 chicks). In small broods (2 to 4 chicks) they fed all chicks evenly. This result is in line with allocation rules in respect to chick competition. In small broods, the hatching dates of the oldest and youngest chick are closer together than in large broods. So size differences among the chicks are smaller. This means in small broods chicks are likely competitive and receive a similar amount of food from the male. In large broods however size differences between the old and the young chicks are much bigger, which means that chick competition will favour the older chicks.

Females, on the other hand, did not show a preference for smaller chicks like we expected, but did feed all chicks evenly, irrespective of brood size. Our results contrast to the studies of Budden & Beissinger (2009), Stamps *et al.* (1985), Leonard & Horn (1996) and Gottlander (1987) who showed that females were preferentially feeding the younger chicks, most likely to compensate for the male’s feeding preferences of large chicks and to ensure the survival of the younger chicks. Not finding any specific feeding pattern of the female in the Hoopoe makes it difficult to know if there is female control over food allocation. If females control which chicks they feed, it might be that there are no big differences in chick hunger. It is possible that older chicks in the short-term need more food than younger chicks (Dickens *et al*. 2008). So the older chicks will be fed by both the male and female because of a higher food demand and the younger chicks with a lower demand are only fed by the female. This would lead to a more or less even feeding pattern of the female. Or it could be that the female feeding pattern is only partly under her control and partly governed by chick competition. This means she would preferentially feed the smaller chicks but because the older chicks are so dominant it is difficult to get access to the smaller chicks. So it’s not always possible to feed the smaller chicks and this in total leads her to feed both old and young chicks.

Causes for sex-specific feeding patterns

Male and female Hoopoes differ in their feeding behaviour. Females normally enter the nestbox to feed while males often feed from the outside, that is they perch at the rim of the entrance hole and feed from this position. Females do enter the nestbox more often most likely because they are the only ones incubating, cleaning the box and mothering the chicks (own observation). This behaviour of the parents was also found in the study of Stamps *et al.* (1985) with budgerigars. Females often stay longer in the nestbox to clean it and to care for the chicks, while males only shortly visit the box to feed and then leave again. This difference in feeding behaviour may mainly explain why males most often fed the large chicks, because there was a difference in the feeding pattern when they enter the nestbox to feed or feed from the outside. When entering the box, both males and females feed all chicks evenly, while they feed older chicks more often than younger ones when they don’t enter the box to feed. This shows that there is actually not a difference in the food allocation behaviour of males and females, but a difference in the frequency of entering the box to feed. Because females mostly enter the box to feed, this leads overall to a more even feeding pattern, with no preferences for specific chicks. The males, on the other hand, often do not enter the box to feed, which leads to a feeding pattern tending to favour the older chicks. So parents might decide to enter the nestbox to feed when they want to control which chicks they feed. Because inside the box they are better able to distinguish and select the neediest chicks, which show their need for food by begging (Aviles *et al*. 2011). And when they do not enter the box to feed, they accept that the food will be distributed according to the outcome of chick competition, because the chick that is reaching highest to the entrance hole and thus is closer to the feeding parent is most likely to get the food (Dickens *et al*. 2008).

Sex-specific prey distribution patterns

Such variation in feeding patterns between males and females also exists concerning the prey items. When looking at what prey is fed to which chicks, we found that females feed the same amount of biomass to all the chicks, while males feed more biomass to older chicks and less biomass to younger chicks. When splitting the data to whether they enter the nestbox or not, it was found that both parents feed more biomass when they enter than when they don't enter. Parents may invest more time in distributing large prey items given the high investment in search time (Grieco 2002a). In contrast, when bringing small prey items they want to reduce the time at the nest to get new food quickly and thus do not enter the box. Concerning the feeding pattern when entering and not entering the box, the same result was found when all data were analysed together. Females in both cases feed even amounts of biomass to all chicks. It is possible that there is not enough variation among the biomass of the prey items fed that there could be any differences. As we found, females also feed even amounts of biomass over the day, which also shows that there is not much variability of the prey sizes fed. So either females show no control over what prey items they feed to which chicks, or they always feed prey items of about the same size, so it is not possible to find any differences in the prey size distribution pattern. They might even actively choose smaller prey so that also smaller chicks are able to swallow it and they can feed evenly (Wiebe & Slagsvold 2009). Males on the other hand, feed more biomass to older chicks, both when they enter the nestbox to feed and when they do not enter. This result is interesting because it shows that there must be male control over what prey is fed to which chick. It could be that because males on average feed bigger prey items than females, the big prey is too big for the youngest chicks to swallow and is thus given to older chicks (Wiebe & Slagsvold 2009). Such patterns have also been found in other studies. Kalam & Urfi (2008) for example found that in painted stork, bigger prey was fed to older chicks and smaller prey to younger chicks. And Campos & Lekuona (1997) found that in the purple Heron, early in the season when chicks were still small, smaller prey was fed than later on when chicks were bigger. But in the Hoopoe old chicks always begged irrespective of the prey brought (own observation). And because males feed older chicks overall more often than young ones, older chicks should also sometimes receive small prey items. So this means there is control of the males especially over the small chicks. When males bring small prey items, which they do less frequently, they specifically feed it to small chicks, while big prey possibly can only be eaten by older chicks.

Brood reduction

Since the hypothesis could be confirmed that male and female Hoopoes show differences in their feeding patterns, we wanted to know if male quality or prey quality has an influence on the feeding pattern and whether this could lead to brood reduction. But no shift in the patterns could be found; females fed all chicks evenly regardless of male and prey quality and males always fed older chicks more than younger ones. So the hypothesis could not be confirmed, but the patterns found here might not really be consistent. Firstly, because we only filmed each nest one day, this specific day could have been influenced by different factors. For example, on a rainy day smaller prey would have been available than on a sunny day (Arlettaz *et al*. 2010a). Secondly, we do not know how often the male gives the prey to the female outside of the box, but field observations indicate this happens quite often in the early nesting stages (unpublished data). This means a male could actually bring a lot of prey, but never feeds the chicks. So to better investigate male feeding patterns and any variability between the days, repeated filming of the same boxes would be advantageous. We also showed that the bigger the average biomass fed in a nest was, the less often the parents had to feed, and vice versa. The same result was also found by Fournier & Arlettaz (2001). This means it is also possible that it doesn't make much sense to split the broods to whether males feed a lot or little and prey items fed are large or small because they might just compensate. When they mostly bring small prey items, they feed more often and all chicks still get enough food. In a study with blue tits, Grieco (2002b) found a similar pattern, parents had to travel further to find big prey items and the feeding rate therefore was lower. So feeding big or small prey items might not really reflect habitat quality, but the decision of parents to travel further to find bigger prey or vice versa. It is also possible that the female feeding pattern does not change towards neglecting the youngest chicks because resources were not limited. Hatching asynchrony can be an adaptation to an unpredictable environment, with brood reduction happening when conditions are unfavourable and resources are scarce (Clark & Wilson 1981). So when it was a year with sufficient food supply, in most broods no brood reduction occurred because younger chicks still obtained enough food. To better investigate these patterns, data about the feeding patterns of different years should be compared. This would help to know if in bad years, for example with lots of rain (Arlettaz *et al*. 2010a), the female's feeding pattern was different in broods with insufficient food supply by the male.

Feeding position

The question now arises what determines whether a bird enters the nestbox to feed or not. We found that there is a difference in the respective probability between males and females. This could be because the value of the brood is different for males and females. Males can invest into extra-pair copulations (EPC) to increase their reproductive output (Kempenaers & Dhondt 1993). Therefore their investment in the brood might decrease because paternal care trade-offs with future reproduction. So when they are not sure about their unique paternity in a brood they should decrease their efforts in favour of future offspring (Houston & McNamara 2002). Females on the other hand, normally are sure about their maternity and thus should be more interested in raising the whole brood. This could translate in the female entering more often, because this way she can better control the food distribution. An exception when the female cannot be sure about the maternity might be the occurrence of conspecific brood parasitism, but this has not been found in this Hoopoe population (Leippert 2005). Similarly, the occurrence of extra-pair paternity has been found to be low in this population (Leippert 2005).

But there is also a difference between individual birds in the probability to enter the nestbox to feed. Maybe there are genetically-based differences in birds' personality (van Oers *et al.* 2005). It is known from many species that individuals can differ in their personality, meaning that there are shy and bold individuals which differ in their foraging behaviour, aggression, response to stress and risk-taking behaviour (Carere *et al*. 2005). Variation in the propensity to enter the nestbox could therefore reflect individual differences in characters. Additionally, the propensity to enter is likely to be plastically adjustable. We found that there is a time effect, meaning that already a few days later (measured on ± day 13 and 14 of the oldest chick) both parents fed more often from the outside than on day 12. The reason for this might be that at a later stage, size differences and the competitive differences among chicks are getting smaller. Less parental control may therefore be necessary and it may pay to feed in relation to chick competition, meaning from the outside of the box. But the frequency of entering declined quite strongly for only two days. Because the data of day 13 and 14 came from an experiment, it could also be that the disturbance it caused led to the parents entering less often. Birds often reduce the activity at the nest by fewer visits in the presence of disturbance (Tarwater *et al*. 2009), but it could also mean that they minimize the time spent at the nest. To be sure about this, a control would be needed where chicks are not manipulated. But because older chicks are being fed more often when parents feed from the outside, this will mean a disadvantage for the smaller chicks, which will get bigger with time. And if the proportion of entering of all feeds really decreases much more when there is more disturbance, it might in some cases even lead to the youngest chicks not obtaining enough food and die. If this is the case, it would be important for the conservation of the Hoopoe to keep any kind of disturbance to a minimum, such as human disturbance by catching the birds or by people walking by the nestboxes or by predators (like snakes and small mammals (Martin-Vivaldi *et al*. 1999), but also other birds like magpies (own observation)).

There are several studies with other bird species which found a similar sex-specific feeding pattern with males feeding preferentially the larger or more dominant chicks and females feeding the smaller or less dominant chicks (Budden & Beissinger (2009) with green-rumped parrotlets; Stamps *et al.* (1985) with budgerigars; Leonard & Horn (1996) with tree swallows; Gottlander (1987) and Lifjeld *et al.* (1992) with pied flycatchers; Krebs & Magrath (2000) with crimson rosellas; Dickens & Hartley (2007) with blue tits). The bird species examined in these studies are all cavity-breeders, which also breed in nestboxes like the Hoopoes. This could imply that in these species the same mechanism works like in the Hoopoe, that feeding patterns are not distinct for males and females, but that their behaviour how to feed differs. Unfortunately, in these studies it is not always specified whether the adult birds enter the nestbox to feed or if they feed from the outside. But regarding the similarities with the Hoopoe the same mechanism might be true for different species of cavity-breeders that were found to show differences in feeding patterns between males and females. This means food distribution is driven by chick competition when they feed from the outside of the box and parental control over food allocation happens when they enter the box.

In other systems like open breeders, there are often no differences in feeding patterns for males and females found when feeding nestlings (e.g. Slagsvold (1997b) and Weatherhead & McRae (1990) found no preferences of parents in American robins; Frederick (1987) also found no preferences of parents in White ibises; Smiseth *et al.* (2003) and Smiseth *et al.* (1998) found a preference for older and closer chicks respectively larger chicks by both parents in bluethroats). This supports our assumption because it shows that there are no differences in feeding patterns between males and females when there is no possibility of entering or not entering. When comparing with the results found for the Hoopoe, there seems to be a difference in the food allocation strategy. In the studies about American robins and White ibis parents might have controlled food distribution while in the ones with bluethroats they seem to feed according to the outcome of chick competition.

In this study we could show a so far unrecognized mechanism causing sex-specific feeding patterns in a bird species, which could also occur in other species of cavity-breeding birds. So in future studies, it should be considered that the position while feeding could have an influence on the feeding pattern found. In the Hoopoe, it could be tested in further studies what factors really determine if a bird enters the nestbox to feed or not. This would give further insight into the birds' behaviour and their reaction to disturbance.

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Figures

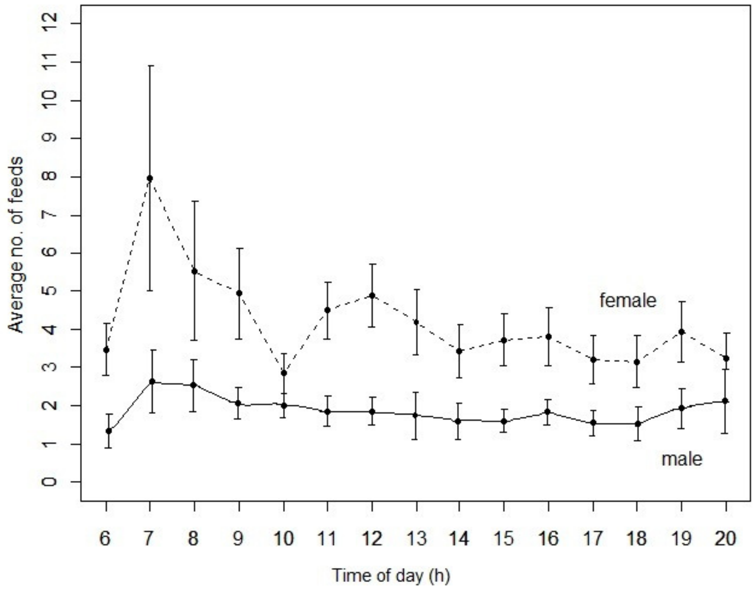

Figure 1: Average number of feeds by females and males per time interval (6=5:30-6:30; 7=6:31-7:30 etc.). Females feed more in the morning, while males feed evenly over the day. Females also feed overall more frequently than males.

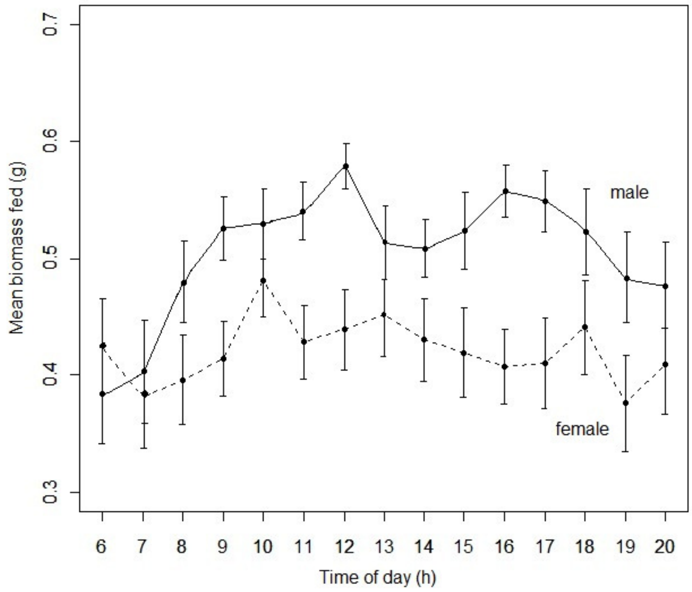

Figure 2: Mean biomass (g) fed by females and males per time interval. Males feed less biomass in the morning, while females feed even amounts of biomass over the day. Males overall feed more biomass than females.

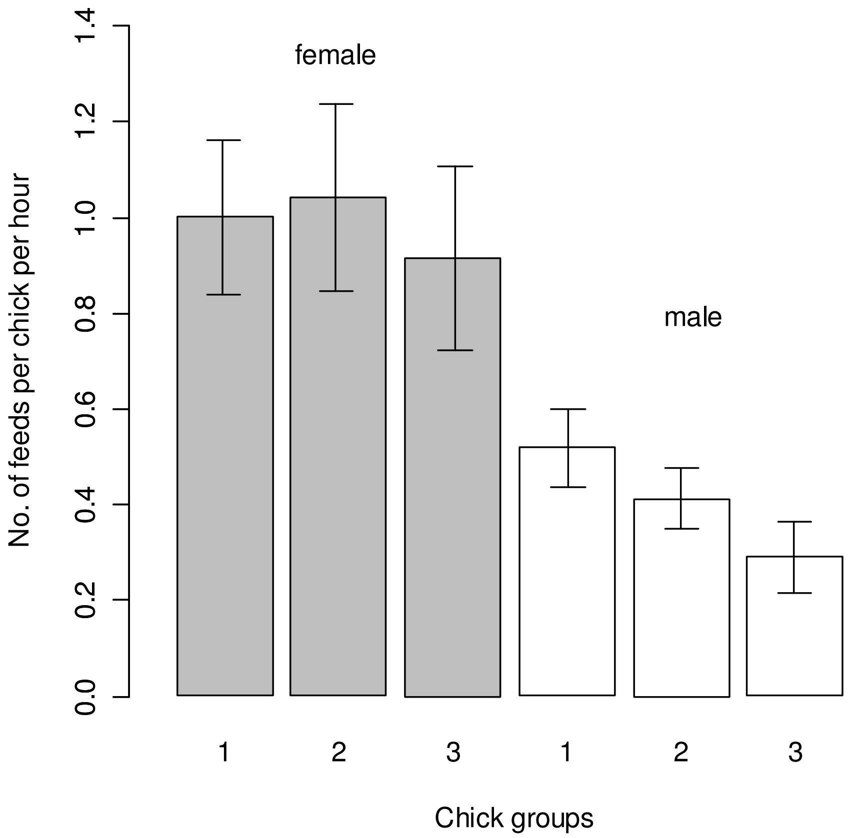

Figure 3: Number of feeds per hour and per chick by females and males to different chick groups (group 1= old chicks, group 2= intermediate chicks, group 3= young chicks). Females feed all chicks evenly, while males feed older chicks more than younger ones.

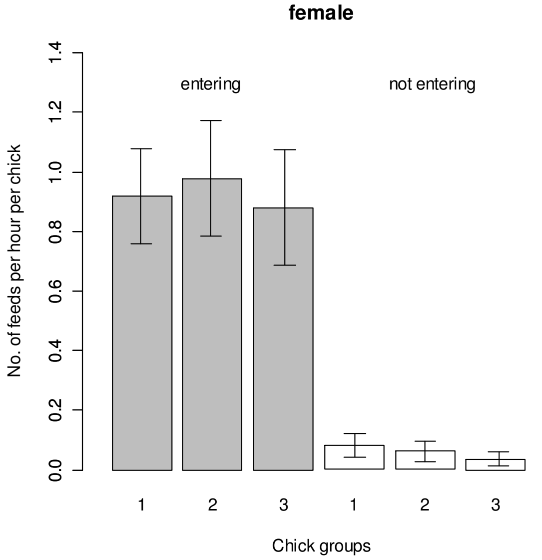

Figure 4: Number of feeds per hour and per chick by females to the different chick groups when entering and not entering the nestbox to feed. When entering, they feed all chicks evenly. When they don't enter they feed older chicks more than younger ones.

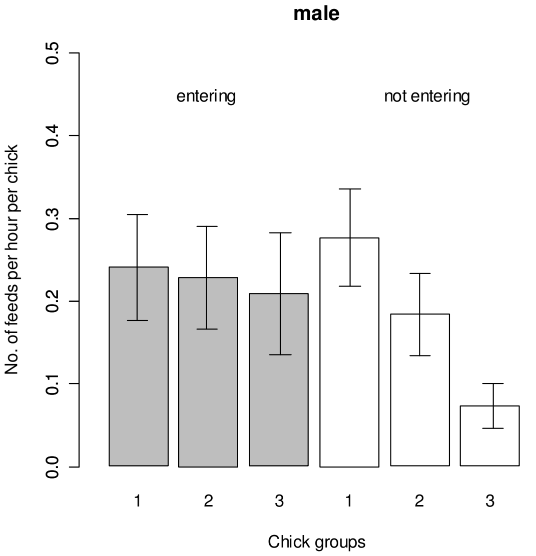

Figure 5: Number of feeds per hour and per chick by males to the different chick groups when entering and not entering the nest box to feed. When entering, they feed all chicks evenly. When they don't enter they feed older chicks more than younger ones.

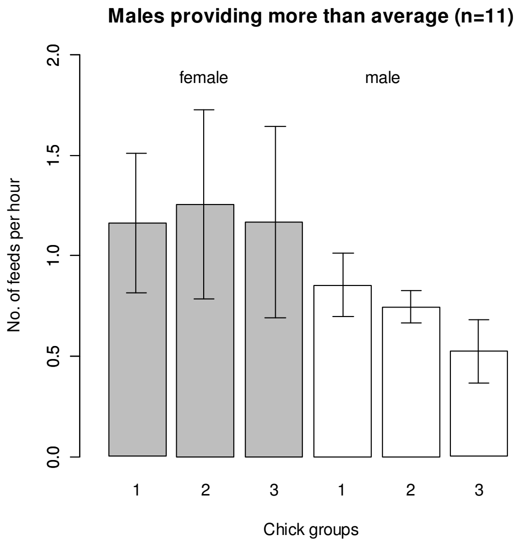

Figure 6: Number of feeds per hour and per chick by females and males to the different chick groups for nests where the male fed more often than on average. The females feed all chicks evenly while the male feeds older chicks more than younger ones.

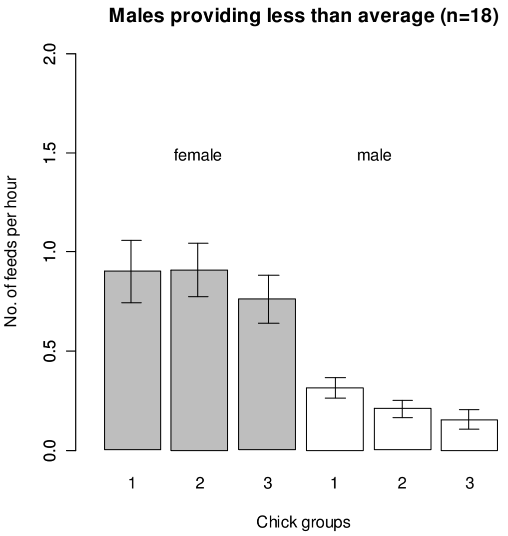

Figure 7: Number of feeds per hour and per chick by females and males to the different chick groups for nests where the male fed less often than on average. The females feed all chicks evenly while the male feeds older chicks more than younger ones.

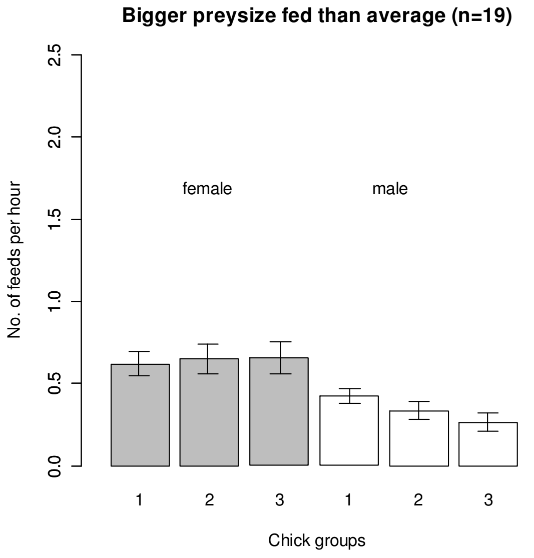

Figure 8: Number of feeds per hour and per chick by females and males to the different chick groups for nests where more biomass (bigger prey) was fed than on average. The females feed all chicks evenly while the male feeds older chicks more than younger ones.

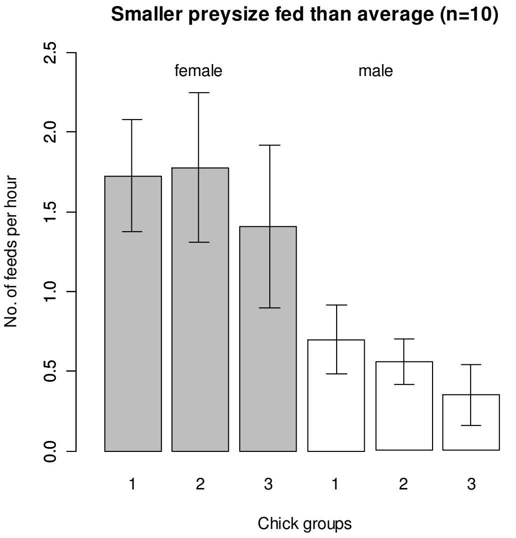

Figure 9: Number of feeds per hour and per chick by females and males to the different chick groups for nests where less biomass (smaller prey) was fed than on average. The females feed all chicks evenly while the male feeds older chicks more than younger ones.

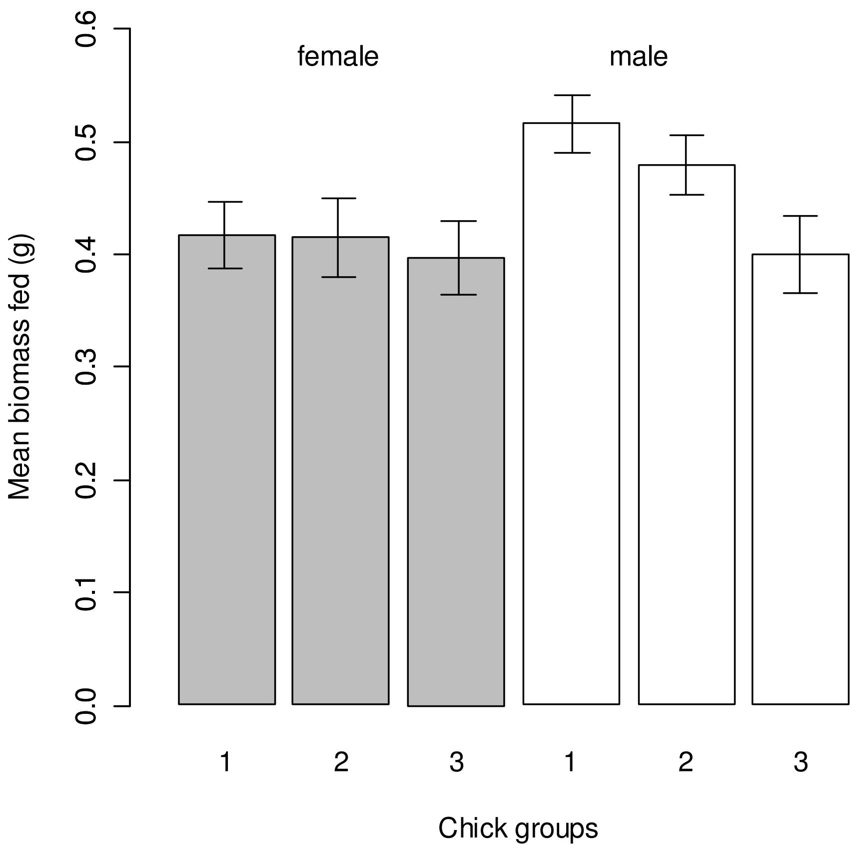

Figure 10: Mean biomass (g) fed by females and males to the different chick groups. The female feeds even amounts of biomass to all chicks, while the male feeds more biomass to older chicks and less biomass to younger chicks.

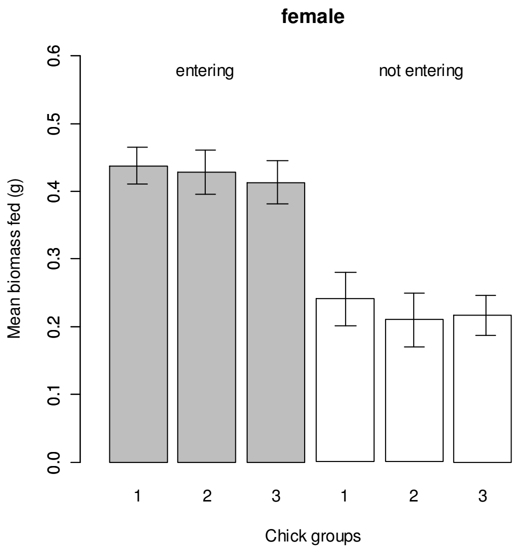

Figure 11: Mean biomass (g) fed by females to the different chick groups when entering and not entering the nestbox to feed. When entering, they feed more biomass than when they don’t enter. The female feeds even amounts of biomass to all chicks, both when entering and not entering.

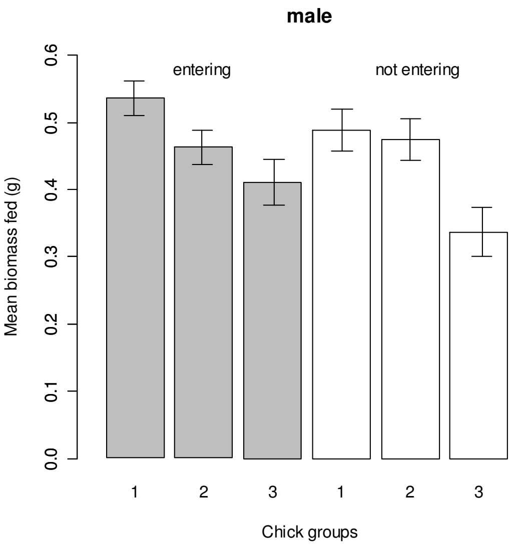

Figure 12: Mean biomass (g) fed by males to the different chick groups when entering and not entering the nestbox to feed. When entering, they feed more biomass than when they don’t enter. They feed more biomass to older chicks and less biomass to younger chicks both when they enter and not enter.

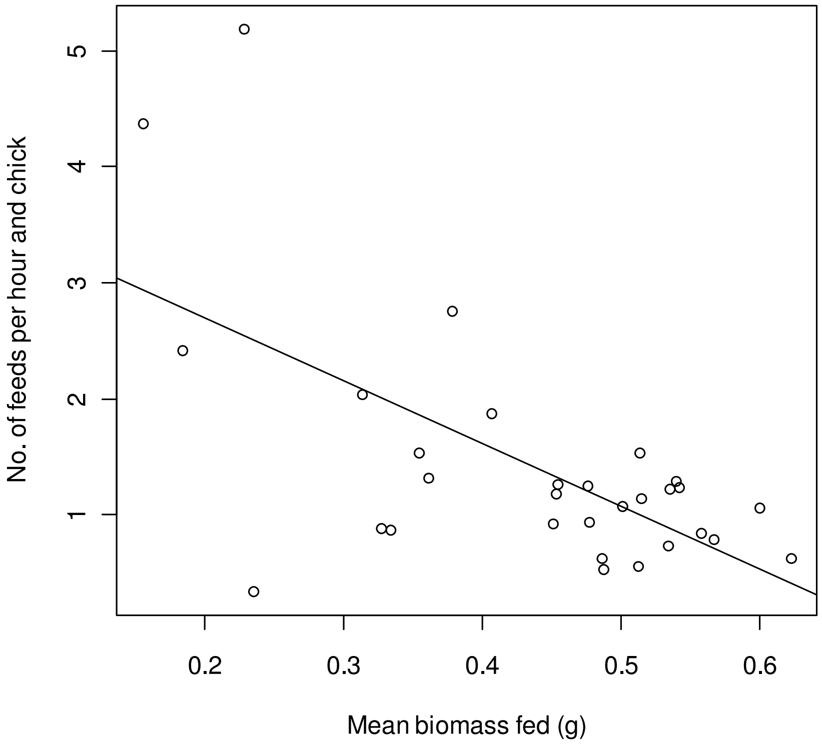

Figure 13: The mean biomass (g) fed in all nests correlates with the number of feeds per hour per chick in all nests.