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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.

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, Korpimaki, 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 ± 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.