



Information warfare in avian families: sex-specific begging responses to need and social environment in canary nestlings



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Begging behaviour is a crucial component of parent–offspring communication. It is used by offspring to trigger the transfer of parental resources while at the same time allowing parents to access cryptic information about their offspring's need. But in a brood of more than one, offspring may gain indirect fitness benefits from responding to the need of its (related) siblings, not to withdraw all resources, especially if these are needier and would possibly contest more vigorously. Thus each offspring is thought to adjust its begging behaviour to its own intrinsic need as well as to its social environment, which is also shaped by the parents potentially having control over the distribution of resources. Here, we experimentally satiated the heaviest nestling within canary broods, *Serinus canaria*, in order to analyse: (1) whether nestlings honestly communicate their intrinsic hunger level; (2) whether nestlings adjust their begging behaviour to the need of their siblings; and (3) how parents respond to these begging strategies. Only female nestlings responded honestly, begging significantly less when satiated. Male nestlings, by contrast, did not alter their begging according to the level of satiation. Nestlings only weakly responded to the need of their siblings, and again only female nestlings did so. Thus female nestlings appear to be more sensitive to both intrinsic need and changes in their social environment, potentially owing to their lower competitiveness. Parents preferentially fed needier nestlings irrespective of the observed sex differences in begging strategies. They appear to control food distribution according to (cryptic) signals of need, which is important to take into account when studying the adaptive significance of any begging behaviour and strategy.

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Communication between parents and offspring during the period of parental care is crucial for optimizing the transfer of resources, both for the caregiver, typically the parent, and the recipient, the offspring. In altricial bird species, offspring communicate with their parents via begging behaviour, which typically precedes parental feeding. Begging signals cryptic information about the offspring's need (Royle, Smiseth, & Kölliker, 2012) and aims at triggering a parental response, typically in terms of a transfer of food (Cotton, Kacelnik, & Wright, 1996; Dor & Lotem, 2010; Mock, Dugas, & Strickler, 2011). The latter is vital at least until fledging, as altricial nestlings depend on the parents' provisioning of food because only the parents have access to often limited food resources. Thus triggering an optimal response from the parents is crucial for the nestlings' development and survival.

Indeed, begging signals are the main indicators used by the parents when taking their feeding decision (Godfray & Johnstone, 2000), which is empirically supported by studies showing an increase in parental provisioning in response to increased offspring begging (e.g. Dor & Lotem, 2010; Mock et al., 2011; Royle et al., 2012).

However, begging may not only represent an honest signal of need in the context of parent–offspring communication (Godfray, 1991; Godfray & Parker, 1991; Hinde & Godfray, 2011). If parents raise more than one offspring at a time, the offspring may have to compete for and communicate about the distribution of parental resources with their siblings (Godfray, 1992; Godfray & Parker, 1992; Rodríguez-Gironés, Cotton, & Kacelnik, 1996; Roulin, Kölliker, & Richner, 2000). Competition can result in increased begging (Macnair & Parker, 1979; Mock & Parker, 1998; Smiseth, Lennox, & Moore, 2007), for example because the amount of food that the parents are able to provide for each nestling decreases with increasing number of siblings. Sibling rivalry is reinforced by an intrabrood conflict, because each nestling is more related to itself than to its sibling(s), and will therefore try to skew parental investment in its favour (Mock & Parker, 1997). Begging behaviour

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may then become further increased by this rivalry, with each sibling increasing its begging in order to get better access to food (Rodríguez-Gironés et al., 1996).

Nevertheless, siblings are related, especially in socially monogamous birds, which should lead to at least some form of collaboration among them (Hamilton, 1964; Mock & Parker, 1998; West, Pen, & Griffin, 2002). Nestlings hence face a trade-off between helping relatives in order to gain indirect fitness by not withdrawing all their resources and competing with them in order to obtain direct fitness benefits, in particular since begging is thought to be costly (Kilner, 2001; Moreno-Rueda, 2010). Communication between relatives should evolve towards an optimal level of signalling with low costs for the siblings (Bergstrom & Lachmann, 1998; Boncoraglio, Caprioli, & Saino, 2009; Brilot & Johnstone, 2003). Taken together, adapting begging to the intrabrood environment not only permits increased indirect fitness but also energy saving in signalling when siblings are needier and thus would contest more vigorously (Johnstone & Roulin, 2003; Roulin, 2002). Context-dependent begging therefore integrates information about the individual's own state and need but is also affected by sibling competition, such as the position within the sibling hierarchy (Price, Harvey, & Ydenberg, 1996). Thus the costs and benefits of the signalling vary not only with the individual's own state but also with the need of its siblings.

Any offspring strategy will ultimately depend on the parents, who have control over the resources and often also over the outcome of sibling rivalry. Asynchronous hatching, for instance, which results from the onset of incubation prior to clutch completion, introduces a size hierarchy. This hierarchy in turn handicaps later hatching nestlings in sibling competition (Bonisoli-Alquati, Boncoraglio, Caprioli, & Saino, 2011; Forbes & Glassey, 2000; Slagsvold, 1997) and may even lead to their death and thus brood reduction (Ricklefs, 1965). Also, after the chicks hatch, parents can affect sibling rivalry via feeding favouritism. For instance, parents may preferentially feed heavier nestlings (Shiao, Chuang, & Wang, 2009), or nestlings of a particular sex (Mainwaring, Lucy, & Hartley, 2011) or the nestling closer to them, which could be either the largest or the neediest (Tanner, Kölliker, & Richner, 2007). Any parental favouritism influences the adaptive significance of offspring begging strategies, as it skews the cost – benefit relationships between favoured nestlings and their sibling(s). This renders it highly important to include parental feeding behaviour when studying the adaptive significance of nestling begging.

To study these different sources of variation in begging in canaries, *Serinus canaria*, we experimentally manipulated the hunger levels of one nestling per brood and tested: (1) whether nestlings communicate their intrinsic hunger level via begging; (2) whether nestlings adjust their begging according to the need of their siblings; and (3) how parents reward the observed begging strategies. We specifically selected the heaviest and thus typically most competitive nestling for an experimental reduction of its hunger levels, because this is thought to lower the level of competition inside the nest most substantially. We expected, on the one hand, a reduction in begging of the individual that was supplementary fed and, on the other, an increase in begging of its siblings, as the chances of obtaining food are elevated while the costs of withdrawing resources are reduced. Finally, we expected parents to respond to the most intensively begging individuals, thus according to offspring need.

METHODS

Experimental Set-up

This experiment was performed during 2 consecutive years using 1-year-old canaries from our outbred laboratory-based

population (33 pairs in 2013, 17 pairs in 2014). Once selected for the experiment, individuals were kept in single-sex aviaries at a room temperature of 19–24 °C and an artificial long daylight schedule (14:10 h light:dark cycle) in order to induce reproduction. After 5 weeks, pairs were formed and allocated to a single breeding cage (GEHU cages, 50 × 64 cm and 40 cm high) containing a nest cup and nesting material. None of the parents were used in both years. Each breeding cage was provided with sand supplemented with shell grit, cuttlefish bones, ad libitum canary seed mixture (Van Camp, Antwerp, Belgium) and ad libitum water and egg food (Van Camp, Belgium) twice a week. From hatching onwards, fresh egg food was provided daily, supplemented with germinated seeds or green peas. Blood or tissue samples (in case of death before blood sampling) were used for molecular sex determination (Griffiths, Double, Orr, & Dawson, 1998).

Parental Provisioning and Nestling Begging

We measured parental provisioning for each nest 10 or 11 days after hatching of the first nestling following the methods described in Estramil, Eens, and Müller (2014). Briefly, before the experiment, each nestling was weighed and marked on the head with a red nontoxic marker for individual recognition on the video. Based on the weight measurements we calculated for each nestling its weight deficit (=within-nest size difference) compared to the heaviest nestling (focal nestling = FN) by subtracting its weight from the weight of the FN (the within-nest size value of the FN thus equals 0) for subsequent statistical analyses. All nestlings were hand-fed until satiation with a syringe (Orlux handmix, Versele Laga, Belgium), and subsequently food deprived for half an hour within their nest (i.e. we removed all food from the cage). As such, levels of hunger for all nestlings were standardized. The FN was then either fed again (satiated) or not fed (control) in order to manipulate the hunger level of the most competitive nestling. Right after this treatment, fresh food was placed in the cage and the video recording started.

Videos were analysed with video analysis software (NOLDUS Observer XT 10.0, Noldus Information Technology, Wageningen, Netherlands). Only the first feeding bout was considered for this analysis in order to have controlled hunger levels for all nestlings. A feeding bout ended when the parents left or if the female started brooding. The number of feedings per nestling was calculated as the total number of food transfers into the nestling's beak by the parent as described in Estramil, Eens, and Müller (2013) and Müller, Boonen, Groothuis, and Eens (2010). Canaries regurgitate pre-digested food, which they transfer in a series of dips into the gapes of their nestlings. Typically, several nestlings are fed per feeding bout. During the feeding bout begging was scored according to nestling posture and duration following Kilner (2001; 1: open beak; 2: open beak and head back; 3: open beak and stretched neck and body; 4: open beak, stretched body and stretched legs). The total begging score was calculated as the sum of every begging score per s per nestling during the begging bout. Canary nestlings do not generally make begging sounds until approximately the age of 14 days (N. Fresneau, personal observation).

The experimental procedures slightly differed between years; in 2013 only one type of treatment was applied per nest (among nest comparison), while both treatments were applied for each nest in 2014, with at least 2 h between manipulations (within- and among-nest comparison). Half of the nests received the control treatment first, and the other half were satiated first. In total we had 33 nests (16 in 2013 and 17 in 2014) in which the FN received supplementary food and 33 nests (16 in 2013 and 17 in 2014) with the control treatment. Brood size ranged between two and four nestlings. There were no significant differences in the mean begging score

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