



## Biparental care and offspring begging strategies: hungry nestling blue tits move towards the father

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Despite the fact that in many bird species offspring are provisioned by two parents, few studies to date have examined the implications of biparental care for offspring solicitation behaviour. Male and female parents can differ in their potential value to individual offspring if they follow different allocation rules and/or have different provisioning rates. If such differences occur, offspring should use different rules when soliciting to the male and female parent. This study looked at how the begging behaviour of nestling blue tits, *Cyanistes caeruleus*, is influenced by their hunger, size and by the sex of the provisioning adult. Nestling hunger was manipulated across size ranks, using periods of hand feeding or food deprivation. While nestling hunger influenced all aspects of nestling begging behaviour, nestling size and the sex of the provisioning adult only affected the position of nestlings in the nest cup. When hungry, nestlings moved closer to the male parent and the largest nestlings in a brood primarily obtained the closest positions. This may be the result of offspring responding to a difference between the sexes in parental food allocation rules.

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Both the visual and vocal components of begging behaviour in nestling birds have been shown to contain information on offspring need (reviewed in Kilner & Johnstone 1997). However, as well as communicating offspring need to parents, begging signals also reflect the competitive environment in which they are performed (Smith & Montgomerie 1991; Price et al. 1996; Leonard & Horn 1998; Leonard et al. 2000) and as such can be viewed as an adaptive strategy reflecting nestling need, relative competitive ability and parental response (Godfray 1995; Johnstone 2004).

Where nestlings hatch asynchronously, later hatched nestlings often remain smaller and in worse condition than their older siblings for the whole of the nestling period (reviewed in Magrath 1990). As a consequence, they may

have greater short and long-term need than older siblings. However, they may also be inferior competitors, for example large nestlings can dominate positions close to parents (Kilner 1995; Cotton et al. 1999) and parents often preferentially feed nestlings that are closer to them (McRae et al. 1993; Kilner 1995; Leonard & Horn 1996). Parents may also bias their provisioning towards large, high quality offspring despite there being no difference between the behaviour of the largest and smallest offspring in the brood (Smiseth & Amundsen 2002). As a result, nestlings of different sizes may experience very different costs and benefits in relation to begging tactics (Godfray 1995; Glassey & Forbes 2002). In support of this, studies have generally shown that younger, smaller nestlings beg at greater intensities and for longer periods than their older nestmates (Price et al. 1996; Cotton et al. 1999; Krebs 2001). Theoretical models also predict differences in the begging strategies of different sized nestlings within the brood in response to competitors (Godfray 1995; Johnstone 2004) and several empirical studies support this (Smith & Montgomerie 1991; Price et al. 1996; Leonard & Horn 1998; Leonard et al. 2000) although others do not (Kacelnik et al. 1995; Cotton et al.

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1996). However, despite the growing evidence that begging behaviour can be context dependent (Royle et al. 2002), few studies have examined the influence of biparental care on offspring solicitation.

Where there is biparental care, the benefit nestlings receive from solicitation may depend on the sex of the parent that they solicit, as there is evidence that within nests male and female parents can differ in how they allocate resources to different types of offspring (reviewed in Slagsvold 1997; Lessells 2002). Several studies have shown that nestling sex, size and need can differently affect how much male and female parents invest in individual offspring (e.g. Stamps et al. 1987; Kölliker et al. 1998; Krebs et al. 1999). The sexes can also differ in how they respond to offspring begging (Kilner 2002) and in the strength of their preference to feed offspring close to them (Porkert & Spinka 2004). If such differences occur, it will be adaptive for offspring to use different rules when soliciting to the male and female parent. It would be particularly profitable where there are simple cues that allow offspring to discriminate between parents and if parents consistently feed from different locations at the nest. Nestlings often change positions in hungry broods (McRae et al. 1993) and can learn to beg in the most profitable locations in the nest (Budden & Wright 2005). In the great tit, *Parus major*, the two parents feed from different, consistent and thus predictable, locations (Kölliker & Richner 2004; Lessells et al. 2006). Kölliker et al. (1998) suggest that by forcing offspring to choose between parents, great tit parents can reduce the time cost of allocation to preferred offspring, as nestlings move closer to, and beg more intensely towards, the parent that is most likely to feed them. Even if parents follow the same food allocation rules, they may still differ in their potential value as a resource to offspring if they provision at different rates or bring food items of different quality and feed from different, yet individually predictable locations (Slagsvold 1997). If this is the case, then competition for 'begging patches' (Kölliker et al. 1998) near to the two parents will not be equal and the more competitive offspring will dominate positions next to the more profitable parent (Slagsvold 1997).

This study looked at how the begging behaviour of nestling blue tits, *Cyanistes caeruleus*, is influenced by the sex of the provisioning adult. We suspected that biparental care would influence begging behaviour, as parents often feed from different locations (Dickens & Hartley 2007). In addition, parents follow different food allocation rules, as the male parent has a stronger preference to feed the closest nestlings than the female (Dickens & Hartley 2007) and feeds the largest fledglings of the brood (Slagsvold et al. 1994). Thus, we examine the effect of parental sex on both the begging displays of nestlings and how they are positioned in the nest, with respect to nestling size. As competitive ability may influence how close nestlings can get to the provisioning adult, we manipulated nestling hunger in both the largest and smallest nestlings of the brood to examine the effect of size on nestling movement in the nest cup. Specifically, this study aimed to determine how both the relative size of nestlings within the brood and their hunger influence which of the

two parents nestlings move closest to and how intensely they solicit each parent.

## METHODS

### Fieldwork

We studied the breeding population of blue tits in two small deciduous woods near Lancaster University, U.K., during the spring of 2003. All birds in the study nested in wooden nestboxes of a standard size (width = 15 cm, height = 20 cm, depth = 15 cm). All nestboxes were regularly monitored from the start of each breeding season to establish laying date of the first egg, clutch size, hatch date and hatching success, and checked at the end of the breeding season to establish fledging success. Nestlings were ringed with numbered metal British Trust for Ornithology rings at 6 days posthatching. Breeding adults were caught at the nest during the second half of the nestling period and fitted with a metal and colour ring combination if they were not already ringed. Adults were sexed in the hand according to the presence or absence of a brood patch, as only females brood nestlings.

At 10 days old, nestlings are rarely brooded, and both parents are working at approximately their maximum provisioning rate for the nestling period (Perrins 1979). When the first nestling to hatch in each brood was 10 days old, feeding interactions between parents and nestlings were filmed for 1 h at each focal nest ( $n = 25$ ). Because of technical problems with videotaping, data from three of these nests could not be used. In addition, in one of the remaining 22 nests only the female parent provisioned nestlings during the observation hour.

Prior to filming, the hunger of four focal nestlings in each nest was manipulated by removing nestlings from the nest, taking them to warmed dummy nests nearby and carrying out a treatment of either food deprivation or hand feeding. The two largest and two smallest nestlings (according to mass) in each nest were chosen as focal nestlings. The mean mass of the two groups was significantly different within nests (the two largest nestlings  $\bar{X} \pm \text{SD} = 9.7 \pm 0.72$  g; the two smallest nestlings =  $8.0 \pm 0.95$  g; paired  $t$  test:  $t_{21} = 17.57$ ,  $P < 0.001$ ). As nestlings at this age gain, on average, under 1 g per day (Perrins 1979), the mass difference between large and small nestling categories represents between 1 and 2 days growth. The relative size of nestlings will often be the result of hatching order, as blue tits can commence incubation prior to laying the last eggs of the clutch, although the size ranking of individual nestlings can change over the nestling period and the extent of differences between ranks also represents conditions during growth (I. R. Hartley, personal observation).

The four focal nestlings were randomly allocated to either a fed or deprived experimental treatment, so that each of the two treatments was carried out on both a large and small nestling. At the start of the procedure, all of the focal nestlings were fed, until satiation, with Nectarblend chick rearing softfood (Haiths, Cleethorpes, U.K.). Nestlings were fed until they would no longer gape in response

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