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Parental influence on sibling rivalry in great tit, *Parus major*, nests

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Sibling and parent–offspring conflicts arise mainly over the amount and distribution of parental care, especially food. In altricial bird species where the young depend on parents for obtaining food, parents may control sibling competition by the choice of their respective provisioning locations. In great tits, the parents use fixed provisioning positions on the nest rim that are determined early in the breeding cycle and maintained until fledging. The two parents may choose positions that are close to each other, or far apart, and thereby increase or relax the pressure for optimal feeding positioning among nestlings. As an inspiration to this study we previously found that the two parents provide food from closer positions if the nest is infested by ectoparasites. Here, we tested the hypothesis that the parental choice of relative provisioning locations could be strategically used to control nestling competition. We forced parents to feed from either one or two provisioning locations and assessed the induced change in nestling movement, weight gain, and food distribution among siblings. We show that the angular distance between male and female locations influences the level of behavioural competition and affects nestling weight gain and food distribution. It is the first evidence for hole-nesting birds, where it was assumed that the nestling closest to the entrance hole was fed first, that the apparent choice of feeding positions by parents could be a way of controlling sibling competition and thereby also taking partial control over the outcome of parent–offspring conflict.

Keywords: food provisioning; great tit; parent–offspring conflict; parental care; *Parus major*; scramble competition

Begging in nestling birds has become one of the model systems to investigate parent–offspring conflict (Wright & Leonard 2002). Nestling birds solicit food through different begging behaviours such as vocal and visual signals (calling, gaping, stretching neck, flapping wings), and by jockeying for positions near a parent's feeding location (Mock & Parker 1997; Wright & Leonard 2002). The evolution of begging has been modelled in two different ways: in the first approach, parents are assumed to have no control over food distribution, and the system is considered as driven by a scramble competition among siblings (Parker et al. 1989; Godfray & Johnstone 2000). The outcome of each feeding bout is then determined by the ability of one nestling to beg more and/or from a better location than its nestmates (Rydén & Bengtsson 1980; Kilner 1995; Ostreiher 2001; Kilner 2002). In species with a dominance hierarchy among nestlings, for example, resulting from hatching asynchrony (Bengtsson & Rydén 1981; Ostreiher 1997), stronger and older nestlings may obtain more food than is optimal from a parent's point of view (Parker et al. 1989). In the second approach, begging is considered to reflect a nestling's true need, which makes the system evolutionarily stable and results in honest signalling of need by nestlings to their parents (Godfray 1991, 1995).

In line with scramble competition models, begging intensity beyond true need can increase with brood size (Kacelnik et al. 1995; Price 1996, 1998; Wright et al. 2002; Neuenschwander et al. 2003) and with previous feeding experience, such as the level of begging required to obtain food (Kedar et al. 2000). Similarly, competition between nestlings, and subsequent food provisioning, can vary

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with certain phenotypic offspring traits such as size or sex (Teather 1992; Oddie 2000). In fact, the two approaches are not mutually exclusive (Royle et al. 2002) but rather the two extremes of a continuum leading from full parental control to no parental control. What happens in real nests is probably a subtle combination of the two extreme situations described by the models (Parker et al. 2002). In addition, different components of begging may differ in their trend towards being honest signals or the result of scramble competition. For example, the jockeying of nestlings for favoured positions in the nest of altricial birds (McRae et al. 1993) is typically an aspect of begging that may be viewed as predominantly shaped by scramble competition (Kölliker & Richner 2004). Parents of several species allocate food according to the outcome of sib competition, and feed the nestling located closer to them (Rydén & Bengtsson 1980; Gottlander 1987; Smith & Montgomerie 1991; McRae et al. 1993; Kacelnik et al. 1995; Ostreiher 2001; Kilner 2002). This could lead to stronger offspring monopolizing the best positions in the nest.

The importance of scramble competition for favourable positions by great tit nestlings was shown by the finding of an increase in nestling positioning activity from experimentally reduced to enlarged broods (Neuenschwander et al. 2003). This effect occurred despite full compensation by parents for the altered brood size in terms of their provisioning rate, that is, individual nestlings obtained the same quantity of food irrespective of brood size. Great tits show biparental care and feed the young from nonrandomly chosen locations on the nest rim (Kölliker et al. 1998). The angle between male and female feeding position varies across nests between 0° and 180°, and the individual feeding location of each parent appears to be stable over the nestling period (Kölliker & Richner 2004). This has potential consequences for food competition among nestlings: if both parents feed from the same position, there is one single best feeding site for nestlings to compete for, if they feed from opposite positions, there are two sites, albeit with half of the former profitability. Thus, in this case the nestlings must choose between the male and the female feeding locations. Experimental manipulation of nestling hunger showed that hungry nestlings preferentially moved to the female feeding location, where they were also more likely to be fed, although parents provided food at similar rates (Kölliker et al. 1998). Even in the absence of a feeding parent, nestlings orient towards a parent's expected feeding location, probably using the nest entrance as a reference point (Kölliker & Richner 2004). This indicates that nestlings are able to learn their parents' feeding locations and that scramble competition for access to these feeding sites can occur even before parents arrive.

The use of different male–female feeding locations might be a parental strategy to avoid time-consuming decision making on which offspring to feed at any given feeding bout, with the possible addition of differential competition rules at male and female locations. The jockeying of offspring to occupy these locations can thus be seen as an optimal foraging strategy under scramble competition (Kölliker & Richner 2004). This hypothesis assumes that parents actively choose their feeding locations, which is supported by our previous finding that experimental parasite infestation with hen fleas, *Ceratophyllus gallinae*, had a significant influence on the angular difference in male–female feeding locations: the presence of ectoparasites during egg laying reduced the angle between the two parents, whereas ectoparasites present during the nestling period tended to increase that angle (Fig. 1). These results show that the angle between the two parental feeding locations is determined in part by an active decision by one or both parents in response to (probably multiple) environmental cues. However, the functional significance of variation in parental feeding angles remains to be elucidated, and is the purpose of the present study.

This finding inspired us to investigate experimentally the consequences of the variation in feeding location of great tit parents on food competition and distribution, and on nestling weight gain. If parents strategically use relative feeding location to control scramble competition (Slagsvold 1997), the predictions are that maximum spacing of parents reduces competition among nestlings and will thus lead to increased weight gain and lower heterogeneity in nestling development compared to a situation where both parents use very close feeding locations. At the other extreme, parents can choose feeding positions close to each other and thereby increase competition among young. This strategy may be used if parents aim to reduce brood size. To test the hypothesis that the parental positioning affects nestling competition, we manipulated the sites from which the parents could feed their nestlings in the nests to have either one unique or two distinct feeding locations. When parents were forced to use a single feeding site, we predicted stronger competition,

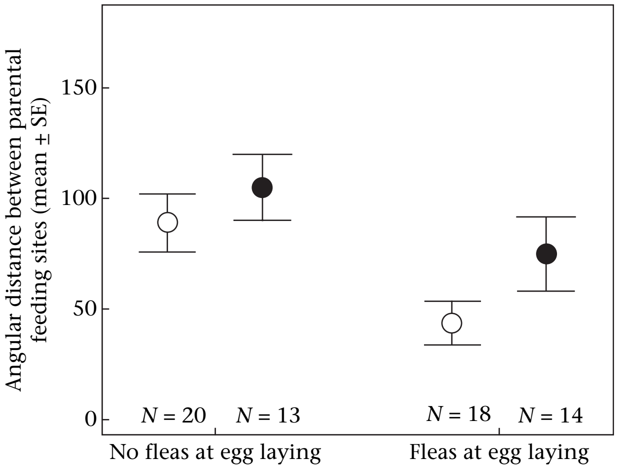

Figure 1. Data from a study in 1995 ($N = 65$) showing active parental adjustment of feeding location angles in response to an ecological factor. Shown is the angular distance between male and female feeding sites in relation to two fully crossed and randomized factors: presence/absence of fleas during egg laying and presence/absence of fleas during nestling period (○: no fleas during nestling period; ●: fleas during nestling period). Experimental addition of fleas during egg laying led to reduced angular difference between parental feeding locations on the nest rim ($F_{1,62} = 8.44$, $P = 0.005$). Inversely, the addition of fleas during the nestling period tended to increase that angle ($F_{1,62} = 3.05$, $P = 0.085$).