ANIMAL BEHAVIOUR, 2007, 74, 977–983
doi:10.1016/j.anbehav.2006.11.034

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

MARION TANNER*, MATHIAS KÖLLIKER† & HEINZ RICHNER*
*Zoological Institute, University of Bern
†Zoological Institute, University of Basel

(Received 24 August 2006; initial acceptance 6 November 2006; final acceptance 28 November 2006; published online 31 August 2007; MS. number: 9090)

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

Correspondence and present address: M. Tanner, Zoological Institute, Baltzerstrasse 6, CH-3012 Bern, Switzerland (email: marion.tanner@esh.unibe.ch). M. Kölliker is at the Zoological Institute, Vesalgasse 1, CH-4051 Basel, Switzerland (email: mathias.koelliker@unibas.ch).

0003–3472/07/$30.00/0

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,

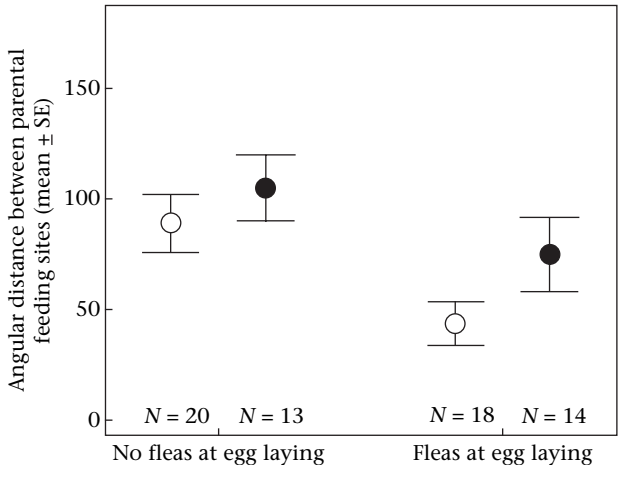

Figure 1. Data from a study in 1995 ($N = 65$) showing active parental adjustment of feeding location angles in response to an ecological factor. Shown is the angular distance between male and female feeding sites in relation to two fully crossed and randomized factors: presence/absence of fleas during 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 ($F_{1,62} = 3.05$, $P = 0.085$).

uneven food distribution among nestlings, higher heterogeneity in mass change and overall lower weight gain due to the increased competition, at least if parents did not compensate for increased competition by provisioning more food.

METHODS

Data Collection

The study was carried out in spring 2003 using a great tit population breeding in nestboxes in the 'Bremgartenwald' and in the 'Könizbergwald', near Bern, Switzerland. Nestboxes were checked every 3 days to monitor nest building. After the completion of nest building, boxes were checked daily for egg laying, start of incubation and hatching. When nestlings were 6-day-old, the chosen feeding location of each parent was determined using video observations from inside the nestbox. The nestboxes ($N = 68$) were equipped with infrared cameras, and filmed for 2 h and 15 min each. From the video films we recorded for each feeding event the sex of the feeding parent, determined unambiguously using the sexual dimorphism in the brightness of the black cap, and its feeding location measured as the head position just before feeding. Position was expressed as the (clockwise) angle between the centre of an adult's head and the entrance hole. Then each parent's feeding location was determined as the median angle of its positions (Kölliker et al. 1998; Kölliker & Richner 2004). From these films, breeding pairs were then divided into those where male and female fed their nestlings from approximately the same location (angle $< 90°$), and those with two clearly distinct feeding locations (angle $> 90°$). We used only the second group for experimental manipulation of the number of possible feeding sites.

Experimental Manipulation

On the morning of the ninth day after hatching, 38 broods composed of 4–11 nestlings where male and female naturally used two distinct feeding locations were assigned randomly to one of the following treatments: in the first treatment feeding was only possible at one location; in the second treatment there were two possible positions from where the male and female could feed the brood. To provide one or two possible feeding locations, a plexiglas and metal fence was fixed inside the nestbox a few centimetres above the brood (Fig. 2). Depending on the treatment, this barrier had one or two openings, from which the parents could feed the nestlings. The two openings were located 90° to the left and right of the entrance hole, whereas single openings were placed randomly 90° to the left or the right of the entrance hole. At the same time nestlings were ringed with numbered aluminium rings (Station Ornithologique Suisse, Sempach), and weighed. Parents and young were left for 2 days to become accustomed to this experimental set-up and then video recorded for 2 h and 15 min on the morning of the 11th day after hatching. Before filming, nestlings were marked on their heads using spots of acrylic paint to make them individually recognizable on the video recordings. The colour used was chosen to be hardly visible under the dim light inside a nestbox, but contrasting well with nestling plumage on recordings with infrared-sensitive cameras. Consequently, it was possible to identify nestlings on the video recordings without the markings disturbing the parents' feeding behaviour. Birds were never seen pecking at the markings. On the evening of the 11th day after hatching, nestlings were weighed again, and the barrier was removed.

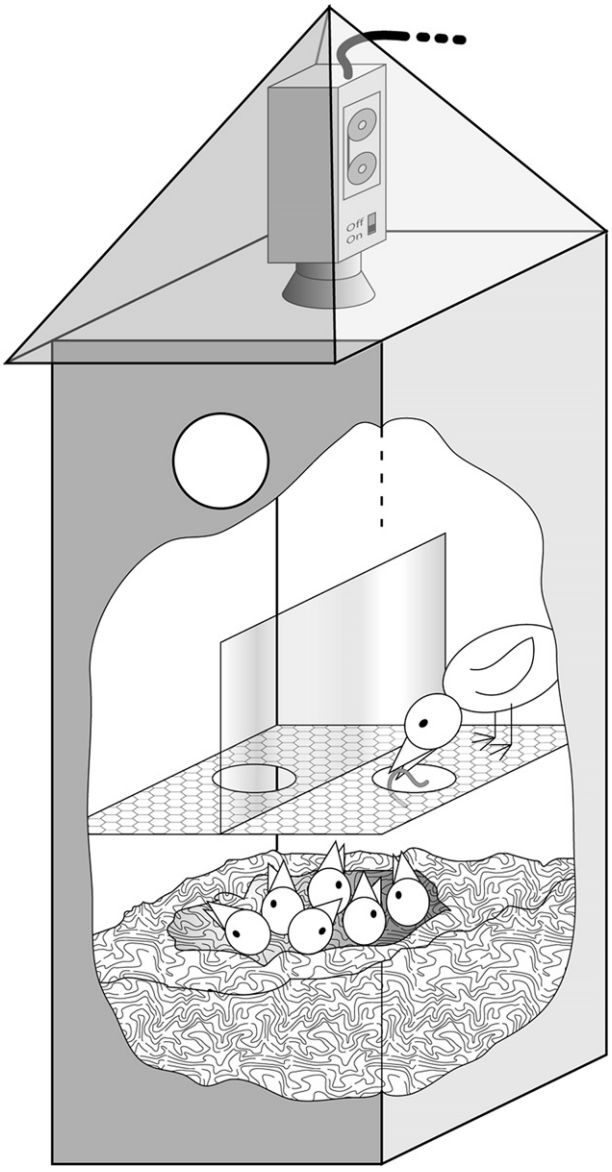

Figure 2. Schematic drawing of experimental set-up (shown here is the treatment with two feeding locations). An infrared camera is installed in the roof of the nestbox. A plexiglas and metal partition is fixed to the walls of the nestbox above the nestlings. The parents can feed through the holes in the horizontal plexiglas partition.

Data Analysis

For each nestling we calculated weight gain as the difference in mass between the beginning and the end

of the experiment (ca. 60 h). The experiment was conducted between days 9 and 11 after hatching because of the high food provisioning rate by parents at this age, and because nestlings are then in a phase of nearly linear weight increase, before body mass reaches a plateau (Gosler 1993). We therefore assumed that a difference in weight gain during this phase could have consequences on development in general. Change in tarsus length as a measure of skeletal body size was not assessed since at this age tarsus length is close to asymptotic size and hence, no effect of our 60 h manipulation on tarsus growth was expected. The video recordings were used to determine the sex of the feeding parent, the feeding location (right or left), and the identity of the fed nestling. Heterogeneity in food distribution and weight gain was calculated as the intrabrood standard deviation of these variables. As an estimation of the level of scramble competition, we also measured the displacement of one randomly chosen nestling during and between parental visits. In each nest one nestling's head marking was drawn randomly from the list of all the head markings present in the nest. On the video recordings the screen was divided into 15 zones of 5 cm^2 each and the displacement was calculated as the number of squares the nestling moved through, both between parental visits and during parental presence, as measured by the position of its beak. To test for the relevance of the use of one target nestling, we measured the displacement of a second randomly chosen nestling in a subsample of eight nests, and found that the displacement of nestmates was highly correlated (during visits: Spearman rank correlation: $r_S = 0.97$, $P = 0.00039$; between visits: $r_S = 0.81$, $P = 0.021$). As the space available to nestlings in the nest is very limited, the movement of any chick forces the others to move at the same time, at least by being displaced, so that the movement of one target chick can be used to quantify the overall level of movement in the nest. This overall movement was divided into the movement between parental visits, and movement during parental presence. Due to technical problems while filming, data on food provisioning and nestling movements were available for only 34 of the 38 experimental nests.

The nestboxes used for our experimental manipulation had also been used for the purpose of another experiment where in each nest either a food or flea treatment was applied before egg laying. Our experiment on food locations was fully crossed with respect to this treatment, and the correlation between this treatment and our manipulation of feeding locations was highly nonsignificant (Spearman rank correlation: $r_S = 0.1$, $P = 0.53$), showing that they were properly randomized. There was no statistical interaction between this treatment and our manipulation of feeding locations in the statistical analyses of our experiment (all $P > 0.55$). Thus, the food/flea treatment was kept in our models for statistical control, but was not used for any further interpretation.

Data were analysed using JMP IN Statistical Software Version 5.1 (Sall et al. 2005), and R (R Development Core Team 2004). Each nest was considered as an independent data point. The level of movements of one focal nestling in each nest was analysed using repeated measures ANOVA, with movements between and during parental visits being the repeated measures. If required data were log transformed to meet the assumptions of normality and homoscedasticity (Shapiro–Wilkinson test: all $P > 0.1$; Bartlett test: all $P > 0.1$). Hatching date and brood size, as well as nestling mass on day 9 after hatching, were included in the models as covariates. Nonsignificant covariates and interactions were backward eliminated. Brood size was similar in nests with one and two feeding locations ($F_{1,34} = 0.2$, $P = 0.63$), as was mean weight before manipulation ($F_{1,35} = 0.1$, $P = 0.79$).

RESULTS

Nestling Weight Gain

As predicted, if distinct parental feeding locations reduce sibling rivalry, our experiment shows that the mean weight gain of nestlings in nests with one feeding location was significantly lower ($F_{1,33} = 4.8$, $P = 0.036$) than in nests with two feeding locations (Fig. 3). Mean weight gain decreased with hatching date ($F_{1,33} = 13.3$, $P < 0.001$). Against the prediction, the intrabrood standard deviation in weight gain was not significantly different in nests with one or two feeding locations ($F_{1,34} = 2.2$, $P = 0.14$), although we observed a trend for a higher heterogeneity in nests with one feeding location, as expected. Heterogeneity was higher later in the breeding season ($F_{1,34} = 20.6$, $P < 0.001$).

Food Distribution

The average number of prey items received by a nestling was similar in nests with one or two feeding locations ($F_{1,30} = 0.7$, $P = 0.39$). Parents decreased their feeding rate later in the breeding season ($F_{1,30} = 8.6$, $P = 0.006$). As expected, the intrabrood standard deviation in feeding rate of individual nestlings was larger in nests with one possible feeding location than in nests with two locations ($F_{1,31} = 15.8$, $P < 0.001$; Fig. 4).

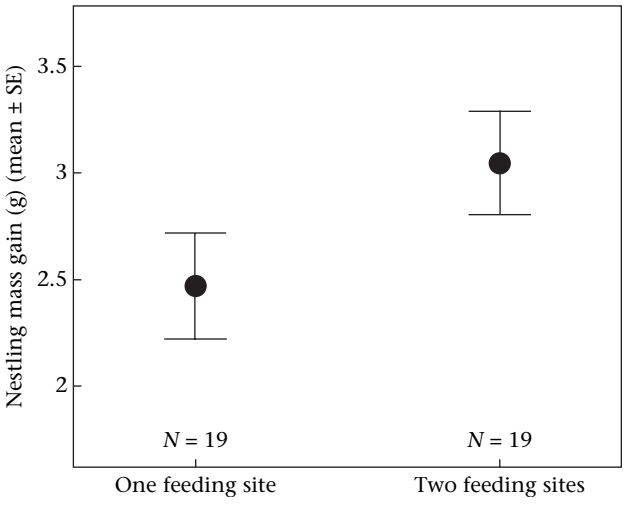

Figure 3. Mean mass gain in grams of nestlings in nests with one and two parental feeding sites.

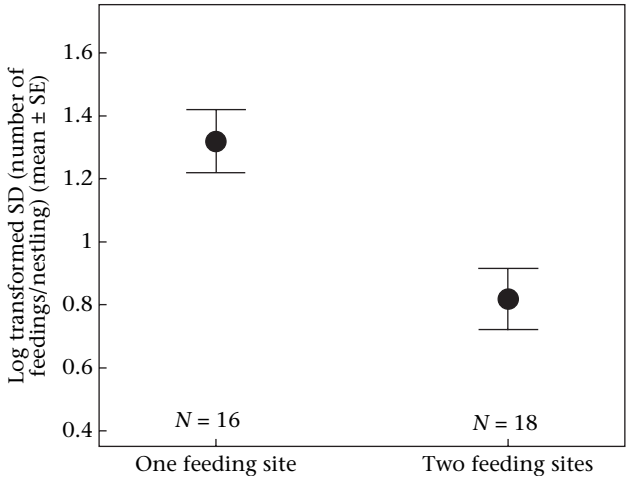

Figure 4. Heterogeneity in food distribution among siblings, measured as within-nest standard deviation of number of food items brought per nestling, in nests with one or two possible feeding locations. Log transformed data to meet the assumption of homoscedasticity.

Scramble Competition

Nestlings in nests with one feeding location moved more than nestlings in nests with two feeding locations ($F_{1,32} = 5.4$, $P = 0.026$) as predicted. This effect was similar when analysing movements between one visit and the next one (Fig. 5a), or the amount of movements during parental visits (interaction effect: $F_{1,32} = 0.1$, $P = 0.73$; Fig. 5b). Nestlings' movements were more frequent during visits than between visits ($F_{1,32} = 39.9$, $P < 0.001$).

DISCUSSION

We found that in nests with only one feeding site, mean weight gain was reduced and food more unevenly distributed among nestlings. Nestlings fed from one or two sites were on average provisioned with the same quantity of food, showing that overall feeding rate was not affected by our treatment. It thus suggests that the observed effect on mean weight gain in nests with one feeding site must arise via the increased competition for food (Neuenschwander et al. 2003), unless there was differential provisioning in prey quality.

From the observation that within pairs male and female parents used fixed food provisioning locations but variable positions among pairs, we hypothesized that this behaviour may serve to modulate the level of sibling competition (Slagsvold 1997). The results from the experiment reported here overall support this hypothesis. As expected we observed a decreasing mean weight gain of the entire brood when fathers and mothers were forced to feed from the same position on the nest rim. This effect was apparently mediated by an increased competition between nestlings, as they were forced to move and scramble more to obtain food. Such a detrimental effect of mobility on nestling growth has already been found in great tit nestlings when competition was increased by brood size manipulation (Neuenschwander et al. 2003). This increased mobility took place before a parent's arrival at the nest, but also just after the arrival of a parent before providing food. This confirms that jockeying for positions between siblings is based on the dynamics of two behavioural interactions: one that takes place before a parental visit, and a more intense one at parental arrival. The importance of chick positioning before parents arrive at the nest is explained by the observation that nestlings have knowledge of their parents feeding locations, and move to these sites even in the absence of any parent (Kölliker & Richner 2004).

In line with our predictions, we found a less even food distribution when the parents were allowed to use one position only to feed their nestlings. This is an indication that the choice of a single feeding location for both parents in a nest could be a way of biasing food distribution towards more competitive nestlings. This result is in line with the study by Ostreiher (2001), who found that when the feeders' arrival was predictable,

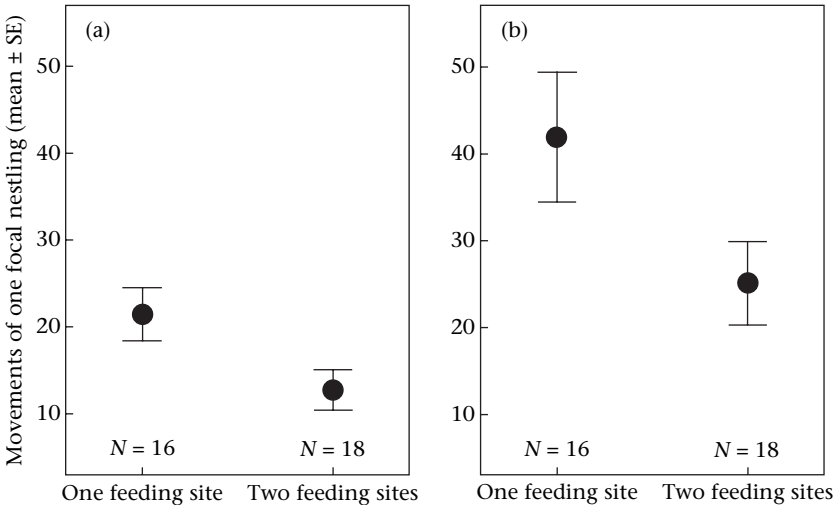

Figure 5. Mean number of movements during a 2 h and 15 min video film of one randomly chosen focal nestling in nests with one or two feeding locations: (a) between parental visits, (b) during parental visits.

first-hatched nestlings obtained a higher proportion of food. However, we found no significantly higher intrabrood heterogeneity in weight gain in nests with only one feeding position, which would be expected if there was a stronger detrimental effect of the increased competition on the growth of smaller and weaker nestlings. This could be due to the rather good food availability in the year of our study, as nestlings were on average relatively heavy compared to other years (B. Doligez, unpublished data), possibly concealing an effect of our treatment on intranest heterogeneity in nestling weight gain. Also, it is possible that the approximate 60 h of feeding location manipulation was not long enough to allow variation in feeding rate to individual nestlings to translate into variation in weight gain. Finally, this result could be due to differential allocation of food resources to various body components in nestlings of different size. Between 9 and 11 days of age, nestlings have to invest heavily in mass growth, but also in feather development, wing length (Gosler 1993) and immunocompetence (Brinkhof et al. 1999). Differential allocation between mass and wing growth was found in marsh tits, *Parus palustris* (Nilsson & Svensson 1996). Barn swallow, *Hirundo rustica*, nestlings supplemented with extra food invested in immunocompetence rather than growth (Saino et al. 1997). Thus, it is conceivable that in our study, smaller nestlings needed to invest mostly in mass increase, whereas older nestlings might invest in feathers or immune function, for example. In such a case, an uneven distribution of food could still result in a relatively homogeneous growth of body mass.

Parents did not compensate for the higher competition in nests with one feeding site by increasing their feeding rates. We cannot completely exclude a difference in the quality of food provided to nests with one or two feeding locations, as the size and quality of each prey brought to the nest could not be assessed. However, in a study on tree swallows, *Tachycineta bicolor*, it has been found that most of the variation in quantity and quality of food is explained by the number of feeding trips (McCarty 2002) suggesting that most of the variation in provisioned food may be assessed by measuring food provisioning rates.

From the common observation that parents of hole-nesting birds feed nestlings closer to themselves and thus seem to accept the outcome of nestling competition (Rydén & Bengtsson 1980; Gottlander 1987; Kacelnik et al. 1995; Kölliker et al. 1998), one might conclude that nestlings are in control of food distribution. As shown here, by varying the feeding angle between male and female along the nest rim, parents can strongly influence the level of scramble competition. Furthermore, the choice of fixed feeding locations by parents gives parents also more control over the outcome of parent–offspring conflicts. A similar adaptation, although on a different timescale, was found by Kilner (2002) in canaries (*Serinus canaria*), where females changed the place from where they fed in response to manipulation of hunger level in the brood, increasing the necessity for nestlings to compete under apparently unfavourable conditions. With this control over competition levels in their nest (Slagsvold 1997; Kölliker et al. 1998), parents could induce brood reduction under harsh environmental conditions. The behavioural choice of a feeding location may be a strategy for parents to maximize their marginal fitness returns without having to make costly decisions on which nestling to feed at each feeding bout. Such a strategy may be more efficient in species with large broods and hence a proportionally higher cost of time-consuming decision processes by parents.

Acknowledgments

We thank Anne Berthouly, Serge Zaugg, Cécile Roche, Aude Cassier and Blandine Doligez, as well as Philipp Heeb and Isabelle Werner for their help during fieldwork. Professor Valentin Rousson was a great help with statistics. We thank Eric Champod for illustration of Fig. 2. The study was financially supported by the Swiss National Science Foundation (grant no. 3100A0-102017 to H.R.). Experiments were conducted under a licence delivered by the Ethical Committee of the Office of Agriculture and Nature of the Canton of Bern, Switzerland.

References

Bengtsson, H. & Rydén, O. 1981. Development of parent–young interaction in asynchronously hatched broods of altricial birds. *Zeitschrift für Tierpsychologie*, **56**, 255–272.

Brinkhof, M. W. G., Heeb, P., Kölliker, M. & Richner, H. 1999. Immunocompetence of nestling great tits in relation to rearing environment and parentage. *Proceedings of the Royal Society of London, Series B*, **266**, 2315–2322.

Godfray, H. C. J. 1991. Signalling of need by offspring to their parents. *Nature*, **352**, 328–330.

Godfray, H. C. J. 1995. Signaling of need between parents and young: parent–offspring conflict and sibling rivalry. *American Naturalist*, **146**, 1–24.

Godfray, H. C. J. & Johnstone, R. A. 2000. Begging and bleating: the evolution of parent–offspring signalling. *Philosophical Transactions of the Royal Society of London, Series B*, **355**, 1581–1591.

Gosler, A. 1993. *The Great Tit*. London: Hamlyn.

Gottlander, K. 1987. Parental feeding behaviour and sibling competition in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica*, **18**, 269–276.

Kacelnik, A., Cotton, P. A., Stirling, L. & Wright, J. 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. *Proceedings of the Royal Society of London, Series B*, **259**, 259–263.

Kedar, H., Rodriguez-Girones, M. A., Yedvab, S., Lotem, A. & Winkler, D. W. 2000. Experimental evidence for offspring learning in parent–offspring communication. *Proceedings of the Royal Society of London, Series B*, **267**, 1723–1727.

Kilner, R. 1995. When do canary parents respond to nestling signals of need? *Proceedings of the Royal Society of London, Series B*, **260**, 343–348.

Kilner, R. M. 2002. Sex differences in canary (*Serinus canaria*) provisioning rules. *Behavioral Ecology and Sociobiology*, **52**, 400–407.

Kölliker, M. & Richner, H. 2004. Navigation in a cup: chick positioning in great tit, *Parus major*, nests. *Animal Behaviour*, **68**, 941–948.

Kölliker, M., Richner, H., Werner, I. & Heeb, P. 1998. Begging signals and biparental care: nestling choice between parental feeding locations. *Animal Behaviour*, **55**, 215–222.

McCarty, J. P. 2002. The number of visits to the nest by parents is an accurate measure of food delivered to nestlings in tree swallows. *Journal of Field Ornithology*, **73**, 9–14.

McRae, S., Weatherhead, P. J. & Montgomerie, R. 1993. American robin nestlings compete by jockeying for position. *Behavioral Ecology and Sociobiology*, **33**, 101–106.

Mock, D. W. & Parker, G. A. 1997. *The Evolution of Sibling Rivalry*. Oxford, New York, Tokyo: Oxford University Press.

Neuenschwander, S., Brinkhof, M. W. G., Koelliker, M. & Richner, H. 2003. Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behavioral Ecology*, **14**, 457–462.

Nilsson, J.-A. & Svensson, M. 1996. Sibling competition affects nestling growth strategies in marsh tits. *Journal of Animal Ecology*, **65**, 825–836.

Oddie, K. R. 2000. Size matters: competition between male and female great tit offspring. *Journal of Animal Ecology*, **69**, 903–912.

Ostreiher, R. 1997. Food division in the Arabian babbler nest: adult choice or nestling competition? *Behavioral Ecology*, **8**, 233–238.

Ostreiher, R. 2001. The importance of nestling location for obtaining food in open cup-nests. *Behavioral Ecology and Sociobiology*, **49**, 340–347.

Parker, G. A., Mock, D. W. & Lamey, T. C. 1989. How selfish should stronger sibs be? *American Naturalist*, **133**, 846–868.

Parker, G. A., Royle, N. J. & Hartley, I. R. 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecology Letters*, **5**, 206–215.

Price, K. 1996. Begging as competition for food in yellow-headed blackbirds. *Auk*, **113**, 963–967.

Price, K. 1998. Benefits of begging for yellow-headed blackbird nestlings. *Animal Behaviour*, **56**, 571–577.

R Development Core Team. 2004. *R: a Language and Environment for Statistical Computing*. Vienna, Austria: The R Foundation for Statistical Computing.

Royle, N. J., Hartley, I. R. & Parker, G. A. 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends in Ecology & Evolution*, **17**, 434–440.

Rydén, O. & Bengtsson, H. 1980. Differential begging and locomotory behaviour by early and late hatched nestlings affecting the distribution of food in asynchronously hatched broods of altricial birds. *Zeitschrift für Tierpsychologie*, **53**, 209–224.

Saino, N., Calza, S. & Moller, A. P. 1997. Immunocompetence of nestling barn swallows in relation to brood size and parental effort. *Journal of Animal Ecology*, **66**, 827–836.

Sall, J., Creighton, L. & Lehman, A. 2005. *JMP IN: the Statistical Discovery Software, 5.1*. Cary, North Carolina: SAS Institute Inc.

Slagsvold, T. 1997. Brood division in birds in relation to offspring size: sibling rivalry and parental control. *Animal Behaviour*, **54**, 1357–1368.

Smith, H. G. & Montgomerie, R. 1991. Nestling American robins compete with siblings by begging. *Behavioral Ecology and Sociobiology*, **29**, 307–312.

Teather, K. L. 1992. An experimental study of competition for food between male and female nestlings of the red-winged blackbird. *Behavioral Ecology and Sociobiology*, **31**, 81–87.

Wright, J. & Leonard, M. L. 2002. *The Evolution of Begging: Competition, Cooperation and Communication*. Dordrecht, Boston, London: Kluwer Academic.

Wright, J., Hinde, C., Fazey, I. & Both, C. 2002. Begging signals more than just short-term need: cryptic effects of brood size in the pied flycatcher (*Ficedula hypoleuca*). *Behavioral Ecology and Sociobiology*, **52**, 74–83.