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Navigation in a cup: chick positioning in great tit, *Parus major*, nests

MATHIAS KÖLLIKER & HEINZ RICHNER

Division of Evolutionary Ecology, Institute of Zoology, University of Bern

Parent birds often feed from predictable sites at the nest and nestlings compete for access to positions close to them. Such scrambling for stable parentally favoured positions may relate to optimal foraging theory. For efficient foraging, nestlings should be able to associate begging payoffs with the available positions in the nestcup and use this information to position themselves before parental arrival at the nest. We tested this prediction experimentally in the great tit by keeping nestlings temporarily in the laboratory where they were housed individually in nestboxes identical to their natural boxes. After a period of food deprivation, we quantified their positioning, taking the nest entrance as a reference. Parental feeding locations were measured from videos made at the natural nests, again relative to the nest entrance. As predicted, nestlings in the laboratory boxes chose positions significantly closer to parental feeding sites than expected by chance. Thus, they had knowledge about their parents' habit of feeding from predictable sites, enabling them to navigate and forage efficiently in the nestcup.

The competition between nestlings for parentally favoured positions in the cup of altricial bird nests is a begging component commonly proposed as driven by scramble competition (McRae et al. 1993; Kacelnik et al. 1995; Budden & Wright 2001; Rodríguez-Gironés et al. 2001; Kilner 2002; Neuenschwander et al. 2003). Under scramble competition, siblings compete for parental resources and parents passively distribute the resources following the outcome of competition (Parker et al. 2002a, b). Theoretical models have shown that scrambling can be, besides the selection for honest signals of need by active parental choices (Godfray 1991), one possible mechanism underlying the resolution of the parent–offspring conflict and the evolution of conspicuous begging displays (Parker et al. 2002a).

Nestling competition for access to favourable positions in the nest may, from a nestling's perspective, be viewed as a problem relating to optimal foraging theory (Kacelnik et al. 1995; Slagsvold 1997; Kölliker et al. 1998; Budden &

Wright 2001). To specify the foraging theoretic context, we refer to this hypothesis as the 'foraging hypothesis of sibling rivalry'. Parents are considered sources providing food at continuous input and offspring as foragers maximizing food intake by scrambling for and begging at optimal positions (and optimal intensity; Kedar et al. 2000). Parental food provisioning relates to a 'continuous input' situation of optimal foraging if (1) it consists of repeated, distinct events (i.e. provisioning is distributed in time; Milinski & Parker 1991), (2) food is unevenly distributed between offspring during any given feeding visit, and (3) feeding success is highest at certain predictable positions in the nest (i.e. provisioning is clumped in space; Milinski & Parker 1991). Predictable, parentally favoured sectors in the nestcup have been observed repeatedly and in a number of different bird species (e.g. Greig-Smith 1985; Gottlander 1987; Smith & Montgomerie 1991; Leonard et al. 1994; Malacarne et al. 1994; Kacelnik et al. 1995; Kilner 1995, 2002; Leonard & Horn 1996; Ostreiher 1997, 2001). These sectors have been termed 'activity centres' (Malacarne et al. 1994; Lotem 1998) or, in analogy to optimal foraging theory, 'begging patches' (Kölliker et al. 1998), and they tend to correspond to positions close to where parents feed. The presence of predictable begging patches implies that nestlings may be

Correspondence and present address: M. Kölliker, Department of Biology, Indiana University, 1001 East 3rd Street, Bloomington IN 47405-3700, U.S.A. (email: mathias.koelliker@swissonline.ch). H. Richner is at the Division of Evolutionary Ecology, Institute of Zoology, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland.

able to measure and remember the begging payoffs associated with the available positions in the nest (Kacelnik et al. 1995), and to navigate and forage correspondingly.

Consistent with the requirements of the foraging hypothesis of sibling rivalry, great tit parental food provisioning consists of highly repeated, distinct events. Parents mostly feed one single nestling during any given visit (the great tit is a typical 'single-prey loader'; e.g. Perrins 1979), use highly predictable feeding locations (Kölliker et al. 1998), and nestlings at positions close to the parental feeding location have greater chances of being fed (Rydén & Bengtsson 1980; Bengtsson & Rydén 1981; M. Kölliker, unpublished data). In addition, and as expected if nestling positioning is a form of scramble competition, the frequency of position changes from one parental visit to the next increases with brood size (Neuenschwander et al. 2003). Thus, if great tit nestlings behave as optimal foragers and have knowledge of parental feeding locations, we predicted that they should approach predictable parental feeding locations in the absence of parents.

Most empirical studies have quantified nestling positioning during the parental visit when the parent, as the target of competition, is immediately available (see references above). They have not discriminated between simple scrambling during parental visits and a more sophisticated form of scrambling involving nestling knowledge of parental feeding locations. To directly test the prediction that nestling great tits have knowledge of parental feeding locations and choose positions accordingly, we performed an experiment where we temporarily separated nestlings from their parents at 10 days of age and then quantified their positioning. Parental feeding locations were measured later at the natural nest. We predicted that the distance between the angle chosen by the test nestlings in the laboratory box and the angle of a parent's feeding location should be less than that expected from random nestling positioning. We also present a detailed analysis of the assumptions of stable parental feeding sites and dynamic nestling positioning.

METHODS

Navigation Experiments

The study was conducted in 1997 with a great tit population breeding in nestboxes in the 'Bremgartenwald', a forest adjacent to Bern, Switzerland. Great tits have been breeding in nestboxes in this population since 1992. The data were gathered during a cross-fostering experiment on the quantitative genetic basis of nestling begging call intensity (Kölliker et al. 2000).

When the nestlings were 10 days old, we selected two nestlings of intermediate size from each brood as test nestlings (Kölliker et al. 2000). After transfer to the laboratory, we placed the test nestlings individually in the laboratory boxes. To provide conditions as natural as possible during the laboratory trials, we used the same type of nestboxes as the ones in the forest for the housing

of nestlings (inner measures: $12.3 \times 12.3 \times 26$ cm), built artificial nests with moss, and added four nestling-sized cotton wool balls (fixed at $45°$, $135°$, $225°$ and $315°$) to simulate the squeezing among siblings in the natural nestcup.

When placing a nestling in the laboratory box, we always put it in the centre of the artificial nestcup with its head orienting towards the entrance hole. Nestlings were then food deprived for 150 min (Kölliker et al. 2000). Food deprivation did not affect nestling growth or survival. The change in body mass from the day of testing to 4 days after the experiment did not differ between the test nestlings and the unmanipulated nestlings (ANOVA: controlling for between-nest variation: $F_{1,162} = 0.020$, $P = 0.887$), and nestlings used in the experiment had a similar fledging success as their unmanipulated nestmates (logistic regression with binary dependent variable (fledged: yes/no): $\chi_1^2 = 0.462$, $P = 0.497$).

We filmed the nestlings in the laboratory boxes at the end of the food-deprivation period for later quantification of positioning. The video camera was installed on a tripod vertically above the laboratory box and on the side of the nest entrance.

Using the videos, we quantified nestling positioning that occurred prior to manual stimulation of begging for the recording of their begging calls (Kölliker et al. 2000). Nestlings therefore chose positions without human interference. Their positions were quantified by subdividing on the video monitor the surface of the laboratory box into 12 equally large arcs, each encompassing $30°$. Nestling position was taken as the arc into which the centre of the nestling's head fell (Kölliker et al. 1998). The entrance hole was taken as the circular origin.

After food deprivation, we fed each nestling with one bee larva to partly compensate for food deprivation, marked them individually with small spots of acrylic paint on their heads, and brought them back to their natural nests. They were placed back in the natural nest at a random position in the nestcup. To obtain the data on feeding locations of the parents, we filmed the activities in the nest during the next 90 min. For quantification of parental feeding locations, we subdivided the nest on the video monitor into 12 equally large arcs (each encompassing $30°$) and took the position of the parent's head shortly before feeding (when they typically 'freeze' for a short moment; Bengtsson & Rydén 1981). Again, we took the entrance hole as the circular origin.

The parental feeding location was estimated by the circular mean from the last 10 visits of each parent on the 90-min videos. Feeding visits were considered from the end of the films backwards. The first quantified parental visit occurred an average $\pm$ SD of 59 ± 19 min after the start of the film, which ensured that test nestlings had enough time to return to hunger levels typical for their broods. One hour after return to natural nests, the postural begging intensity (measured on an ordinal scale; for details see Kölliker et al. 1998) of food-deprived nestling great tits did not differ significantly from the postural begging intensity of unmanipulated control nestlings (Wilcoxon one-sample signed-ranks test: $S = 180.5$, $N = 66$, $P = 0.230$). We took a fixed number of feeding

visits (rather than a fixed time span) per parent to obtain constant accuracy in the estimates of mean parental feeding locations and their variance.

It is important to note that the experimenter did not affect nestling positioning through the manual stimulation of begging (position was quantified before stimulation), and he was blind with respect to parental feeding locations (which were quantified after the experiments on nestling positioning).

Statistical Analyses

The number of subjects used in the experiment was 106 nestlings from 53 nests. One nest was excluded because of technical problems during filming at the natural nest. Final sample size was 104 nestlings and 52 nests, respectively. Among the 104 test nestlings, 26 showed no sign of activity. They mostly seemed to be sleeping. Analyses of nestling positioning were conducted and are presented both including and excluding these 26 inactive nestlings.

We used circular statistical methods (Batschelet 1981; Fisher 1993) to calculate means, measures of variability and correlation coefficients. We did not explicitly consider a central position in the nestcup. This position, although often a quite favourable one (e.g. Greig-Smith 1985; McRae et al. 1993), does not add to the directionality in nestling positioning in which we were interested. It is by definition equally distant from any potential parental feeding location.

We tested two nestlings per nest, which were not independent from each other statistically. To circumvent this problem but retain the full information content of the data, we used resampling techniques where only one nestling per nest was selected randomly at each resampling step. Thus, each sample drawn from the full sample consisted of 52 nestlings from different nests (i.e. they were independent statistically) with a random combination of nestlings between nests at each turn. We conducted the random resampling with replacement, which is bootstrap sampling (Fisher 1993; Chernick 1999), to obtain accurate estimates of variability. We drew by this method 5000 bootstrap samples from the database.

For each bootstrap sample, we calculated the median absolute angular distance between nestling positioning in the laboratory and the parental feeding location at the nest. The median, rather than the mean, was chosen because of the positive skew in the distribution of observed angular distances.

Because great tit mothers and fathers often use distinct locations for feeding (Kölliker et al. 1998), the angular distance was calculated towards the closer of the two available parental feeding locations. By choosing the closer parental feeding site, we potentially overestimated the accuracy of nestling positioning and had to control for this potential bias statistically (see below). In addition, great tit parents have an overall tendency to feed from the rear of the nest (Kölliker et al. 1998). It is possible that the nestlings in the laboratory trials also tended to position themselves towards the rear, for reasons unrelated to

parental feeding locations per se (e.g. because the camera was installed on the side of the nest entrance).

We controlled statistically for these two potential sources of a bias by using permutation tests. For each bootstrap sample, we randomly re-paired measures of nestling position and parental feeding location 50 times and, as done previously for the real parent–offspring pairs, calculated from these random pairings the median angular distance of nestling positioning to the closer of the two available parental feeding locations. By using this method, we controlled for the potential bias when calculating angular distances to the closer of two parental feeding locations by including the same bias in the null expectation generated through the permutation test. Also, the comparison between the median angular distance of the real estimates and the estimates from the random pairings was done within the empirical overall distribution of nestling positions and parental feeding locations, ensuring that any overall tendency in a certain direction was excluded from our statistical test.

Statistical significance in this analysis was assessed by means of bootstrap P values (Fisher 1993). Estimates for nestling positioning towards parental feeding locations are provided with bootstrap 95% confidence intervals. One-tailed P values were calculated as one minus the proportion of bootstrap samples where the observed median angular distance was smaller than the median angular distance expected from the random permutations (Fisher 1993). Our alternative statistical hypothesis of nestling positioning towards parental feeding location was directional a priori (i.e. angular distance was expected to be smaller, and not larger, than expected by chance). To avoid one-tailed testing but retain the directionality of our alternative hypothesis, we calculated directional P values and asymmetric 95% bootstrap confidence intervals (Rice & Gaines 1994). The one-tailed P values obtained from bootstrap sampling were multiplied by 1.25, according to the convention set by Rice & Gaines (1994). P values calculated based on this approach were denoted as P_{boot}. Correspondingly, for the 95% confidence intervals, the upper and lower error tails from the bootstrap distribution were taken as 3.75% and 1.25%, respectively.

Analyses between nests of the overall directionality of parental feeding locations and the stability of parental feeding locations (see below) involved permutation tests without bootstrap sampling because the data were already on the appropriate statistical level (i.e. the nest). For these analyses, P values were nondirectional and two-tailed, and calculated based on 5000 permutations. They were denoted as P_{perm}.

Predictability of Nestling Positioning and Parental Feeding Locations

The relative predictability of parental feeding locations and nestling positions was quantified from data collected independently from the experiment described above, in 1995 ($N = 65$ nests) and 1996 ($N = 12$ nests). The data from the 2 years were analysed separately (and towards different aspects of stability of parental feeding locations;

see below) because the breeding pairs sampled in 1996 were mostly pairs contained in the 1995 sample. In all these nests, we marked all the nestlings at the age of 10 days after hatching with small spots of Bordeaux red acrylic paint on their heads (Kölliker et al. 1998). Videos were taken at the age of 10 days in 1995, and at both 6 days and 10 days in 1996. We quantified both nestling positions and parental feeding locations at the age of 10 days, whereas for the brood age of 6 days, only data on parental feeding locations were available (nestlings were not individually marked at age 6 days). Nestling positions were taken before the parent arrived at the nest and before nestlings had started begging, and a categorical measure of individual postural begging intensity was taken at parental arrival (for details see Kölliker et al. 1998). In each nest, one nestling was food deprived and one fed to satiation for 2 h prior to the start of filming (Kölliker et al. 1998). The positioning activities of these two nestlings were included in the analysis because we were interested in the description of the per-brood averages of levels of nestling positioning activities only. In this analysis, the behaviour of the two manipulated nestlings effectively cancelled out each other's effect.

For both the analysis of nestling positioning and parental feeding locations, an initial parental feeding visit (v_0) was set as a baseline to which the subsequent six visits (v_i: $i = 1$–6) were correlated in turn by use of circular correlation. We calculated circular correlations based on the coefficient r_t (Fisher & Lee 1983; Fisher 1993), which estimates the degree of 'linear' association between two circular variables (Fisher & Lee 1983) and can be considered the circular counterpart to the Pearson's correlation coefficient of linear statistics (Fisher 1993). The change in the value of r_t with increasing degree of time spacing (in terms of number of feeding visits) between v_0 and v_i represents an estimate for the decay of predictability over time and thus can be used as a measure for the extent of position changes for both nestlings and parents. To temper the potential impact of the individual feeding visit set as the initial visit (v_0), we ran the analysis eight times, starting by taking the first feeding visit analysed from the videos as the first initial visit, the second as initial visit number two, and so forth. The mean r_t of the eight runs was taken as the final measure of predictability.

We calculated r_t for the parental feeding locations from the between-parent (co-)variation in feeding location, and for mothers and fathers separately. As a consequence, we obtained one point estimate for r_t for the whole sample of nests and for each sex, respectively. We calculated r_t for nestling positions from the within-nest and between-nestlings (co-)variation in positions, resulting in 65 estimates of r_t. Nestling positions were considered separately for visits by mothers and fathers, and the values of r_t from maternal and paternal visits were then averaged to get the final measure of nestling predictability. For nestling positions, it was possible to calculate 95% bootstrap confidence intervals for r_t. This analysis was carried out on the 1995 sample ($N = 65$). The 1996 sample ($N = 12$) was used to assess the stability of parental feeding locations over 4 days (locations at brood age 6 days versus age 10 days).

All the statistical analyses and simulations were conducted using SAS statistical software, version 8.2 for Windows (SAS Institute 1999). Algorithms for circular statistics, bootstrap sampling and permutation tests were written as SAS-macros following the methodology of Fisher (1993) and Chernick (1999).

RESULTS

Nestling Positioning towards Parental Feeding Locations

As predicted, nestlings preferentially chose positions in the laboratory box towards the direction of a feeding location of one of their provisioning parents. The absolute angular distance between nestling positioning and the closest available parental feeding location was smaller than the angular distance expected from chance alone (Fig. 1). In the analysis based on the full sample, nestlings chose positions towards directions 48.8° from a parental feeding location, which was 23.3° (32.3%) closer than expected from random positioning (Fig. 1a). This effect was statistically significant ($P_{boot} = 0.044$). Somewhat more accurate nestling positioning was suggested when the 26 inactive nestlings were excluded. In the analysis based on the subsample, nestlings chose positions towards directions 38.5° from a parental feeding site (Fig. 1b). This was 22.6° (37.0%) closer than expected from random positioning ($P_{boot} = 0.014$).

Maternal and paternal feeding locations were chosen by nestlings at comparable frequencies. The proportion of cases with preference for the maternal location was 0.529 in the full sample (bootstrap confidence interval: 0.432–0.663; $P_{boot} = 0.257$), and 0.469 (bootstrap confidence interval: 0.358–0.597; $P_{boot} = 0.841$) in the subsample.

As expected if nestling positioning was dynamic and did not reflect a potential nestling preference towards a typical position within the nestcup, there was no significant
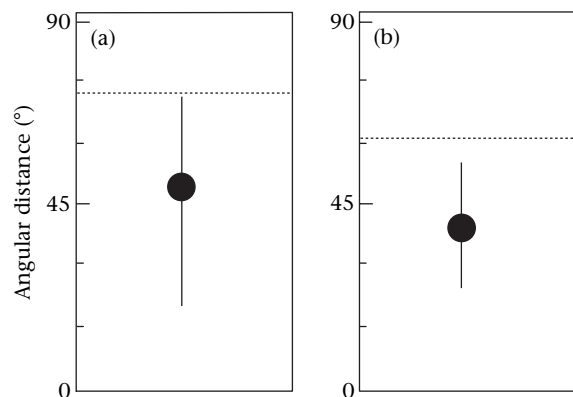

Figure 1. Nestling positioning towards parental feeding locations: (a) full sample $N = 105$ nestlings; (b) subsample excluding 26 inactive nestlings. The dashed line indicates the angular distance between nestling positioning and parental feeding location expected through random nestling movements (estimated by use of permutation tests). The mean and bootstrap 95% confidence intervals are shown.

correlation between nestling positioning in the laboratory and at the nest close in time to when parental feeding locations were quantified (i.e. approximately 60 min after return to the nest; $r_t = 0.002$, $N = 98$, $P_{perm} = 0.772$).

Distribution of Parental Feeding Locations and Nestling Position Choices

Among parents, there was ample variation in feeding locations between mothers and between fathers (Fig. 2). Both sexes had an overall tendency to prefer locations at the rear of the nest. Maternal feeding locations were centred around the mean ± circular SD direction of 161 ± 71.02° (Rayleigh test: $r = 0.46$, $N = 52$, $P_{perm} < 0.001$; Fig. 2a), and paternal feeding locations centred around the mean ± circular SD direction of 188 ± 54.50° (Rayleigh test: $r = 0.64$, $N = 50$, $P_{perm} < 0.001$; Fig. 2b). The mean absolute angular distance between feeding locations of great tit mothers and fathers was 73.3° (range 0.2–174.0°). All these observations are quantitatively very close to the ones described in Kölliker et al. (1998).

Positions chosen by nestlings in the laboratory trials were distributed widely over the circle (Fig. 2c). Excluding the 26 inactive subjects (Fig. 2c; white bar), there was a slight but significant tendency for nestling positioning towards the right-hand rear of the nestbox (mean ± circular SD direction = 238 ± 99.70°; Rayleigh test: $r = 0.22$, $N = 78$, $P_{perm} = 0.002$; Fig. 2c).

Dynamics of Nestling Positioning and Predictability of Parental Feeding Sites

The 'decay' plot presented in Fig. 3 reveals that feeding locations of mothers and fathers were constantly predictable over time, whereas the predictability of nestling positions decayed rapidly and significantly from one parental visit to the next. Parental feeding visits were stable not only over a couple of visits, but also over several days. The correlation between the mean maternal/paternal feeding location (based on 10 visits) at brood age 6 days versus brood age 10 days was strong and highly significant for both mothers ($r_t = 0.81$, $N = 12$, $P_{perm} < 0.001$) and fathers ($r_t = 0.94$, $N = 11$, $P_{perm} < 0.001$).

The predictability from an initial visit to its first subsequent visit (0–1) was similar and not significantly different for nestling positions and parental feeding locations, but contrary to parental feeding locations, the predictability of nestling positions decayed rapidly afterwards (Fig. 3). Although nestling predictability remained statistically significant throughout the six visits analysed here (note that the 95% confidence intervals never cross the X axis in Fig. 3), the extent of predictability decreased substantially and to quite low values of r_t.

DISCUSSION

We have shown that great tit nestlings have knowledge of their parents' feeding locations and position themselves
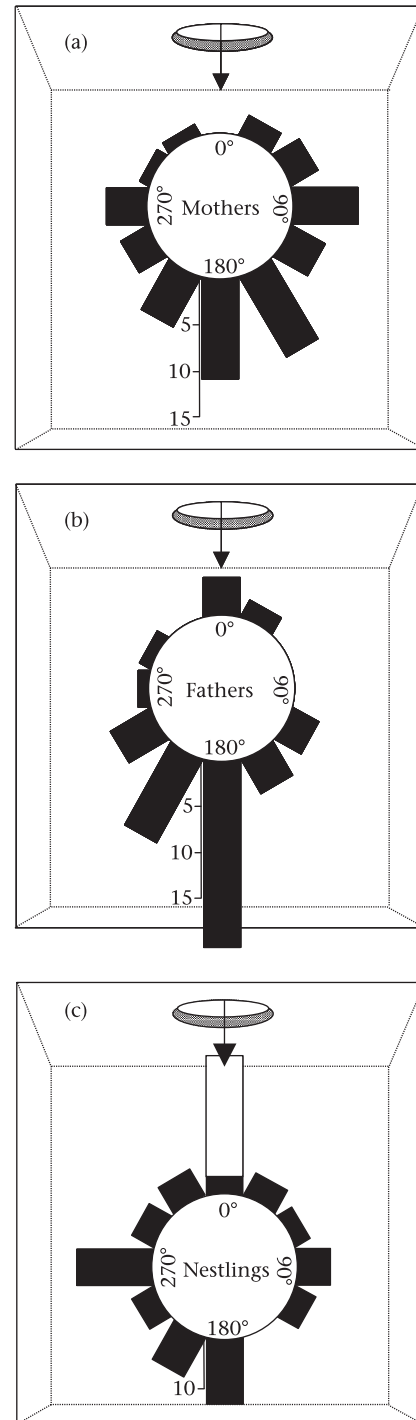

Figure 2. Circular distribution of the typical (a) maternal and (b) paternal feeding locations around the nestcup at natural great tit nests, and of (c) nestling positioning in laboratory boxes. The typical individual maternal and paternal feeding locations were calculated as the mean location of 10 feeding visits. The axis added to the bar at 180° indicates the number of (a) mothers, (b) fathers or (c) nestlings. Note that, due to the interdependence, the univariate distributions displayed in (a), (b) and (c) do not allow conclusions to be drawn on the within-nest angular distances either between maternal and paternal feeding locations or between nestling positioning in the laboratory and a parental feeding location. The white bar in (c) corresponds to the 26 inactive nestlings.
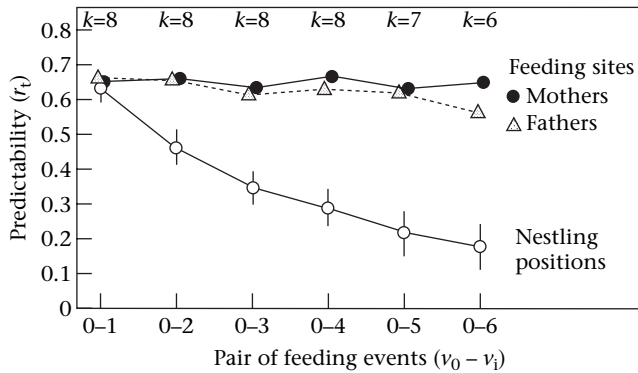
Figure 3. Decay plot for the predictabilities of parental feeding locations and nestling positions. The X axis indicates the spacing in terms of the number of parental visits between the correlated variables. The Y axis is the predictability, calculated as the circular correlation coefficient r_t. The predictability at 0–1 corresponds to r_t between the initial and the first subsequent feeding visit, 0–6 to r_t between the initial and the sixth subsequent feeding visit. The first eight feeding visits from the videorecordings were each set as initial visit in turn, and the average values of these eight runs are shown (indicated by k). k is declining with increasing spacing due to the insufficient number of total feeding visits available at some nests. Bootstrap 95% confidence intervals are shown for nestling positions. Nestling positions were quantified before parents arrived at the nest. Data are from 1995.

in the direction of those locations without a parent being present. Our results suggest that nestlings are able to associate begging payoffs (higher when closer to the parent; see Introduction) with specific locations in the nestcup. This capacity would allow competitive and/or hungry nestlings to occupy 'pole positions' before parental arrival when the parent as the target of competition is not available. The cavity entrance appears to be a cue that nestlings use for orientation, but it is not the target for competition.

The only straightforward 'landmark' available for orientation in our experimental setting was the nest entrance hole. All other cues were excluded experimentally. Nestlings may also use information from nest and cavity structure for orientation, however. Use of an innate geomagnetic compass (see e.g. Wiltschko & Wiltschko 2002), which is somewhat speculative because the great tit is a nonmigratory bird, was also ruled out because the laboratory boxes were installed with the nest entrance holes towards the west whereas the entrance holes in the forest tend to orient towards east. Thus, the effects reported here may underestimate the navigational capacities of great tit nestlings. Further research is required to reveal the full set of cues that nestling birds may use for navigation in the nest.

A critical requirement for interpreting our results as nestling navigation in the nestcup is that nestlings did not use typical positions to which parents may have actively adjusted their feeding locations (e.g. if a nestling in a given position stood out by begging very intensely). We reduced the risk that our test nestlings would stand out from the rest of the brood by feeding them before returning them to the nest, and by starting

quantification of parental feeding locations 1 h, on average, after the start of videorecording (when begging levels of food-deprived nestlings had returned to average levels; see Methods). Additional analysis confirmed that this competing scenario is unlikely in the great tit. There was no correlation between the position chosen by the nestling in the laboratory and the position occupied in the natural nest close in time to when parental feeding locations were quantified. Such a correlation would be required, however, if nestlings in the laboratory chose their typical positions and parents later approached these typical positions at the natural nest. This lack of correlation was expected from our additional results of dynamic changes in nestling positions shown in Fig. 3.

The foraging hypothesis of sibling rivalry assumes predictable parental feeding locations and dynamic nestling positioning. The great tit largely conforms to these assumptions. The predictability of parental feeding locations remained very stable over time, even over periods as long as several days and potentially most of the nestling period. The mean of as few as 10 feeding visits provided a very good estimate of the typical parental feeding location over several days. Even though parents were somewhat variable in their location choice from visit to visit (average $r_t \cong 0.65$; Fig. 3), most probably due to some degree of active choices towards immediate individual nestling positions (M. Kölliker, personal observations), this variation was restricted to a limited sector only. Simultaneously, the decay in the predictability of nestling positions over time was considerable, showing highly dynamic position adjustments by nestlings throughout the nestcup, and the lack of typical nestling positions (see also Neuenschwander et al. 2003). Whereas a nestling needs only one parental visit to get an accurate estimate of the typical parental feeding location, a parent would need to update the positions of all nestlings at each visit to achieve a similar precision in the longer run (see Fig. 3).

Our analyses suggest that nestling great tits approached parental feeding sites through positioning by approximately 23° as compared to random choices. To get a heuristic estimate of the benefit associated with the observed effect, we fitted regression models describing within-brood food distribution as a function of postural begging and angular distance of individual nestlings for both maternal (feeds$_m$ = 1.8894 + 0.5491 postural begging − 0.0084 angular distance) and paternal (feeds$_p$ = 1.9494 + 0.5030 postural begging − 0.0083 angular distance) feeding (data from 1995). Both the postural begging intensity and the angular distance were significant ($P < 0.001$). Fixing the postural begging intensity at the population average (1.74; i.e. assuming average postural begging behaviour), substituting the observed effect size into the equations, and summing the predictions for maternal and paternal provisioning suggests an increased feeding success through positioning on the order of 0.4 feeds per hour per nestling. This corresponds to an approximate 8% competitive advantage over a (hypothetical) randomly moving nestling. An 8% competitive advantage might be biologically relevant, especially under conditions of limited food availability.

This reasoning raises the question as to how the ability of great tit nestlings to approach parental feeding locations is expressed in real broods where choices are not as free as in our laboratory trials. It is conceivable that nestlings may use their ability for directional positioning in a condition-dependent manner (i.e. only when hunger trespasses a certain level). Such a system would result in a dynamic, hunger-driven turnover of nestlings at favourable positions. In addition, competitive ability might interact with hunger (Gottlander 1987; Price et al. 2002), skewing nestling positioning and parental food allocation under conditions of low food availability (i.e. when competitive nestlings stay hungry enough to maintain a favourable position) and equalizing nestling positioning and food allocation when food is plentiful (i.e. when more competitive nestlings get easily satiated and have higher marginal gains in inclusive fitness by allowing access to a more hungry sibling; e.g. Mock & Parker 1997).

It is commonly argued that, in cavity-nesting birds, parents are constrained to feed from the nest entrance hole (e.g. Leonard et al. 1994; Kacelnik et al. 1995; Leonard & Horn 1996; Lotem 1998; Rodríguez-Gironés et al. 2001). Great tit parents differ widely in their feeding locations, with an overall tendency to feed from the rear of the nest (Fig. 2; Kölliker et al. 1998), and mothers and fathers tend to feed from distinct locations on the nest rim (this study; Kölliker et al. 1998). Thus, cavity nesting per se does not explain stability of parental feeding locations in cavity-nesting birds nor make the entrance hole the target of competition between nestlings. Stable feeding locations may actually be beneficial to parents because such a habit allows them to save time and to transfer food efficiently (e.g. Rodríguez-Gironés et al. 2001). This benefit may come at the cost of losing some control over food allocation by creating selection on nestlings to exploit parental predictability through learning and optimal foraging. These arguments suggest that parent birds may actively choose their feeding locations. Their choices may be influenced or constrained by a number of factors such as nest structure (Ostreiher 2001), external ecological factors, the competitive situation in the brood (Kilner 2002), the age of the nestlings (i.e. older nestlings may be more able to block the nest entrance hole; Litovich & Power 1992; Kilner 2001), and/or the feeding location of the other parent (Kölliker et al. 1998). Additionally, parents may not just stick to their habit and accept passively the outcome of scramble competition between their offspring (Davis et al. 1999), but may actively modulate the begging payoffs associated with certain positions in the nestcup (Kölliker et al. 1998). They may adjust their feeding locations to each other, which may affect the overall level of sibling rivalry in the brood (Kölliker et al. 1998; Lessells 2002), and/or each parent may establish independent competition rules for access to their respective 'begging patches' (Kölliker et al. 1998), for example, by active choices limited within a small sector around their typical feeding sites. Thus, nestling positioning may not be pure scrambling for access to passive parents because parents actively set up and modify rules under which nestlings have to forage.

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