ANIMAL BEHAVIOUR, 2006, 72, 1249–1257
doi:10.1016/j.anbehav.2006.02.024

Consistent feeding positions of great tit parents

C(KATE). M. LESSELLS*, ERIK H. POELMAN*, A. CHRISTA MATEMAN* & PHILLIP CASSEY†
*Netherlands Institute of Ecology (NIOO-KNAW), Heteren
†Centre for Ornithology, School of Biosciences, University of Birmingham

*(Received 17 June 2004; initial acceptance 19 August 2004;
final acceptance 28 February 2006; published online 2 October 2006; MS. number: 8169)*

When parent birds arrive at the nest to provision their young, their position on the nest rim may influence which chick or chicks are fed. As a result, the consistency of feeding positions of the individual parents, and the difference in position between the parents, may affect how equitably food is divided among the chicks. We studied the positions of parent great tits, *Parus major*, landing on the nest to feed their chicks. Individual parents were consistent in their position within observation periods, on different days within the same breeding attempt, and at breeding attempts in different years. Within each sex, there were individual differences in position within single observation bouts, in average position across days within a breeding attempt, and in average position across years. At the majority of nests, the two parents differed in positions. The distribution of angular distances between the parents differed from that expected if the parents' positions were independent, with the observed median being less than that expected. The angular distance between the parents was not related to 22 different characteristics of the brood and parents. We conclude that consistency (i.e. a departure from a random uniform distribution) in position is explained by habit formation, and to a lesser extent by an overall preference for particular locations, and by nest configuration. We also conclude that there is little scope and no evidence for the parents strategically adjusting their angular separation.

The incomplete relatedness between family members in sexually reproducing species creates genetic conflicts of interest (Parker et al. 2002). These conflicts include both sexual conflict between the parents and parent–offspring conflict, and act as selection pressures for an intriguing array of ways in which family members might conflict or cooperate. For example, sexual conflict between the members of a pair over parental investment is almost universally expected, with each parent's selfish optimum involving the other parent doing a relatively large share of the work. But there are also ways in which parents may be selected to cooperate: in general, parent–offspring conflict results in the optimal division of investment between offspring for both parents being more even than that for the offspring. Parents might be able to cooperate in achieving closer to their own optima by providing parental care in such a way that offspring cannot simultaneously solicit care from both parents. This would limit the extent to which individual offspring could monopolize parental care (Slagsvold 1997; Lessells 2002).

In birds, some species with biparental care 'divide' the brood after fledging, each parent taking sole care of part of the brood (see Lessells 2002 for a list of studies showing brood division). Preventing chicks from selfishly monopolizing care is one explanation (in addition to many others; see, for example, McLaughlin & Montgomerie 1985) to explain brood division. A form of brood division may occur even before the chicks have left the nest: Kölliker et al. (1998) showed that the positions from which individual parent great tits, *Parus major*, fed their chicks were remarkably consistent within a period of observation, and that at the majority of nests the two parents fed from significantly different positions. They also showed that the difference in feeding positions of the two parents (measured by the angular separation) differed significantly from that expected on the basis of the distribution of feeding positions of all males and all females. They concluded that the parents seemed to adjust their feeding locations to each other, and that the different locations of the two parents forced the chicks to choose between them.

The difference in feeding positions of parents in the majority of nests and the departure of the observed

Correspondence: C. M. Lessells, Netherlands Institute of Ecology, Centre for Terrestrial Ecology, PO Box 40, 6666 ZG Heteren, The Netherlands (email: k.lessells@nioo.knaw.nl). E. Poelman is now at the Laboratory of Entomology, Wageningen University, PO Box 8031, 6700 EH Wageningen, The Netherlands. P. Cassey is at the Centre for Ornithology, School of Biosciences, University of Birmingham, Edgbaston B15 2TT, U.K.

0003–3472/06/$30.00/0

distribution of angular separations from the expected distribution raise three general questions. The first is whether, as Kölliker et al. (1998) suggested, the parents do adjust their positions relative to each other, and in addition whether this is a strategic decision that allows them to adjust the equitability of food distribution in relation to environmental circumstances (e.g. allowing strong offspring to monopolize resources when food is scarce to produce adaptive brood reduction; Lack 1954). The second question is what effect the difference in parental positions has on the distribution of food between the offspring. The third question is, regardless of whether the parents have adjusted their positions relative to each other, whether chicks use the information contained in consistency of feeding locations about the identity of the parent to modulate their begging behaviour to the male and female parent.

In this study, we focused on the first of these three questions. We repeated Kölliker et al.'s (1998) analysis of the consistency of individual positions within an observation period, and of the separation between the two parents provisioning a brood. In addition, we examined individual consistency in position across days within a breeding attempt, and also across breeding attempts in different years. We also attempted to identify the ways in which the observed separation between parents differs from the expected distribution, and examined whether the distance between the parents is related to any characteristic of the brood or parents. In doing this we had two general aims: the first was to identify the source(s) of consistency in feeding positions. (For example, do all individuals simply have (the same) preference for a particular location?) The second aim was to examine the evidence that the two parents adjust their feeding locations to each other, and the likelihood that they strategically adjust their separation in relation to environmental circumstances. Our study is similar to that of Kölliker et al. (1998) in being on the same species breeding in nestboxes with the same internal dimensions. One important difference is that we measured the positions of some individuals in more than one year, allowing us to estimate consistency in position across years. We also measured the angular positions of the parents by scoring their X,Y coordinates on a grid, and then converted the coordinates to an angular position, giving considerably greater precision than Kölliker et al.'s (1998) allocation to one of eight sectors around the nest rim.

METHODS

We carried out the study on a population of great tits at the Buunderkamp, an area of mixed woodland in the Veluwe region of the Netherlands. Nestboxes were inspected regularly during the early part of the breeding season to determine clutch size and expected hatching date. We determined actual hatching date (day 0) from daily nest checks, which we continued until the number of hatched young was known, and we collected any unhatched eggs. Chicks were blood sampled (10 µl) from the leg or brachial vein during the nestling period and their sex, and that of unhatched embryos, determined with a reliable molecular technique (Griffiths et al. 1998). Chicks were weighed (±0.1 g) and their tarsus length measured (±0.1 mm) on day 15 ('fledgling' measurements). Adults were caught in the nestbox on or after day 7 (but not before video recording on the same day) and ringed, aged as yearlings (1 year old) or older on the basis of plumage characteristics and of their ringing history, weighed, and the lengths of their third primary (±0.5 mm) and tarsus measured. Nests were inspected after fledging to record any chicks that failed to fledge. In the analyses presented below, initial brood size is generally the number of young hatched in the nest, but in 2001 partial cross-fostering was carried out on day 0–2, and initial brood size is then the brood size following this manipulation. Hatching success is the proportion of the clutch laid that hatched, and fledging success the proportion of the initial brood size that fledged. Sex ratio of the clutch is the proportion of males among the hatched young and unhatched embryos from the clutch laid. We corrected fledgling masses and tarsus lengths for sex, and masses also for the time of weighing (see Table 3 in the Results), before calculating means and standard deviations of these two variables for each brood.

Video Recording

Video recordings were made at 77 breeding attempts by 55 known individual males and 57 known individual females in 1999–2003 inclusive as part of various observations and experiments (not reported here). Mean brood size at the time of video recording ±SD was 9.03 ± 0.91 chicks (range 5–13). The chicks were either undeprived (control), or one or all of the chicks had been food deprived for 2 h before the recording. For this paper, we generally analysed data from only one video recording per breeding attempt (1999 and 2002: control 10-day chicks; 2001: one-deprived 10-day chicks; 2002 and 2003: control 9-day chicks), but for 2000 we analysed data from three recordings for each brood (control 10-day chicks; one-deprived 9- or 11-day chicks; all-deprived 9- or 11-day chicks). In all analyses using data from more than one year, we used only the control recordings from 2000. In analyses where pseudoreplication might be a problem, we used only the first recording from each individual or pair (as appropriate). In analyses of within-year across-days consistency we used data only from 2000.

For all video recordings, we used Sony video camcorders with 'nightshot' facility (i.e. recording in the infrared with an integral infrared lamp for illumination) housed in a second wooden box that replaced the lid of the nestbox. This second box was put in place at least a day before video recordings began. All experimental pairs were breeding in nestboxes with internal dimensions $12.5 \times 12.5 \times 22.5$ cm (identical to the nestbox dimensions in Kölliker et al.'s 1998 study; M. Kölliker, personal communication). The cameras filmed near-vertically downwards. Positions of the parents were determined on frozen frames of video playback, and were interpolated by eye to the nearest 10th of a grid square on a 10×10 grid on a transparent overlay attached to the monitor

screen drawn to match the internal box dimensions in that recording (i.e. approximately ±1.25 mm). Any nest visits when the other parent was already in the box were excluded from the analyses (5.65% of visits; $N = 3487$).

For each nest visit, we scored the position of the adult as it landed on the nest (one point in the middle of the back between the folded wings, and a second point at the base of the beak at the junction with the feathers) from the video recording, along with its sex. (On the infrared recordings the males' crown feathers appear glossy, and those of the females sooty.) We also noted the extreme X and Y coordinates of the nest cup and used these to determine the coordinates for the centre of the nest cup. We used these X,Y coordinates and those of the parents at each nest visit to calculate the angular positions of the parents at each nest visit. It is these angular positions that we analysed in this paper.

Statistical Analysis

Statistical methods for analysing circular data were taken from Batschelet (1981) and Fisher (1993). The position of a parent during multiple visits can be summarized by the mean vector, the direction of which, φ, describes the average angular position of the adult, and the length of which, r, describes how consistent the angular positions are, ranging from 0, when the angular positions 'cancel each other out', to 1, when all the angular positions are identical. In general, r varies with sample size, a smaller sample size favouring higher r (Batschelet 1981). The number of feeding visits per parent scored from a recording ranged from 3 to 64 for males and 5 to 46 for females. We used the calculated r values based on different numbers of measurements because, if anything, the calculated r values increased (not decreased as expected) with the number of measurements (Spearman rank correlations, r_S, between the consistency of angular position (r) and sample size: male beak: $r_S = 0.096$; male back: $r_S = 0.039$; female beak: $r_S = 0.127$; female back: $r_S = -0.004$; all $N = 103$; all $P > 0.2$). Thus the increase in precision in the estimate of r obtained by using the larger sample sizes when available appears to more than counteract any bias caused by sample size. We used Rayleigh tests to determine whether a set of angular measurements are more consistent than a random (uniform) distribution. In Rayleigh tests of consistency across days or between years, we analysed the mean angular position for a video recording, and not the individual angular positions, to avoid pseudoreplication. We used Watson–Williams tests to determine whether two (or more) samples of angular positions differed significantly from one another.

In some cases, our data do not meet the assumptions of the statistical test used (e.g. sample size too small per group). In these cases, and in analysing the frequency distribution of angular distances between the members of pairs, we used randomization tests to attach a P value to a parameter or test statistic (Fisher 1993; Manley 1997). The general procedure used in these tests was to reallocate randomly the measured values of variables across the measured units while maintaining sample sizes per group or subgroup, and then to recalculate the parameter or test statistic of interest for these randomized data. The proportion of 1000 iterations in which the parameter or test statistic was more extreme than the observed value was taken as the P value.

P values are two tailed unless otherwise stated.

Ethical Note

Broods were never abandoned in response to any of the procedures we used. Food deprivation was carried out for scientific purposes other than those reported in this paper. Chicks were kept warm during food deprivation and did not show signs of stress at the end of the deprivation period. The number of times a chick was food deprived (≤ 2, always on different days) had no detectable effect on the probability of surviving until fledging (logistic regression controlling for year: number of times deprived: $\chi^2_1 = 0.05$, $P = 0.83$) or fledgling mass (hierarchical mixed model with brood as a random effect, and sex and the number of times deprived as within-brood effects: number of times deprived: $F_{1,381} = 0.08$, $P = 0.78$). For comparison, rainfall during the nestling period does affect fledgling mass (Radford et al. 2001). The necessary permission to carry out experimental procedures was granted by the Animal Experimentation Committee (DEC) of the Royal Dutch Academy of Arts and Sciences (KNAW).

RESULTS

Positions of the Parents

Angular positions of parents were available for 55 individual males and 57 individual females. Both sexes of parents were consistent across nest visits within a single observation period in both their beak and back positions (Rayleigh test: % of tests significant at $P < 0.05$: male beak: 100%, $N = 55$ tests; female beak: 95%, $N = 57$; male back: 98%, $N = 55$; female back: 98%, $N = 56$). Males were more consistent than females in both their beak and back positions, and within each sex back positions were more consistent than beak positions (Table 1). Significantly consistent positions of individuals might by associated with individual differences, but might also simply arise if all birds (or all birds of each sex) have the same preference for some position in the nest (e.g. the front). Further analysis showed that at least part of the consistency is associated with individual differences, because beak and back positions were significantly different between individuals within each sex (Watson–Williams tests: male beak: $F_{54,678} = 116.52$; female beak: $F_{56,559} = 39.31$; male back: $F_{54,678} = 281.78$; female back: $F_{56,559} = 140.47$; all $P < 0.001$).

There was also evidence for a general preference for some parts of the nest: there was no left–right bias in the position of the beak or back for males or females (largest $\chi^2_1 = 0.89$, $P > 0.3$), but beak positions were generally in the back half of the nest (one-sample t test for difference from 90°: males: $t_{54} = 7.41$, $P < 0.001$; females: $t_{56} = 6.15$,

Table 1. Consistency (*r*, the mean vector length) of angular positions of great tit parents landing on the nest

	Mean *r*±SD (*N*)		Males versus females
Angular position	Males	Females	Test statistic *P*
Within a recording session*			
Beak	0.938±0.074 (55)	0.884±0.166 (57)	2.28±0.023†
Back	0.957±0.010 (55)	0.938±0.117 (57)	2.11±0.023†
Beak versus back: *Z*‡	3.13	2.45	
P	0.002	0.014	
Across days§			
Beak	0.986±0.030 (13)	0.975±0.028 (13)	20 NS
Back	0.952±0.102 (13)	0.980±0.018 (13)	45 NS
Beak versus back: *T*	25	43	
P	NS	NS	
Across years**			
Beak	0.856±0.162 (14)	0.856±0.284 (14)	0.207 NS
Back	0.726±0.359 (14)	0.890±0.182 (14)	0.607 NS
Beak versus back: *T*	21	33	
P	NS	NS	

*Angular position at each nest visit within a recording session (one per individual). Because *r* is expected to vary with the number of observations on which it is based, the statistical test for comparing males and females was based on *r* values calculated from the first 10 positions recorded during the recording period. $N = 37$ males and 50 females.
†Mann–Whitney *U* test.
‡Wilcoxon matched-pairs test.
§Average angular position for a recording session across different days within the same breeding attempt (one breeding attempt per individual).
**Average angular position for a recording session across different years (one recording session per year per individual).

$P < 0.001$; Fig. 1a). Back positions were approximately equally distributed between the front and back of the nest (one-sample *t* test for difference from 90°: males: $t_{54} = 0.26$, $P > 0.5$; females: $t_{56} = 0.89$, $P > 0.2$; Fig. 1b). Unsurprisingly, most males and females faced backwards in the nest as judged by their average beak and back positions (% facing backwards: males: 85%, $N = 55$; females: 79%, $N = 57$). There was no difference between males and females in their front–back position in the nest (Mann–Whitney *U* test: beak: $Z = 0.064$, $P = 0.95$; back: $Z = 0.177$; $P = 0.86$).

Angular positions were available for recordings made on 3 days within the same breeding attempts for 13 pairs. Both sexes of parents were consistent across days in both their beak and back positions (Rayleigh test, *P* values based on 1000 calculations of *r* from three randomly generated angular positions: % of tests significant at $P < 0.05$: male beak: 92%, $N = 13$ tests; female beak: 92%, $N = 13$; male back: 77%, $N = 13$; female back: 92%, $N = 13$; Table 1). Consistency did not vary significantly between sexes or between beak and back (Table 1). As before, consistency may be generated if all birds (or all birds of each sex) have a consistent preference for some position in the nest. However, individuals of each sex again differed significantly in their angular positions, so at least part of the consistency is associated with individual differences (Watson–Williams tests: male beak: $F_{12,26} = 70.05$; female beak: $F_{12,26} = 39.50$; male back: $F_{12,26} = 38.84$; female back: $F_{12,26} = 84.74$; all *P* (randomization tests) <0.001).

Recordings were made in more than 1 year for 14 males and 14 females. Both sexes of parents tended to be consistent in their positions across years (Table 1). Many of the individuals were recorded in only 2 years so Rayleigh tests on individuals were mostly nonsignificant. However, when exact probabilities were assigned using distributions of *r* values calculated from randomly chosen angular positions, and combined for individuals of each sex, combined *P* values were highly significant (Fisher's test for combining probabilities, Sokal & Rohlf 1969: male beak: $\chi^2_{28} = 75.50$; male back: $\chi^2_{28} = 60.16$; female beak: $\chi^2_{28} = 77.10$; female back: $\chi^2_{28} = 80.54$; all $P < 0.001$). Individuals of each sex differed significantly in their angular positions (apart from back positions of males, which were marginally nonsignificant; Watson–Williams tests (*P* values from randomization tests): male beak: $F_{13,18} = 2.711$, $P = 0.008$; female beak: $F_{13,18} = 3.650$, $P = 0.004$; male back: $F_{13,18} = 2.121$, $P = 0.058$; female back: $F_{13,18} = 6.746$, $P < 0.001$). This analysis shows that individuals were consistent from year to year in the position that they landed on the nest, over and above any preference by all individuals, or individuals of one sex, for some particular position. Figure 2 illustrates the consistency of angular positions of individuals across years for a representative sample of males and females.

If individuals are influenced by the position of their mate, consistency is expected to be higher across different years when mated to the same rather than a different partner. Equally, if landing position in the nest is determined by peculiarities of the specific nestbox (including habitat features influencing approach path), consistency is expected to be higher across years when breeding in the same rather than a different nestbox. Although sample sizes are small for such comparisons, there is no suggestion

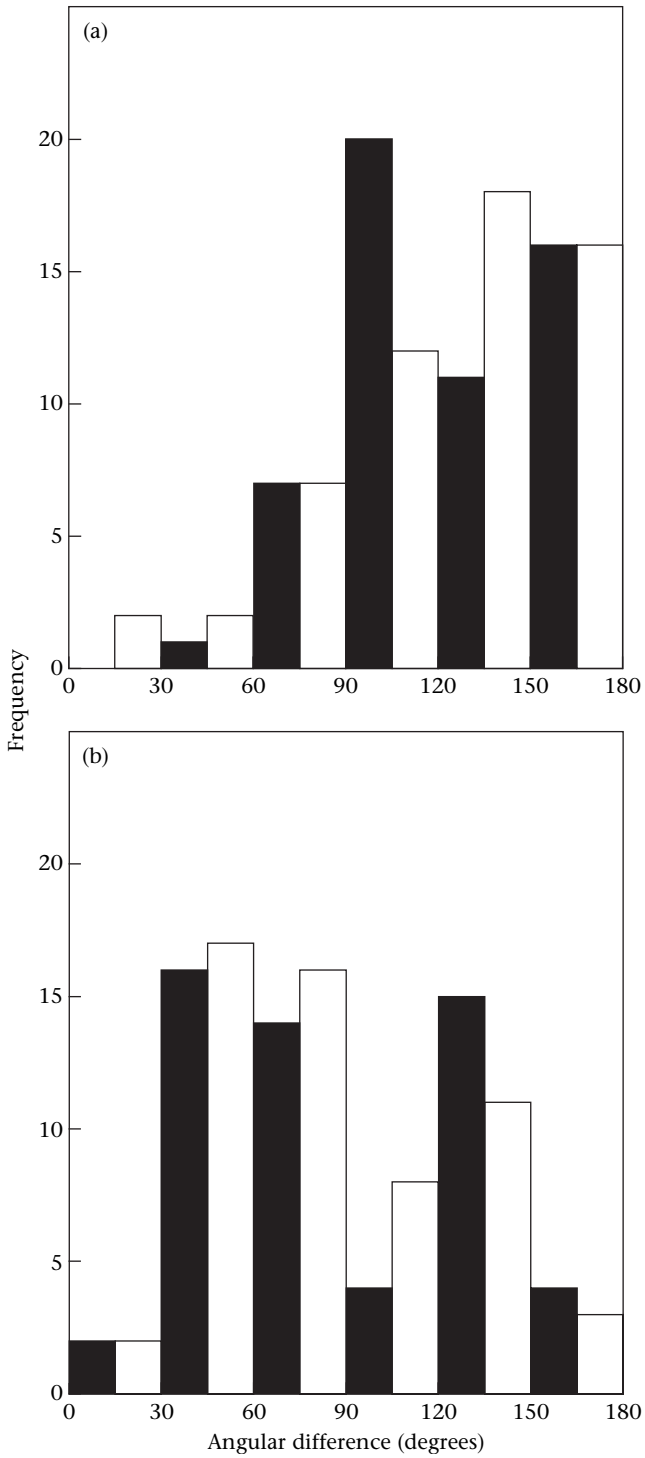

Figure 1. Position of the (a) beak and (b) back of male (■; $N = 55$) and female (□; $N = 57$) great tit parents. The X variable is the absolute angular difference between the average angular position of the individual and the front of the nest.

for such differences. In eight comparisons of consistency between breeding with the same or different mate or nestbox, mean consistency was higher on two occasions with the same nestbox, and five occasions with a different mate or nestbox (Table 2). None of these differences was significant in a directional test (Table 2).

Angular Distance Between Parents

Angular positions of both parents were available for 69 unique pairs (Fig. 3). Mean angular separation of beak positions ±SD was $62.9 \pm 49.0°$ and of back positions $65.2 \pm 48.2°$. In the majority of nests, the angular positions of the male and female were significantly different (Watson–Williams test: % of tests significant at $P < 0.05$: beak: 80%, $N = 69$ tests; back: 85%, $N = 69$).

Significant differences in the angular positions do not demonstrate that the positions of the two parents are nonindependent, because such differences could be generated by consistent use of independently chosen positions. To test whether parental positions are independent, we compared the observed distribution of angular distances with an expected distribution under independent choice of positions. This expected distribution was generated by randomly sampling one male and one female from the data set of 69 pairs and calculating their angular distance for both beak and back. This was done 10 000 times (with replacement). The expected distribution generated in this way takes into account the nonuniform distribution of feeding positions around the nest circumference. To compare observed distributions with the expected distribution, we used a Kolmogorov–Smirnov one-sample test. The distribution of beak angular distances was not significantly different from the expected distribution ($D = 0.159$, $N = 69$, $P < 0.1$), but the distribution of back angular distances was ($D = 0.204$, $N = 69$, $P < 0.01$). The Kolmogorov–Smirnov one-sample test identifies any departure between an observed and expected distribution, but does not identify the nature of the departure. To test whether the median angular distance between the two parents differed from expected if the parents' positions are independent, we performed 1000 iterations of a randomization test in which the 69 males and females in the sample were randomly reallocated into pairs and the median angular distances for beak and back for these 'pairs' calculated. Both beak and back observed angular distances were less than expected if the parents were independently distributed, but this difference is marginally nonsignificant for beak positions (beak: $P = 0.088$; back: $P < 0.001$; two-tailed probabilities derived from a one-tailed randomization test). In other words, the parents were closer together, if anything, than expected if they had chosen their positions independently.

If the angular distance between the parents provides a means for the parents to vary the equitability of food division between the chicks, parents should adjust this angle in relation to variables that predict the benefit of more or less equitable food division. Conversely, if the angular distance affects the equitability of food division, variables such as the mean and standard deviation of chick mass and size at fledging should be affected by the angular distance between the parents. We therefore investigated the relation between the angular distance between the parents (in both beak and back positions) and year, and a number of variables related to the brood and parental phenotype (see Table 3 for a list of these variables). In some cases, where a relation exists, causation could be in either direction. (For example, parents might

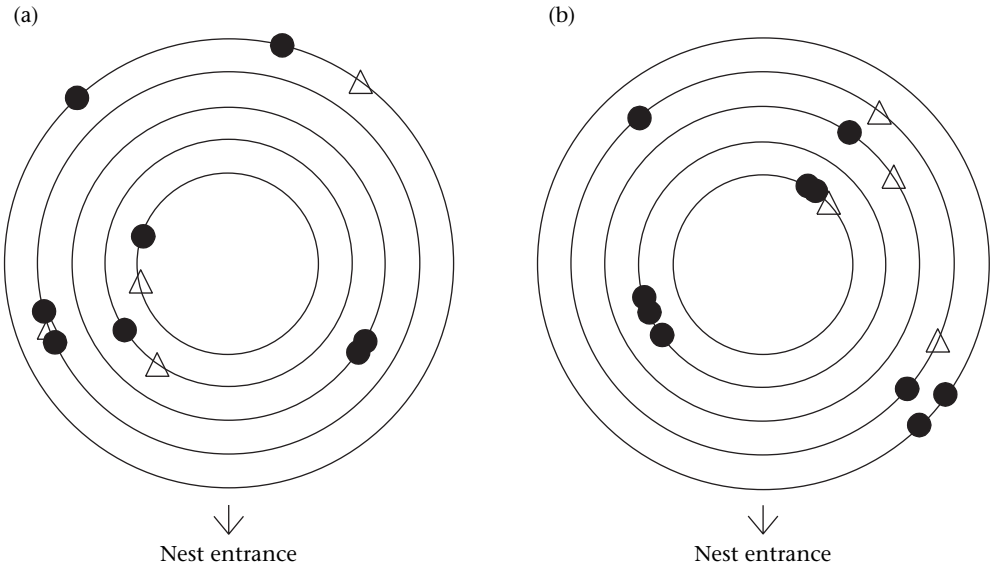

Figure 2. An illustration of the consistency of average angular positions of backs of (a) males and (b) females across years. Each ring represents a different individual; data are presented for five different males and five different females. Each of the points on a ring represents the average angular position in a different year, so the tendency for points to cluster together on each ring indicates that individuals are consistent in their positions across different years. The figure also shows that consistency across years is not greater when breeding with the same mate. Identity of the partner is indicated by the symbol used: within each ring (but not across different rings), each symbol indicates that the bird was mated to a specific individual partner, so that the same symbol represents a pair breeding together in 2 or more years.

adjust their angular distance in relation to initial chick growth, or chick growth might be affected by the angular distance.) However, we were, in the first instance, simply interested in whether such relations existed. Of the 42 relations tested (Table 3), only two were significant at $P < 0.05$, and neither of these was significant after we carried out a sequential Bonferroni correction (Rice 1989). We therefore conclude that there is little evidence for any relation between the angular distance between the parents and the variables tested.

Table 2. Consistency (*r*, the mean vector length) across years of average angular positions of great tit parents landing on the nest for individuals breeding with the same or different mate, and in the same or different nestbox

	Mean $r \pm$SD (N)		Same versus different*	
	Same pair or box	Different pair or box	*U*	*P*
Same or different pairs				
Males				
Beak	0.886±0.197 (7)	0.967±0.090 (12)	63	NS
Back	0.780±0.275 (7)	0.879±0.249 (12)	54	NS
Females				
Beak	0.850±0.323 (7)	0.850±0.294 (10)	42	NS
Back	0.820±0.337 (7)	0.895±0.148 (10)	36	NS
Same or different nestboxes				
Males				
Beak	0.735±0.235 (5)	0.976±0.046 (11)	49	NS
Back	0.592±0.457 (5)	0.869±0.225 (11)	42	NS
Females				
Beak	0.996±0.006 (3)	0.867±0.269 (12)	7	NS
Back	0.997±0.005 (3)	0.920±0.133 (12)	12	NS

One-tailed tests were carried out testing the directional hypothesis that consistency in angular position would be higher when breeding with the same mate than with a different mate, or in the same nestbox than in a different nestbox. In this case, a one-tailed test is appropriate because it is analogous with the one-tailed testing of *F* ratios implicit in conventional ANOVA. ANOVA (usually) considers only the possibility that a given factor increases (and not decreases) the variation in the response variable. The one-tailed test used here considers only the possibility that being with a different mate or in a different box increases (and not decreases) the variation in (=decreases the consistency of) angular position. Unfortunately, ANOVA cannot be used with circular data.
*Mann–Whitney *U* test.

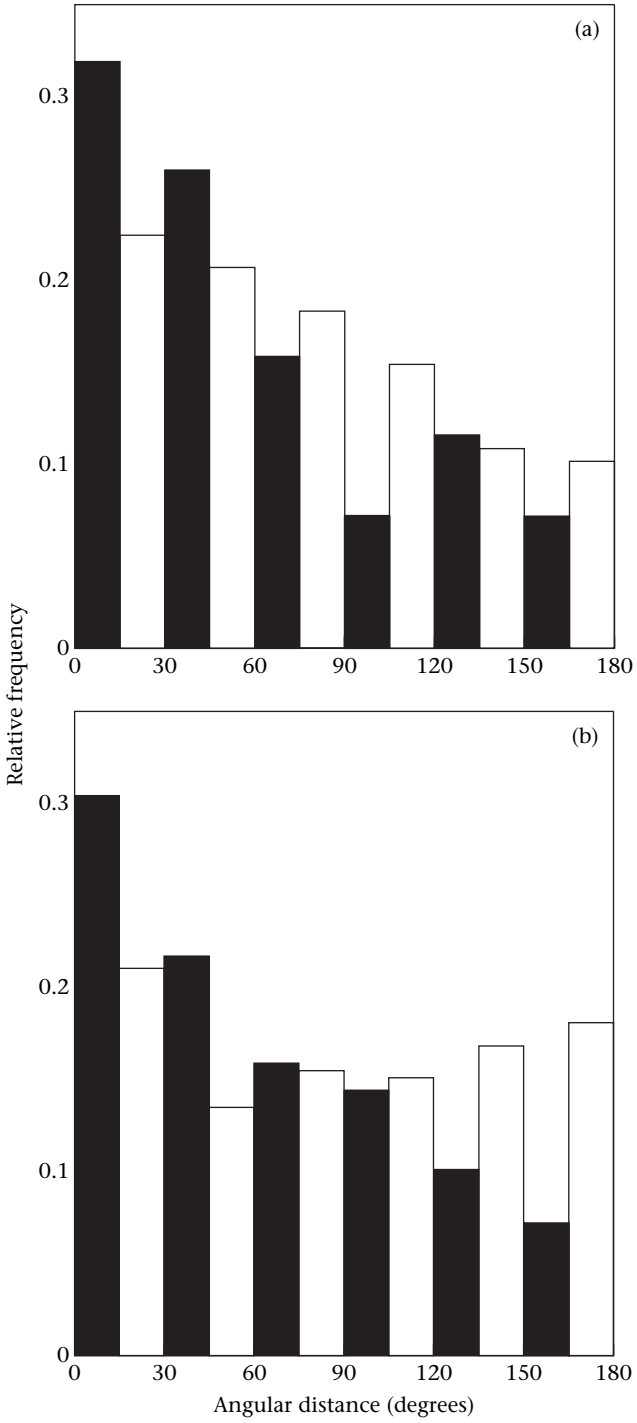

Figure 3. Observed frequency distributions (■; $N = 69$) of angular distance between (a) beak and (b) back positions of pairs of provisioning great tits, and the expected distributions (□) if parents' positions are independent. The expected distributions were generated as described in the text.

DISCUSSION

Individuals were remarkably consistent in the position from which they fed. This consistency occurred not only within observation periods, but also across days within a breeding attempt (at least when the chicks were about 10 days old), and, most surprisingly, across breeding attempts in different years. At the majority of nests, the two parents fed from significantly different positions, and the distribution of angular distances between the parents differed significantly from that expected if the positions of the two parents were independent. We were unable to find significant evidence for an association between the angular distance between the parents and characteristics of the brood or parents.

As a whole, the feeding positions of parents were not randomly distributed around the nest rim. As Kölliker et al. (1998; Kölliker & Richner (2004) found for head positions, average beak positions tended to be towards the rear of the nest, and average back positions were most frequent at an intermediate position between the front and back of the nest. Some authors have emphasized that nest structure may constrain parents to feed from the same position, and suggested that cavity nesters may be more constrained than open nesters, with parents positioned close to the nest entrance (McRae et al. 1993; Kacelnik et al. 1995; Ostreiher 2001). While it is undoubtedly true that some cavity nesters are constrained in this way (e.g. Lessells & Avery 1989, Malacarne et al. 1994), our observations show that this is not always the case, and that parents may feed from different positions, and in some cases from almost diametrically opposite positions on the nest rim (Fig. 3). In particular, our observations caution against assuming that chicks at the 'front' of the nest (with respect to the nest entrance) are those closest to the provisioning parents without confirmation from behavioural observations. Parental positions have been measured surprisingly rarely (but see McRae et al. 1993; Kölliker et al. 1998; Ostreiher 2001; Kölliker & Richner 2004).

Our observations show that individual consistency in feeding position arises from a number of sources. First, the overall preference for some positions in the nest will give rise to some consistency (as measured by r, the mean vector length) even if the angular positions of one individual are independently chosen from this overall distribution. However, the significant differences between positions of individuals of the same sex show that there are additional sources of individual consistency. These might be caused by differences in nest configuration (for example in the placement of the nest cup, even in nestboxes of uniform dimensions) and by 'habit' formation. Both of these appear to play a role. The fact that median angular distances between pairs are shorter than expected based on independent positioning of the two parents suggests that nest configuration may have an influence (although adjustment of the two parents to feed from similar feeding positions cannot be ruled out). However, the constraining effect of individual nest configuration (at least in nestboxes of uniform dimensions) seems at best weak, because mean angular separation was more than 60° for both beak and back positions (remembering that angular distance by definition lies between 0 and 180°), and in the majority of nests the parents fed from significantly different positions. Such differences could still be consistent with nest configuration constraints if males and females differed in locomotor performance. The lack of any sex difference in the overall location preferences argues against this, leaving

Table 3. Correlates of the angular distance between the members of a pair

			Value of test statistic and *P* for the angular distance between pair members in the position of their			
			Beaks		Backs	
	Test statistic*	*N*	Test statistic	*P*	Test statistic	*P*
Year (5 years: 1999–2003)	χ^2	69	4.190	0.381	2.141	0.710
Hatching date†	r_S	69	−0.021	0.866	0.026	0.831
Clutch size†	r_S	69	0.157	0.197	0.206	0.089
Initial brood size†	r_S	69	0.169	0.165	0.222	0.067
Brood size fledged†	r_S	69	0.137	0.260	0.113	0.356
Hatching success†	r_S	69	0.053	0.665	0.099	0.420
Fledging success†	r_S	69	0.052	0.671	0.010	0.932
Sex ratio of clutch	r_S	69	0.104	0.395	0.084	0.491
Sex ratio of brood at recording	r_S	69	0.141	0.247	0.073	0.553
Mean fledgling mass†‡	r_S	69	−0.044	0.723	−0.089	0.466
SD fledgling mass†‡	r_S	67	−0.158	0.199	−0.045	0.719
Mean fledgling tarsus length†§	r_S	69	−0.034	0.780	−0.036	0.769
SD fledgling tarsus length†§	r_S	67	−0.162	0.180	0.020	0.872
Male age (yearling versus older)	χ^2	64	0.352	0.553	3.600	0.058
Male primary length	r_S	40	0.293	0.066	0.034	0.835
Male tarsus length	r_S	64	−0.010	0.938	−0.148	0.244
Male mass	r_S	62	−0.092	0.479	−0.306	0.015
Female age (yearling versus older)	χ^2	65	0.754	0.385	1.766	0.184
Female primary length	r_S	38	0.324	0.047	0.200	0.229
Female tarsus length	r_S	60	−0.016	0.901	−0.048	0.716
Female mass	r_S	59	−0.088	0.509	0.020	0.883
Chick food deprivation**	*T*	13	27	0.197	38	0.603

*χ^2 values are from a Kruskall–Wallis test; r_S is the Spearman rank correlation coefficient; *T* values are from a Wilcoxon matched-pairs test.
†Relations between the angular distance in beak or back positions and these variables were also not significant after controlling for year in a GLM (results not shown).
‡Individual fledgling masses were corrected for the sex difference by adding 0.894 g to the masses of females, and for the diurnal trend in mass using a linear increase of 0.180 g/h. These coefficients were obtained from a hierarchical mixed model with brood identity as a random effect, time of weighing as a between-brood effect, and sex as a within-brood effect.
§Individual tarsus lengths were corrected for the sex difference by adding 0.577 mm to the tarsus lengths of females. This coefficient was obtained from a hierarchical mixed model with brood identity as a random effect, and sex as a within-brood effect.
**Matched comparisons were made for the 13 broods observed on consecutive days in 2000 when either none or all of the chicks had been food deprived for 2 h before observations.

habit formation as the major explanation for the consistency implied by significant differences in position between individuals of the same sex and between members of a pair. Lastly, the somewhat surprising consistency of individual positions across breeding attempts in different years, irrespective of the identity of the mate or specific nestbox, also supports habit formation as an important source of consistency.

The angular distance between the parents' beaks and the shape of the distribution of these angular distances resemble those reported by Kölliker et al. (1998; Kölliker & Richner 2004) for head positions. Also like Kölliker et al. (1998), we found differences (marginally nonsignificant for beak position) between the observed and expected distributions of angular distances between the parents. Kölliker et al. (1998) interpreted this statistical nonindependence between the positions of the parents as a specific form of nonindependence: that the parents adjusted their positions to each other. However, the statistical nonindependence might come about in other ways, for example if the positions that the parents can land in a particular nest are constrained by nest configuration. In our data, median angular differences are less than expected (again marginally nonsignificantly for beak), as would be expected if nest configuration acts as a constraint. We cannot distinguish between these alternative hypotheses without further information. However, the important point is that, although the departure between observed and expected distributions may be consistent with the parents reacting to each other, this does not provide unequivocal evidence that they do so. The consistency in the positions of individual parents from year to year suggests that the amount of any such adjustment must be limited. We also found no relations between the angular distance between the parents and a number of characteristics of the brood and parents. Overall, our data suggest limited scope and no evidence for strategic adjustment of the angular distance between the parents.

Even if the angular distance between the parents is not adjusted strategically, it may affect the distribution of food between the chicks. The lack of a relation between the mean and standard deviation (for the brood) of fledgling mass or tarsus length does not support this. However, this analysis would not reveal changes in the proportion of feeds to each chick (or chick position) from each parent without an overall change in the amount a chick (or chick

position) was fed. Analysis of the positions of chicks fed by each parent from a limited sample of nests shows that there is sometimes some spatial separation (but with an overlap in distributions) in the chicks fed by each parent (C. M. Lessells, unpublished analysis). Further analysis is needed of a larger sample of nests, and also to answer the question whether either beak or back position predicts the position of chicks fed, or if the angular distance between the parents predicts the extent of any spatial separation in the chicks fed.

Lastly, whether or not the positions of the parents have consequences for which chicks are fed, the consistent positioning of the parents would allow the chicks at the majority of nests to identify which of their parents is present. Recent studies have revealed that male and female parents may use different behavioural rules in responding to the begging behaviour of their chicks (Kölliker et al. 2000; Kilner 2002). This would in turn mean that chicks should solicit differently to the two parents, and parental position would provide a cue as to parental identity. Kölliker et al. (1998) showed that chicks did indeed react to parental position: single food-deprived chicks sat closer to the female's feeding position than undeprived chicks, but equally close to the male's feeding position. Further research is needed into the ramifications of consistent parental feeding positions for parent–offspring interactions.

Acknowledgments

We thank Mathias Kölliker for enthusiastic discussion and helpful advice over many years, Henri Bouwmeester and Christiaan Both for help with nestbox monitoring, and Staatsbosbeheer and Dhr. van Notten for permission to work at the Buunderkamp.

References

Batschelet, E. 1981. *Circular Statistics in Biology*. London: Academic Press.

Fisher, N. I. 1993. *Statistical Analysis of Circular Data*. Cambridge: Cambridge University Press.

Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998. A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.

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**, 1723–1727.

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 nest 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.

Kölliker, M., Brinkhof, M. W. G., Heeb, P., Fitze, P. & Richner, H. 2000. The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. *Proceedings of the Royal Society of London, Series B*, **267**, 2127–2132.

Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford: Clarendon Press.

Lessells, C. M. 2002. Parentally biased favouritism: why should parents specialize in caring for different offspring? *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 381–403.

Lessells, C. M. & Avery, M. I. 1989. Hatching asynchrony in European bee-eaters *Merops apiaster*. *Journal of Animal Ecology*, **58**, 815–835.

McLaughlin, R. L. & Montgomerie, R. D. 1985. Brood division by *Lapland longspurs*. *Auk*, **102**, 687–695.

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

Malacarne, G., Cucco, M. & Bertolo, E. 1994. Sibling competition in asynchronously hatched broods of the pallid swift (*Apus pallidus*). *Ethology Ecology and Evolution*, **6**, 293–300.

Manley, B. F. J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. 2nd edn. London: Chapman & Hall.

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., Royle, M. J. & Hartley, I. R. 2002. Intrafamilial conflict and parental investment: a synthesis. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 295–307.

Radford, A. N., McCleery, R. H., Woodburn, R. J. W. & Morecroft, M. D. 2001. Activity patterns of parent great tits *Parus major* feeding their young during rainfall. *Bird Study*, **48**, 214–220.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

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

Sokal, R. R. & Rohlf, F. J. 1969. *Biometry*. San Francisco: W.H.Freeman.