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ORIGINAL ARTICLE

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Sex differences in canary (*Serinus canaria*) provisioning rules

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Abstract I investigated how male and female captive canaries (*Serinus canaria*) decide to divide resources among their nestlings. Specifically, I examined whether parents partitioned food in proportion to the size-related competitive prowess of their young or their postural begging intensity. Females responded to both aspects of nestling behaviour. They allocated food in relation to the height attained by offspring during begging as well as the intensity of their postural display. When the brood was especially hungry, mothers additionally favoured offspring at the front of the nest, nearest their perch position. By contrast, males allocated food only in relation to competitive ability, simply by preferring offspring that reached higher during begging. I compare these findings with previous work on other species and discuss why females changed their provisioning rules in relation to brood hunger.

Keywords Begging · Parent–offspring conflict · Scramble competition · Sibling conflict · Signalling

Introduction

In the theoretical literature, the evolution of nestling begging behaviour has been linked with an evolutionary conflict of interest between parents and their young over the allocation of parental investment (reviewed by Godfray 1995; Mock and Parker 1997). Two types of model describe how begging may function to resolve parent–offspring conflict. In the earliest formal analyses, begging is viewed as a form of scramble competition (reviewed by Mock and Parker 1997), similar to the jostling and shoving performed by schoolchildren competing for sweets thrown in their direction, where all competitors acquire some reward for their efforts (Parker 2000). In more recent theoretical work, begging is assumed to be a signal. Offspring have private information about their need, which they convey to parents by adjusting the intensity of their begging display. Parents then select offspring for provisioning in relation to their begging intensity (reviewed by Godfray and Johnstone 2000).

At first sight, these two functions appear very different. In the former, the parent passively tosses food to offspring and food distribution is determined by the competitive interactions of the offspring alone. By contrast, in the latter, parents actively scrutinize the begging performance of their offspring before carefully deciding which to feed. In practice, it is much harder to draw a distinction. Among passerines, at least, parents seldom toss food in the direction of their young, but carefully place food into a gaping mouth. This act alone blurs the distinction between whether the parent is acting passively or actively. In addition, offspring signals can themselves be a form of competition (Smith and Montgomerie 1991; Leonard et al. 2000) while acts of competition can potentially convey information (Kölliker et al. 1998; Lotem et al. 1999).

Given these practical difficulties, it is a daunting task to distinguish the scramble competition and signalling functions of begging behaviour empirically. Instead, here I consider whether parents scale offspring provisioning in relation to size-related nestling competitive ability or the intensity of the postural begging display (which is not simply a function of relative chick size). For comparison with the traditional theoretical functions of begging, a response to size-dependent competitive prowess most closely corresponds to the scramble competition function of begging because offspring interactions influence the division of food. A response to postural begging intensity may be described by either the signalling (e.g. Godfray 1991; Johnstone 1999) or competitive (e.g. Parker and Macnair 1979; Harper 1986) functions of begging. The aim of this paper is to investigate how well these contrasting responses to nestling begging describe the brood provisioning behaviour of male versus female canaries.

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Three aspects of canary chick behaviour, and their role in influencing food distribution, are of interest here: (1) competition for positions within the nest which favour access to parents; (2) competition to stretch highest towards the parent; and (3) the intensity of the postural display. I experimentally reduced competition among canary chicks for favourable positions within the nest, by using perspex barriers to restrict nestling movement, and tested the following predictions. If competition for favoured locations within the nest influences food allocation then: (prediction 1) restricting competition should markedly change the distribution of food compared with that seen at unmanipulated nests; and (prediction 2) when competition is restricted, chicks in the best position should receive the most food, regardless of their relative size or hunger. If parents respond to postural begging intensity then (prediction 3) it should be correlated with food allocation. In addition, (prediction 4) food allocation must not be better explained by the relative height reached by begging chicks (postural begging intensity is not simply related to chick height because it can increase without a gain in height and is also related to the duration of begging).

Finally, if the competitive interactions of offspring are better at explaining food distribution than postural begging intensity then why should this be? One possibility is that parents have chosen to relinquish control of food distribution, perhaps to promote provisioning efficiency (Göttlander 1987; Ostreiher 1997). If so, we can predict that (prediction 5) provisioning efficiency should be lower when nestling competition is restricted experimentally. Alternatively, offspring may have seized control of food distribution and in so doing may subvert patterns of provisioning preferred by parents (McRae et al 1993; Kacelnik et al 1995; Ostreiher 1997, 2001). I investigated whether, in principle, parents could ever lose control of food allocation to offspring, by comparing parental behaviour at older and younger broods. Just before fledging, individual offspring have a high degree of motor coordination and are potentially big enough to monopolize access to the feeding parent completely. If offspring can control food distribution at all, it should be measurable by this stage in the nestling period. Therefore, if offspring seize control of food distribution then we can predict that (prediction 6) restricting competition for positions within the nest should cause a more marked change in food distribution when chicks are older than when they are younger.

Methods

Study species

Gloster and Fife canaries were kept and bred at the Sub-department of Animal Behaviour at Madingley, Cambridgeshire, UK in 1993–1995, 1997, 1998 and 2000. They were exposed to natural daylight supplemented with artificial light on a 16:8 h light:dark cycle. Between March and July, birds were arbitrarily paired and each pair occupied a double breeding cage (102 × 28 × 40 cm) furnished with a felt-lined plastic nestpan (11.5 cm external diameter) supported on a wooden stand (13 × 14 × 19.5 cm). The modal brood size was three. Within broods, chicks varied in mass as a result of hatching asynchrony, such that the largest chicks were roughly 10% heavier than the medium chicks, and 15% heavier than the smallest chicks. Chicks typically fledged 16 or 17 days after hatching. At both ages tested, chicks had a high degree of locomotory ability in the nest. Eight days after hatching they were covered in pin feathers. By day 13 they were almost completely feathered. Breeding birds were supplied with ad libitum quantities of mixed canary seed, Nectarblend and Easisoak (all purchased from Haith's, Cleethorpes, UK) as well as cress or chick weed, grit, drinking water and bathwater.

Manipulation of chick position in the nest

Chick movement in the nest was restricted by inserting perspex barriers secured with fuse wire which divided the nest cup into three equal sectors, each containing one chick. Chicks were free to display within each sector, but the barriers controlled their relative proximity to the parent. The wooden stand supporting the nest was enclosed on three sides with perspex screens, thus constraining parental access and encouraging parents to feed offspring from the remaining exposed side. All the data presented were collected from parents perching here. The manipulated nest thus controlled the relative lateral distance between parents and their offspring, with one chick occupying the front of the nest closest to the parent, and the remaining two on either side at the back of the nest. In a control treatment, I removed the perspex dividers in the nest, so that chick movement was unrestricted but the screens on the wooden nest stand were retained.

Manipulation of brood hunger

Broods 8 or 9 days old

I manipulated brood hunger in two different ways. In one treatment ('hungry'), the entire brood was food deprived for 1 h before the experiment while their parents temporarily tended one or more foster chicks. In the second treatment ('partly fed'), the brood was food deprived for 40 min, but individual chicks within each brood were then fed different sized meals of Nectarblend, mixed to a standard concentration (6.00 g Nectarblend plus 15.0 ml warm tap water) and administered through a plastic 1.00 ml Monoject syringe. Within broods, each chick received a different sized meal (0 ml, 0.25 ml, 0.50 ml). Between broods, the three meal sizes were stratified with respect to relative chick size. In four treatments, the largest chick was the hungriest, in three it was the medium-sized chick and in the remaining three it was the smallest nestling. In both brood hunger manipulations, chicks were marked with spots of coloured Tippex on the back of their head for identification.

Broods 12 or 13 days old

In this age class, broods experienced only the 'partly fed' treatment. For comparison with broods tested 8 or 9 days after hatching, the three meal sizes were scaled in relation to chick mass (0 ml, 0.35 ml and 0.70 ml). In all other respects, the treatment was identical to that experienced by the younger broods.

Adding chicks to manipulated nests

I drew up a chart of the six possible combinations of chick size (or hunger) and position in the nest, and cycled through the sequence between broods when competition was restricted experimentally. Before testing, each chick in the nest was weighed (except at four nests). After manipulating brood hunger and nest structure, I returned the chicks to their parents and filmed all the action at the nest during the following hour. The perspex screens surrounding the nest allowed me to film parental behaviour in profile. Chicks were returned to their usual, unmanipulated nests after filming.

Treatments

Broods 8 or 9 days old

I combined the brood hunger and nest manipulations to create four different treatments: brood hungry, competition restricted (n=8; 6 broods were tested in 1993, 2 were tested in 2000); brood hungry, competition unrestricted (n=11, all tests were in 1995); brood partly fed, competition restricted; and brood partly fed, competition unrestricted. The latter two treatments were both performed in 1997 on the same ten broods, on alternate days. The sequence was alternated between broods. (The broods tested in 1993 and 1995 were part of separate experiments and could not be tested twice, unlike those used in 1997.)

Broods 12 or 13 days old

This age group experienced just two treatments: brood partly fed, competition restricted and brood partly fed, competition unrestricted. The same nine broods were subjected to both treatments on alternate days and the sequence was alternated between broods. The experiments were conducted in 1998 with entirely different pairs to those used in the 1997 treatments. All the experiments were conducted in a standardized breeding environment, which justifies the pooling of data from different years.

Data collection

From the videotapes, I collected data from the first visit by each parent to the nest at which all three young begged. I counted the number of feeds parents gave each offspring, scoring a dip of the parent's bill into a chick's mouth as one feed. Parents made multiple transfers of food within each visit, with individual offspring receiving between 0 and 64 transfers per visit. I also measured the postural begging intensity of each chick in the brood. Every second during the nest visit, I scored chick posture which was rated in ascending order of vigour (0 = not begging, 1 = gape open, 2 = gape open, head back, 3 = as 2 plus neck stretched, 4 = as 3 plus back vertical) and then summed the rates over the entire begging bout for each chick, as is common practice in the medical and psychological literature (e.g. Fordham and Stevenson-Hinde 1999).

With broods tested 8 or 9 days after hatching, I used a grid drawn over the TV screen to collect data about parental provisioning stances, when competition was unrestricted. When a parent arrived at the nest, it typically froze before starting to regurgitate food. At this point I scored the horizontal coordinate of the centre of the adult's bill and measured the lateral distance between the adult's bill and the centre of the nest. Nests were typically eight units in external diameter, measured with the TV screen grid. In addition to the 10 families in the ‘brood partly fed’ treatment and the 11 families in the ‘brood hungry’ treatment, this dataset includes a further 8 nests tested in 1994. At these nests, also tested 8 or 9 days after hatching, broods had been food deprived for 1 h before the largest chick was fed 0 ml food, the medium chick received 0.50 ml food and the smallest chick received 0.25 ml food.

The final data sets are smaller than the total number of nests used, either because all three young did not beg simultaneously during provisioning; or because it was not possible to film provisioning behaviour of both parents (although both parents were observed feeding nestlings at other times); or because the nest rim was not visible on the videotape, so the parent's position in relation to the centre of the nest could not be scored.

Postural intensity versus relative height

To examine the relationships between postural begging behaviour, relative height and food allocation, I analysed data from medium-sized nestlings because there was no a priori reason to expect these offspring to be favoured through their relative size alone (Lessells 2002). For either parent, each data point in the analysis was drawn from a different family. Canary families differ in postural begging intensity and their responsiveness to postural begging intensity (R. M. Kilner, unpublished data; see Kölliker et al. 2000 for similar results with begging calls in great tits *Parus major*). To control for variation between families, I calculated the postural intensity of the medium nestling relative to the summed postural intensities of the rest of the brood. In effect, the analysis assumes that parents use a form of mean-matching (Harper 1986; Mock and Parker 1997) to determine a response to relative begging intensity. It is just as likely that parents respond to absolute begging intensity, but this possibility will have to be investigated in future work.

I estimated the relative height stretched by medium offspring during begging as the product of the medium nestling's absolute postural begging intensity and its mass relative to the summed mass of the rest of the brood. I checked whether this estimate was correlated with measured relative height with a subsample of 20 nest visits at 10 broods aged 8 or 9 days, tested once when the brood was hungry and once when the brood had been partly fed. I measured the height of each chick in the nest every 5 s during provisioning, using a grid drawn over the TV screen. For each bout of provisioning, I calculated the mean height of the medium nestling relative to the summed mean heights of the rest of the brood. Estimated relative height was correlated with measured relative height ($F_{1,19}$=8.49, P=0.009).

Statistics

The data were analysed with the application StatView produced by SAS Institute, and I checked that they met the assumptions of the statistical tests used with Bartlett's test for homogeneity of variances, a Kolmogorov-Smirnov test for deviations from normality and Bartlett's test for sphericity. Summed canary posture rates are monotonically correlated with parental behaviour (Kilner 1995), chick hunger (Kilner 1995) and begging cost (Kilner 2001). It is therefore reasonable to treat them as ratio data (Gaito 1980) and to analyse them with parametric statistics. The data were transformed where necessary. The P values reported are two-tailed.

Results

Does competition for favourable positions influence food allocation?

Brood hungry

I analysed the data with a repeated measures ANOVA in which the number of food transfers to chicks in three size categories within the brood (big, medium, small) were the repeated measures. Each line of the dataset represented the outcome of a visit to the brood by a parent (= brood visit). A family thus contributed up to two lines in the dataset: a brood visit by the female and a brood visit by the male. The analysis assumes that provisioning behaviour by males and females is independent, although this assumption remains to be tested experimentally. Chick movement (restricted, unrestricted) and parent sex (male, female) were between brood visit factors.

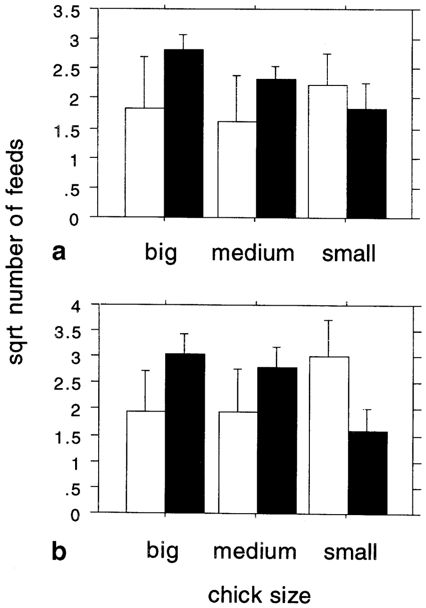

Fig. 1 The influence of competition for favourable positions within the nest and chick size on food distribution by **a** male and **b** female canaries (*Serinus canaria*) when the brood was food deprived before testing ('hungry'). *White bars* show the experimental treatment in which chick movement in the nest was restricted, *black bars* show the control treatment in which chicks were free to move. Means with standard error bars are shown

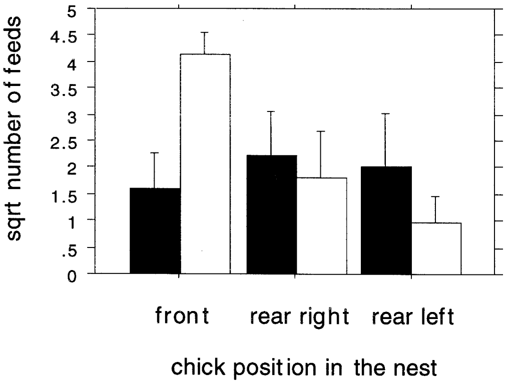

Fig. 2 The influence of chick position in the nest on food distribution when chick movement was restricted experimentally and when the brood was food deprived before testing ('hungry'). *Black bars* show the pattern of food distribution by males, *white bars* show the pattern for females. Means with standard error bars are shown

Prediction 1: does restricting chick movement change the pattern of food allocation? When chick position in the nest was controlled experimentally, the pattern of food distribution with respect to chick size changed significantly (repeated measures ANOVA, chick size × chick movement interaction: $F_{2,62}$=3.35, P=0.042; Fig. 1). To see exactly how restricting chick movement changed food distribution, I analysed the experimental and control treatments separately.

In the control treatment, when chicks were free to move, the smallest nestling obtained significantly less food (repeated measures ANOVA, chick size effect: $F_{2,36}$=5.42, P=0.009) than either the largest (Fisher PLSD, P=0.0022) or medium-sized chicks (Fisher PLSD, P=0.026). Parents did not differ significantly in their behaviour (repeated measures ANOVA, parent × chick size interaction: $F_{2,36}$=0.47, P=0.63).

By contrast, when chick movement was restricted in the experimental treatment, chicks in each size class did not differ significantly in their likelihood of receiving food (repeated measures ANOVA, chick size effect: $F_{2,26}$=0.66, P=0.53). Again, parents did not differ significantly in their response (repeated measures ANOVA, parent × chick size interaction: $F_{2,26}$=0.09, P=0.91).

Prediction 2: does chick position explain the pattern of food allocation? The data were analysed with a repeated measures ANOVA, similar in structure to the previous analysis, with number of food transfers to chicks in the different positions within the nest (front, rear right, rear left) as the repeated measures and parent sex (male, female) as a between brood visit factor. The influence of chick position on food allocation differed between parents when chick position was controlled experimentally, although the result was not statistically significant (repeated measures ANOVA: position × parent interaction: $F_{2,26}$=3.26, P=0.054; Fig. 2). I analysed maternal and paternal behaviour separately, to see how parents differed. Mothers fed chicks at the front of the nest significantly more food (repeated measures ANOVA: position effect: $F_{2,14}$=9.42, P=0.0026) while fathers showed no significant preference for any particular position in the nest (repeated measures ANOVA: position effect: $F_{2,12}$=0.12, P=0.89).

Brood partly fed

I analysed the data with a repeated measures ANOVA, similar in structure to the previous analyses, in which either the number of food transfers to chicks in the three size categories (big, medium, small) or the number of food transfers to chicks in the three hunger treatments (no meal, small meal, large meal) were the repeated measures. Once again, chick movement (restricted, unrestricted) and parent sex (male, female) were between brood visit factors.

Prediction 1: does restricting chick movement change the pattern of food allocation? Restricting chick movement did not significantly alter the pattern of food allocation with respect to chick size (repeated measures ANOVA, chick size × chick competition interaction: $F_{2,56}$=0.24, P=0.79). In neither case was food distribution significantly influenced by relative chick size (repeated measures ANOVA, chick size effect: $F_{2,56}$=1.74, P=0.18). There was no significant difference between the behaviour of mothers and fathers in either their response to chick size (repeated measures ANOVA: chick size × par-

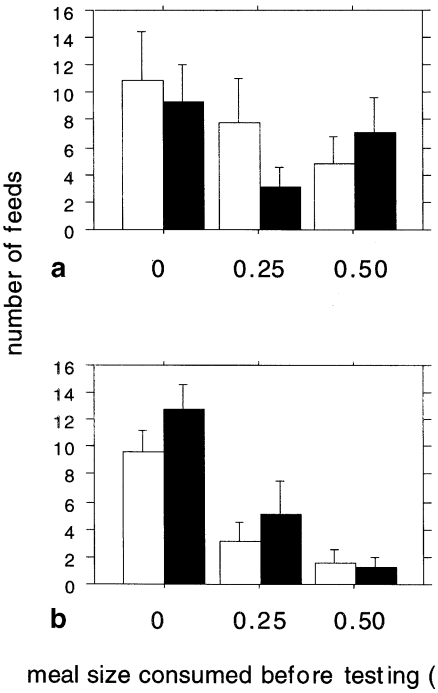

Fig. 3 The influence of competition for favourable positions within the nest and meal size consumed by nestlings prior to testing on food distribution by **a** males and **b** females when broods were 8 or 9 days old. *White bars* show the experimental treatment in which chick movement in the nest was restricted, *black bars* show the control treatment in which chicks were free to move. Means with standard error bars are shown

ent interaction: $F_{2,56}$=1.17, P=0.32) or in the influence of competition on food allocation with respect to chick size (repeated measures ANOVA: chick size × chick movement × parent interaction: $F_{2,56}$=0.60, P=0.55).

Nor did restricting chick movement change food distribution with respect to chick hunger (repeated measures ANOVA, chick hunger × chick competition interaction: $F_{2,56}$=0.36, P=0.70; Fig. 3). The meal size received by chicks prior to testing explained a significant amount of variation in food distribution in both treatments (repeated measures ANOVA, chick hunger effect: $F_{2,56}$=11.87, P<0.0001; Fig. 3), with the hungriest nestlings receiving more feeds than chicks that had eaten a small meal (Fisher's PLSD: P=0.0007) or a large meal (Fisher's PLSD: P=0.0007) before the test began. Again, parents did not differ significantly in either their response to chick hunger (repeated measures ANOVA: chick hunger × parent interaction: $F_{2,56}$=1.71, P=0.19) or in the influence of competition on food allocation with respect to chick hunger (repeated measures ANOVA: chick size × chick movement × parent interaction: $F_{2,56}$=1.26, P=0.29).

Prediction 2: does chick position explain the pattern of food allocation? The data were analysed as described in the equivalent 'brood hungry' section. Whether they were fed by mothers or fathers (repeated measures ANOVA: parent × position interaction: $F_{2,26}$=0.60, P=0.56), there was no advantage for chicks at the front of the nest (repeated measures ANOVA: position effect $F_{2,26}$=0.26, P=0.78). This contrasts with the advantage of occupying the front position when the brood was hungry and fed by mothers (repeated measures ANOVA, chick position × brood hunger × parent interaction: $F_{2,52}$=3.18, P=0.050).

Predictions 3 and 4: does relative height or relative postural begging intensity best explain food distribution? I began by investigating whether relative height and relative postural begging intensity were individually correlated with the number of feeds transferred to nestlings. Data for both parents from every treatment were analysed with a single ANCOVA, in which the dependent variable was the log transformed number of feeds received by the medium nestling, the covariate was either relative height or relative postural begging intensity and parental sex was a factor. Relative height significantly predicted food transfer (ANCOVA, relative height effect: $F_{1,58}$=41.52, P<0.0001) and the relationship did not differ significantly between parents (ANCOVA, parent × relative height interaction: $F_{1,58}$=0.385, P=0.54). Relative postural begging intensity was also related to food allocation (ANCOVA, relative height effect: $F_{1,62}$=28.83, P<0.0001), but this time the relationship did differ significantly between parents (ANCOVA, parent × relative height interaction: $F_{1,58}$=4.61, P=0.036).

To see how the sexes differed, I examined their responses separately using a multiple regression, in which relative height and relative postural intensity were independent variables and the dependent variable was the number of feeds. Estimated relative height and relative postural begging intensity were only weakly correlated (R^2=0.17), which justifies their simultaneous inclusion in the model. For males, relative height accounted for a significant amount of variation in food allocation (partial t=3.05, P=0.006) while relative posture did not (partial t=0.89, P=0.39). The relationship between relative height and food transferred did not differ significantly between brood hunger treatments (ANCOVA: brood hunger × relative height interaction: $F_{1,23}$=1.22, P=0.28), nor was it significantly different between chick movement treatments (ANCOVA: chick movement × relative height interaction: $F_{1,23}$=0.01, P=0.91).

By contrast, female food allocation was significantly related to both relative height (partial t=4.77, P<0.0001) and relative postural intensity (partial t=4.50, P<0.0001). Females provided significantly more food in proportion to relative height when the brood had been partly fed (ANCOVA: brood hunger × relative height interaction: $F_{1,31}$=4.36, P=0.045), while their response to relative posture was unchanged (ANCOVA: brood hunger × relative postural intensity interaction: $F_{1,33}$=0.00, P=0.99). Neither the relationship between relative height and food allocation (ANCOVA: chick movement × relative height interaction: $F_{1,31}$=2.27, P=0.14) nor the relationship between relative postural begging intensity and food allocation (ANCOVA: chick movement × relative height interaction: $F_{1,33}$=0.49, P=0.49) were significantly influenced by the chick movement treatments.

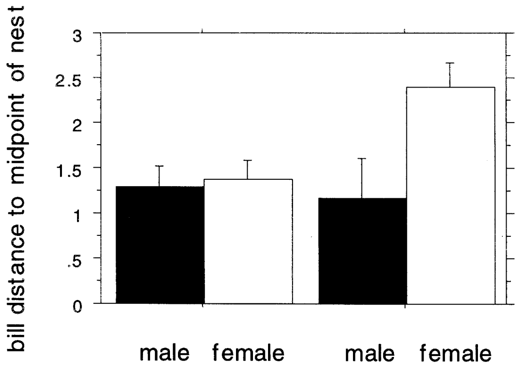

Fig. 4 The influence of brood hunger on the perching stance of males and females at the unmanipulated nest. Bill distance to the midpoint of the nest is measured in arbitrary units from a grid placed over the TV screen during video analysis. Means with standard error bars are shown

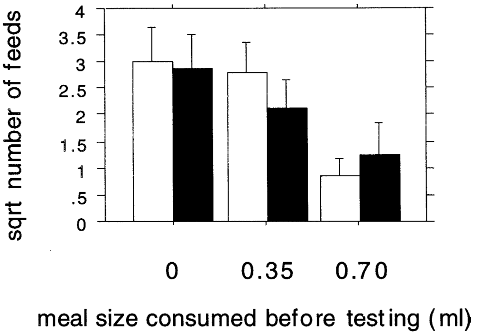

Fig. 5 The influence of competition for favourable positions within the nest and meal size consumed by nestlings prior to testing on food distribution by females when broods were 12 or 13 days old. *White bars* show the experimental treatment in which chick movement in the nest was restricted, *black bars* show the control treatment in which chicks were free to move. Means with standard error bars are shown

Why did mothers sometimes give chicks at the front of the nest more food?

Prediction 5: to improve provisioning efficiency to hungry chicks. There was no evidence to support this suggestion. I compared the rate at which mothers regurgitated food to a ‘hungry’ brood during the nest visit, when chick movement was restricted experimentally, and when chicks were free to move. Their rate of food delivery did not differ significantly between the two treatments (unpaired $t_{17}=-1.17$, $P=0.26$), and was slightly higher when movement was controlled (mean±SE=0.91±0.07 feeds/s) than when chicks were free to move (mean±SE=0.81±0.04 feeds/s).

Prediction 6: because offspring seized control of food allocation. The change in brood hunger was accompanied by a change in the perching stance adopted by mothers as they fed their young at unmanipulated nests. Mothers leaned over the nest, with their bills close to its centre when the brood had been partly fed, but withdrew their bills to the edge of the nest (unpaired $t_{17}=-3.16$, $P=0.006$; Fig. 4) when the brood had been food deprived before testing. The difference in maternal feeding stance may account for the change in the importance of relative chick position in influencing food allocation. Only when mothers had retreated to the edge of the nest could chicks at the front gain any advantage from their position (see Ostreiher 2001). If this switch was caused by chicks seizing control of food distribution, then offspring must have forced the change in female provisioning stance, perhaps because their intense begging drove mothers from the centre of the nest. Male provisioning behaviour should therefore be similarly affected. I compared male and female bill positions, in relation to the centre of the nest, when the brood was hungry and when it had been partly fed. In contrast to females, I found that male bill position was unaffected by brood hunger (ANOVA, parent × brood hunger interaction: $F_{1,47}=3.98$, $P=0.052$), remaining close to the centre of the nest in both treatments (Fig. 4).

I further tested whether, in principle, mothers could ever lose control of food allocation to offspring, by comparing maternal behaviour with older and younger broods. I analysed the data with a repeated measures ANOVA, in which the number of food transfers to chicks in the three hunger treatments (no meal, small meal, large meal) were nested within chick movement (restricted or unrestricted), with chick age as a between brood visit factor. At both ages, and in both chick movement treatments, chick hunger significantly influenced the pattern of food distribution at the nest (repeated measures ANOVA, chick hunger effect: $F_{2,32}=20.64$, $P<0.0001$; Figs. 3b, 5). However, at neither age did controlling chick movement within the nest change the pattern of food distribution with respect to chick hunger (repeated measures ANOVA, chick hunger × chick movement interaction: $F_{2,32}=0.023$, $P=0.98$; Figs. 3b, 5). Consequently, there was no indication that older chicks were better able to monopolize access to mothers than younger chicks (chick hunger × chick movement × chick age interaction: $F_{2,32}=0.51$, $P=0.61$). In summary, it is too soon to dismiss entirely the suggestion that nestlings can seize control of food distribution, but I found no evidence to support the idea.

Discussion

How do the sexes differ in their provisioning rules?

The likelihood that a canary nestling will receive food depends on a complex combination of its size-related competitive ability and postural begging display intensity. The particular blend depends on the sex of the provisioning parent. On arrival at the nest, males consistently leant into the brood, positioning their bills close to the centre of the nest before starting to regurgitate food to their young. Fathers made themselves equally available to each chick in the nest with this provisioning stance which may explain why no individual profited when chicks were experimentally forced to occupy a particular sector of the nest. Once canary fathers started regurgitation, food allocation was solely influenced by the relative height to which nestlings stretched. In this respect, canary paternal behaviour is similar to adult Arabian babblers (*Turdoides squamiceps*) who prefer to feed chicks located at the centre of the nest and so avoid being monopolized by dominant young. When the babblers were experimentally forced to provision chicks close to the nest rim, food distribution became markedly more skewed towards the largest chick in the nest (Ostreiher 2001).

Females differed from males in a number of respects. Before starting to regurgitate food, females adjusted their perching stance at the nest in relation to brood hunger. In trials where the brood had been partly fed before filming, mothers adopted a stance at the nest akin to that employed by fathers. Just as with fathers, no sector of the experimental nest was especially favoured during the ensuing bout of brood provisioning. When the brood had been food deprived before filming, mothers perched with their bill closer to the edge of the nest and subsequently preferred to feed chicks forced to occupy the position directly in front of them. By adopting different provisioning stances it is possible that canary parents favour different patches within the nest, as has been found in great tits (Kölliker et al 1998). However, with canaries there is the additional complication that the preferred provisioning zone for females apparently varies with brood hunger. Once regurgitation had begun, mothers distributed food in relation to the height of their young and the intensity of the postural begging display. There was no indication that maternal responsiveness to either variable was amplified by the relative position of chicks in the nest (Rowe 1999).

Why do the sexes differ in their provisioning rules?

Sex differences in provisioning rules could function to reduce the potential for individual offspring to monopolize access to resources from both parents (Kölliker et al 1998). It is possible that the optimal division of resources among the brood is similar for males and females (Lessells 2002). Parents may cooperate by employing different provisioning rules to achieve an overall pattern of food distribution among the brood that is close to both parents' optima. Although this hypothesis explains why sexually different responses to begging may persist, it does not explain why the role of each sex was similar between families. It would be interesting to determine whether the sexes are themselves physically constrained in their ability to respond to begging, or whether the negotiation of provisioning rules between partners is constrained (McNamara et al 1999), perhaps because one sex always has the upperhand.

Why do females change their provisioning rules in relation to brood hunger?

The switch in provisioning rules associated with brood hunger is curious and not easily explained by these experiments. It seems unlikely that the change in maternal response to begging was precipitated through loss of control of food distribution to offspring. I found no evidence that, in principle, mothers could ever lose control of provisioning to their young. Even when chicks had grown to a large enough size, with sufficient motor skills to prevent their siblings from easily reaching the mother, they could not seize control of food distribution by monopolizing favourable positions in the nest. An alternative interpretation of the evidence is that mothers chose to give offspring control of food distribution. By changing their provisioning stance at the nest when the brood was hungry they may even have incited competition within the brood for favourable positions in the nest.

Why they should do so remains unclear. There was no indication that this tactic promoted the efficiency of food division among the brood. It is conceivable that mothers use the begging intensity of their brood to gauge whether there is sufficient food to sustain the successful growth and development of all their young. By switching provisioning rules, females may have assumed responsibility for initiating, or preventing, brood reduction (Lack 1947; Magrath 1990). When the brood had been food deprived, for example, mothers may have perceived that resources were too low to sustain every member of the brood. Males simply fed whichever nestling stretched the highest, thereby penalizing the smallest chick in the nest. Females reinforced the prejudice, similarly preferring larger nestlings which had successfully competed for the favoured position at the front of the nest. If parents followed these rules for long enough, the smallest nestling would eventually starve.

Once the brood had been partly fed before testing, however, females may have estimated that there were sufficient resources to maintain the whole brood. Males continued to allocate food in proportion to the relative height stretched by young but, with greater variance in begging posture, food distribution with respect to chick size was less skewed. Females further equalized food distribution by responding to relative begging intensity as well as relative height. By following these rules consistently, food would have been divided more or less evenly among the brood and the smallest nestlings would have survived to fledge.

In summary, male and female canaries use different rules to allocate resources within the brood, with males consistently relying on the size-related competitive prowess of individual young. The challenge for future work is to determine how these sex differences in provisioning rules arise and to explain why they persist.

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