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Begging signals and biparental care: nestling choice between parental feeding locations

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Abstract. The evolutionary conflict over the amount of resources transferred between a parent and its offspring may be resolved by honest signalling of 'need' by offspring and parental investment in relation to signalling level. In birds, biparental care is the norm and evidence that male and female parents differ in their investment pattern in individual offspring is growing. In an experiment on great tits, *Parus major*, we investigated how and why parents differ in food allocation when responding to similar chick signals, which supposedly uniquely reflect the chick's nutritional condition. Nestling hunger level was manipulated by food deprivation and hand-feeding. Subsequent filming revealed that parents fed from significantly different locations on the nest and thereby forced chicks to choose between them when competing for favourable positions. Deprived nestlings approached, and fed ones retreated (or were displaced by siblings) from, positions near the female. No such behaviour was observed towards the male. Females allocated more feeds than males to the food-deprived nestlings. The results are discussed in terms of nestling competition for access to 'begging patches'. By varying their 'begging patch' value, parents may exploit competitive inter-sibling dynamics to influence the outcome of competition among chick phenotypes (e.g. 'need', size, sex). Parent birds may thereby exert considerable control over the information content of chick begging behaviour.

Parents are selected to make investment decisions that maximize their lifetime reproductive success, but the conflict with their own progeny may constrain these decisions (Trivers 1974; review in Godfray 1995a). Recent models have shown that the conflict may be resolved by honest signalling of 'need' by offspring and parental investment in relation to signalling level (Godfray 1991, 1995b). Parents achieve honesty by demanding costly signals, which discourages selfish tendencies in offspring otherwise favoured by natural selection (Godfray 1991). Begging signals may have fitness costs to offspring in terms of energy expenditure (Leech & Leonard 1996; McCarty 1996) and/or predator attraction (Haskell 1994).

These models do not consider the case of biparental care (but see Parker 1985), which is the norm among bird species (Clutton-Brock 1991). There is growing evidence that parents can differ in their interest in feeding individual young, which could have important consequences for the evolution of begging signals (Parker 1985; Godfray 1995b). In budgerigars, *Melopsittacus undulatus*, pied flycatchers, *Ficedula hypoleuca*, and tree swallows, *Tachycineta bicolor*, male parents preferentially feed large and female parents small nestlings (Stamps et al. 1985; Gottlander 1987; Leonard & Horn 1996). In contrast, females but not males feed older nestlings more than younger ones in red-winged blackbirds, *Agelaius phoeniceus* (Westneat et al. 1995). In great tits, *Parus major*, and blue tits, *P. caeruleus*, males preferentially feed large fledglings whereas females feed small ones (Sasvári 1990; Slagsvold et al. 1994). Moreover, in some bird species male and female parents differ in how they allocate food in relation to offspring sex (review in Gowaty & Droge 1991).

Because both parents depend on nestling signals for appropriate food distribution (Trivers 1974; Parker & Macnair 1979), these studies raise

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questions about behavioural mechanisms for asymmetries in feeding patterns (Westneat & Sargent 1996). Nestling birds display a variety of behaviours when parents feed at the nest: they compete for favourable positions in the nest (McRae et al. 1993), posture, gape and vocalize (Kilner & Johnstone 1997). The majority of these components of the begging display depend on the individual chick's hunger level (e.g. Gottlander 1987; Smith & Montgomerie 1991; Kacelnik et al. 1995; Kilner 1995; Cotton et al. 1996; Kilner & Johnstone 1997). In general, these studies support the view that bird begging behaviour contains honest information about chick 'need' which parents use when deciding how to allocate food (Godfray 1991; Kilner & Johnstone 1997).

Our aim in this study was to address experimentally the seeming paradox that parents often differ in their pattern of food allocation even though the begging signals towards males and females should be similar if they uniquely transmit information about the chick's nutritional condition. This question has not yet been addressed experimentally (but see Stamps et al. 1985 for observational evidence), although the majority of studies on begging signals have been carried out on species with biparental care. We experimentally created within-brood variation in chick 'need' by food deprivation and hand-feeding and subsequently monitored (1) chick positioning relative to the feeding location of each parent in the nest, (2) chick posturing ('begging intensity'), and (3) the individual parent's food allocation decision. This set-up allowed us to disentangle the potential effects of the individual chick's 'need' from the individual parent's feeding behaviour with regard to their effects on chick begging signals and feeding success.

METHODS

Data Collection

We studied a natural great tit population in the spring of 1995 in the 'Bremgarten' forest near Bern, Switzerland. All pairs nested in nestboxes. At 9 days post-hatching, we ringed all nestlings with numbered aluminium rings, and installed a dummy camera box to accustom the birds to the presence of the camera box the following day. At 10 days post-hatching, we weighed all nestlings to the nearest 0.1 g using a Sartorius balance, ranked them according to body mass, and marked them individually on their heads with small spots of acrylic paint. We temporarily removed the two intermediate-sized nestlings from the nest, randomly assigned them to the 'food-deprived' and the 'fed' treatment groups, and put them separately into warmed artificial nests. Nestlings of the fed treatment group received bee-larvae for the following 2 h until they were satiated, while deprived ones received no food. After the 2 h we placed both nestlings, in a random position, back in their original nest. We then filmed the brood within the nest with a video camera equipped with an infra-red light source (see Christe et al. 1996). The camera box had a built-in camera in the upper part, which allowed us to film close up feeding bouts from a position vertically above the nest cup. In our population, mean brood size ± SD was 7.38 ± 1.28 and eggs hatched over a mean period ± SD of 0.7 ± 0.8 days as determined by daily visits to nestboxes.

As great tits usually resume normal feeding within 15 min of a nest visit by a human (personal observation), we discarded the first 15 min of filming and analysed the subsequent 45 min for 72 nests. The observer of the video had no knowledge of the hunger treatments to which nestlings had been subjected. We measured the following variables at every feeding event.

Parents: (1) time of entry into nestbox; (2) sex; (3) prey size (1 = small; 2 = intermediate; 3 = large); (4) feeding location of the parent (head position shortly before feeding); (5) time of feeding; and (6) division of food among more than one nestling (yes/no).

Nestlings: (1) position of each nestling just before a parent enters the nestbox; (2) begging intensity (posture) of nestlings when parent is at feeding location (0 = calm; 1 = weak gaping; 2 = persistent gaping; 3 = gaping, neck fully stretched; 4 = gaping, neck fully stretched, wing flapping); and (3) identity of the fed nestling.

Statistical Analysis

To determine nestling and parental positions, we divided the surface of the nest cup, on the video screen, into nine equally large areas, one circular in the centre and eight adjacent sectors (see McRae et al. 1993). Parental feeding location was treated as a circular variable. We calculated the mean feeding location of individual parents with 95% confidence intervals, and the mean angular distance between the two parents (absolute difference between the mean male and female location), using circular statistical methods (Batschelet 1981). To analyse whether males and females used the same or different feeding locations within the nest, we carried out Watson–Williams tests for each nest (Batschelet 1981). We subsequently combined the *P*-values using Fisher's method (Sokal & Rohlf 1995) to get a global *P*-estimate for the statistical significance of the difference in parental feeding location.

We calculated distances between parents and nestlings by transforming the pairs of absolute positions into distance scores ranging from 1 (closest possible) to 6 (furthest possible). We calculated for each nestling the mean distance from each parent, a median begging intensity and the mean proportion of feedings received from each parent over the 45 min analysed. The mean of the unmanipulated nestlings' means (or median of the nestlings' medians) were used for comparisons with experimental nestlings.

To understand the behavioural mechanisms promoting potential flexibility in begging behaviours with respect to the individual parent, we quantified aspects of parental behaviour that may affect the 'feeding value' of the parent as a food resource to the nestlings. We calculated for each parent a feeding rate, a median size of food item and a mean proportion of feedings divided among more than one nestling (aspects of potential benefits to nestlings). We also calculated the mean parental assessment time, as well as a mean begging distance and a median index of begging level of nestlings that begged successfully (nestlings fed by the parents), for each nest and parent (aspects of costs to chicks to get the food). We defined begging level as the product of time spent begging and the begging intensity of nestlings that begged successfully. Time spent begging was calculated as the time (s) elapsing between the parent arriving at the entrance hole (when begging starts) and feeding of a chick (when begging in the majority of cases stops). This index correlates positively with energy expenditure in 10-day-old tree swallow nestlings (Leech & Leonard 1996) and might thus give an estimate of energetic begging costs demanded by parents before feeding.

Of the 72 nests recorded, seven had to be excluded from the analysis: technical problems with the video arose in one nest, two nests received no feeding visits, and four nests were visited by one parent only. The final sample therefore consisted of 65 broods. Lower sample sizes in analysis of positioning are due to nestlings that were never visible during the observational period. Each brood was considered as an independent data point. For comparisons of nestlings within broods we used paired statistics (repeated measures ANOVA or Friedman two-way ANOVA by ranks). Before using parametric statistics, we tested the data for normality. All *P*-values are two-tailed. Statistical analysis was carried out using the Systat Statistical Package (Wilkinson 1989).

Ethical Note

To minimize the risk of parental abandonment because of the temporary chick removal, we included only broods with five or more chicks in the experiment. We observed no case of abandonment. We chose a period of 2 h for food deprivation by (1) referring to other studies (e.g. Smith & Montgomerie 1991) and (2) observing continuously the nestlings' reactions to the 2 h of manipulation. In general, nestlings did not show signs of stress at the end of the deprivation period and, on average, lost only 1.9% of their weight. Moreover, food deprivation and temporary removal of chicks had no detectable long-term effects on chick condition or survival: nestlings from the three experimental treatments did not differ in weight at 14 days (4 days after the experiment; Friedman two-way ANOVA by ranks: $F_{r,\,2,69}=0.021$, NS), fledging probability (food deprived: 84%; fed: 84%; unmanipulated: 83%; chi-square test: $\chi^2_2=0.033$, NS) or probability of recruitment to the local breeding population the following year (food deprived: 11%; fed: 15%; unmanipulated: 12%; $\chi^2_2=0.694$, NS). Chicks were marked with small spots of Bordeaux red acrylic paint (Lascaux Studio, Diethelm AG, Brüttisellen, Switzerland). This colour was chosen because it has low visibility under the dim natural light inside a nestbox, but contrasts well with the black head feathers of great tit chicks under the infra-red light source for the camera (personal observation). Parents and chicks were never seen pecking at the markings.

Table I. Mean angular distance between locations of parents feeding nestlings and measures of feeding location of male and female parents across nests

Feeding locations	Male	Female
Mean angular distance (± SD) between parents	77.7 (± 57.4)°	
Median 95% confidence interval (range) of feeding location	16 (0–140)°	16 (0–100)°
Mean absolute feeding location* (± angular deviation)	176.8 (± 54.8)°	155.5 (± 65.3)°

*Feeding location in relation to nestbox entrance hole (=0°). See text for statistical comparison of male and female behaviour.

RESULTS

Parental Feeding Locations

Within nests, male and female parents differed significantly in their feeding locations in 66% of nests (43 out of 65; Fisher combination test (see Methods): $\chi^2_{130}=605$, $P<0.0001$) and were similarly potentially recognizable to nestlings competing for favourable positions in the nest. This is further demonstrated by the observed mean angular distance between parental feeding locations and the high predictability with which both parents used their individual feeding location (shown by the narrow median 95% confidence interval; Table I). Males and females did not differ in the predictability of their location (Wilcoxon signed-ranks test: $Z=0.457$, $N=58$, NS). Females and males both had a significant preference for feeding their nestlings from the rear of the nest (Table I; Rayleigh test: females: $Z=8.0$, $N=65$, $P<0.001$; males: $Z=19.2$, $N=65$, $P<0.001$; Batschelet 1981).

Differences in feeding locations between parents (given that locations were very stable for each parent) might occur even if parents chose their location independently of each other (i.e. randomly). More interestingly for the hypothesis of parentally modified chick positioning, parental feeding locations may depend on each other. To test this hypothesis, we simulated random location choice by pairing randomly in the computer male and female location angles from all the nests 10^5 times. The resulting frequency distribution of angular distances was then compared with the observed one (Fig. 1). As predicted if parents (at least partly) adjusted feeding locations to each other, the two distributions differed significantly from each other (chi-square test: $\chi^2_5=11.81$, $P<0.05$). The difference between the two distributions is mainly due to the bimodality of the observed versus the unimodality of the expected distribution (Fig. 1).

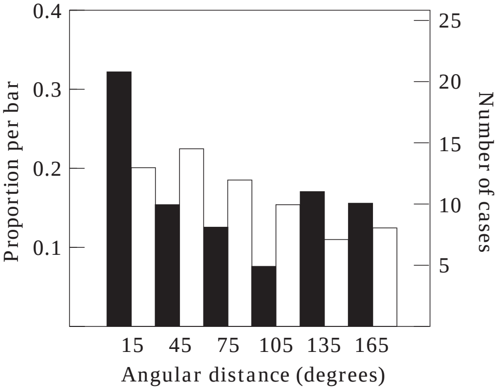

Figure 1. Observed frequency distribution of angular distances between parental feeding locations (■) and the distribution expected if parents chose their locations independently from each other (□). Numbers on the *X*-axis are category centres in degrees (category width=30°).

Effect of Hunger Level on Begging Behaviour

Begging distance to the female parent was significantly affected by hunger level (Fig. 2a; repeated measures ANOVA: $F_{2,62}=6.899$, $P<0.01$), whereas the distance to the male was not ($F_{2,61}=0.823$, NS). Experimental hunger level significantly influenced the chicks' choice between parental feeding locations. Food-deprived nestlings were positioned significantly closer to the female than to the male (paired *t*-test: $t_{63}=2.162$, $P<0.05$) and fed nestlings significantly further away from the female than the male ($t_{62}=-2.255$, $P<0.05$). The mean distance of unmanipulated nestlings to the female did not differ significantly from that to the male ($t_{64}=0.292$, NS).

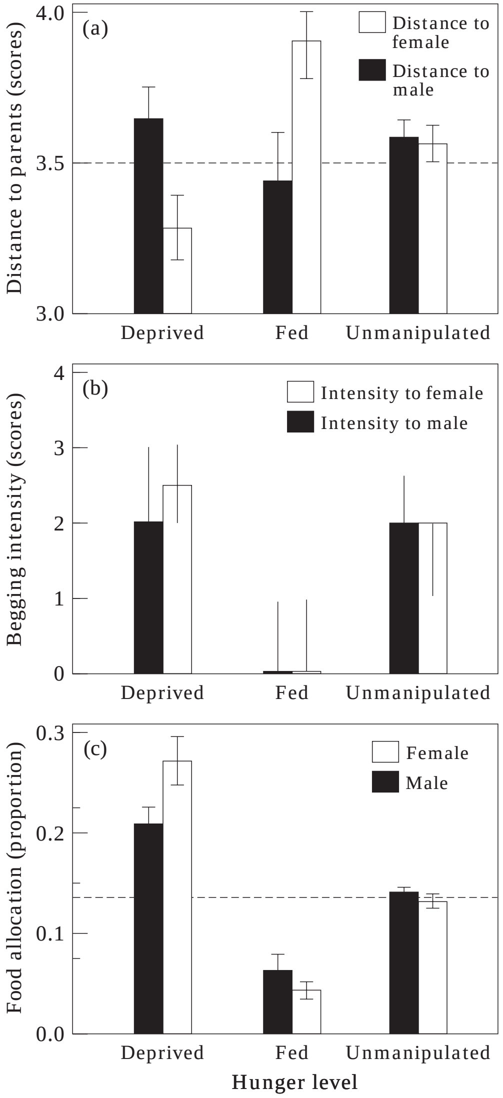

Figure 2. Effect of experimental hunger treatments on nestling begging behaviour and parental food allocation. Nestlings were food deprived for 2 h, fed to satiation or were unmanipulated. (a) Begging distance to male and female parent ($\bar{X}\pm$ SE). The dashed line indicates the prediction for random positioning of nestlings. (b) Begging intensity to male and female parent (median scores and inter-quartile range). (c) Male and female parental food allocation ($\bar{X}\pm$ SE). The dashed line indicates the mean prediction for random parental food allocation (i.e. 1/mean brood size).

Variation in begging intensity towards both the female and male parent was also significantly related to nestling hunger level (Fig. 2b; Friedman: female: $F_{r,\,2,63}=51.238$, $P<0.0001$; male: $F_{r,\,2,63}=40.762$, $P<0.0001$), but food-deprived nestlings begged at a significantly higher intensity to the female than to the male parent (Wilcoxon: $Z=2.367$, $N=41$, $P<0.05$). Fed and unmanipulated nestlings did not beg at significantly different intensities towards the two parents (fed: $Z=-0.338$, $N=28$, NS; unmanipulated: $Z=-1.302$, $N=31$, NS).

Effect of Hunger Level on Food Allocation

Both female and male food allocation were significantly related to nestling hunger level (Fig. 2c; Friedman: females: $F_{r,\,2,63}=70.000$, $P<0.0001$; males: $F_{r,\,2,62}=44.460$, $P<0.0001$), but food-deprived nestlings obtained a higher proportion of female than male feeds (paired t-test: $t_{63}=-1.99$, $P=0.05$). Fed and unmanipulated nestlings obtained a similar proportion of feedings from the two parents (fed: $t_{63}=0.934$, NS; unmanipulated: $t_{63}=1.524$, NS).

Differences between Parents in Feeding Value

Parents provided food at a similar rate, brought prey items of similar size and shared a similar proportion of feedings among more than one nestling (Table II). Males spent on average more time assessing before feeding a nestling than females (Table II). The analysis of the behaviour of successful chicks, as an estimate of the begging behaviour required to be fed, revealed that both parents fed nestlings positioned at similar average distances, but males fed nestlings begging at a higher level (for definition see Methods) than females (Table II).

DISCUSSION

Our study confirms models of honest signalling which predict that (1) offspring begging behaviour reflects variation in marginal benefit to be gained (hunger level) and (2) parents respond to the begging behaviour (Godfray 1991, 1995b; Kilner & Johnstone 1997). Furthermore, nestling positioning appeared to be strongly influenced by the feeding location of each parent and/or the begging intensity demanded. Such flexibility in parent–offspring interaction has been given little theoretical or empirical attention in the past.

Table II. Potential differences between parents in aspects of feeding value to nestlings

Variable	Male	Female	Test statistics	P
Feeding rate (per 45 min)	14.8 ± 9.0	15.0 ± 9.2	$t_{64}=0.164$	NS
Food item size (size classes)	1 (1–3)	1 (1–3)	$Z†=0.189$ $N=28$	NS
Proportion of food items shared among more than one nestling	0.07 ± 0.07	0.07 ± 0.07	$Z=0.246$ $N=63$	NS
Time spent assessing before feeding (s)	2.74 ± 1.13	2.44 ± 0.95	$Z=2.090$ $N=41$	<0.05
Begging distance of successful chicks*	3.11 ± 0.69	3.08 ± 0.66	$t_{64}=0.335$	NS
Begging level of successful chicks*	9.30 (5.5–29.3)	8.32 (3.5–18.0)	$Z†=3.22$ $N=65$	<0.01

Median (range) or $\bar{X}\pm$ SD. A more detailed analysis of food items brought by parents (measures of quantity and quality) for the same population in 1994 showed no significant differences between sexes (I. Werner, unpublished data).
*Successful chicks are nestlings that were fed by the arriving parent at a given feeding visit.
t: paired *t*-test; *Z*: Wilcoxon signed-ranks test; *Z*†: sign test.

Overall, great tit parents fed from significantly different locations on the nest and thereby forced nestlings to choose between them, when competing for favourable positions. The extent of this choice was modulated by parents since they seemed to adjust feeding locations to each other. Experimental chick hunger level had a strong influence on which parent was approached. Nestlings approached the female when food deprived, and retreated (or were displaced by siblings) from positions near the female when fed. No such behaviour was apparent towards the male. Furthermore, food-deprived nestlings begged at significantly higher intensity towards the female than male parent. This result is more difficult to interpret as it might simply be a correlate of differential positioning ('beg less intensely from the parent further away') and may represent the overall decision of hungry nestlings to concentrate begging at the location where the female fed. As expected, both parents allocated food according to experimental chick hunger levels, but females allocated more of their feeds towards food-deprived chicks than males.

Sibling Competition for Access to 'Begging Patches'

Nestling positioning in the nest as a component of begging display has attracted special interest because more competitive chicks (i.e. hungry and/or strong ones; e.g. Kilner 1995) have the potential to monopolize the best positions in the nest, even against the parents' best interest (Gottlander 1987; McRae et al. 1993; Kacelnik et al. 1995; Kilner 1995). Stable parental feeding locations have been reported for several cavity- and open-nesting bird species (see McRae et al. 1993), and are puzzling since chick competition may be enhanced and parental scope for choosing between nestlings reduced (Godfray 1995a; Kacelnik et al. 1995). It has been suggested that cavity-nesting could force parents to feed predictably from the entrance hole, and therefore constrain parents to accept the outcome of inter-sibling dynamics (e.g. Kacelnik et al. 1995). Great tit parents seemed to escape from this constraint by feeding nestlings from locations opposite to the nest entrance hole. They nevertheless used predictable feeding locations. This and our finding of differential chick positioning between the two parental locations suggest that constraints alone cannot account for this feeding behaviour in the great tit.

Our results support the hypothesis that parents gain information about nestling condition and/or phenotype by influencing the dynamics and outcome of direct sibling competition (Kacelnik et al. 1995; Rodríguez-Gironés et al. 1996). This scenario has recently been suggested to account for the initial evolution (and maintenance) of parent–offspring communication from an ancestral parental investment strategy without offspring signalling (Rodríguez-Gironés et al.

1996). Parents with different but predictable feeding locations confront their nestlings with a continuous-input situation of optimal foraging (see Milinski & Parker 1991) where chicks have to compete for access to 'begging patches'. By varying 'patch' value, parents may be able to influence flexibly the relationship between differences in chick phenotypes (e.g. 'need', size, sex) and relative competitive weights (Milinski & Parker 1991) in their 'patch'. They may favour nestlings that yield the highest marginal fitness returns on investment without having to make time-consuming active choices (Kacelnik et al. 1995).

Our finding of strong dependence of 'begging patch' choice on hunger level could be explained by hungry nestlings having a competitive advantage in the female but not in the male 'patch' (analogous to Milinski & Parker 1991, page 151). Choosing different feeding locations may therefore allow parents to favour different nestling phenotypes in their 'patch' and to build up communication with their nestlings individually. Moreover, different feeding locations may reduce the absolute extent of sibling competition for favourable positions in the nest since no chick can monopolize the best position of both parents at the same time.

Our observational evidence suggests a 'rule of thumb' by which parents could favour or disfavour 'needy' chicks. Male 'begging patches' may on average be costlier in terms of begging effort required to be fed: males waited longer before feeding and then fed nestlings begging at a higher level than females. This difference could explain the decision of food-deprived chicks to approach the female rather than the male feeding location, because hungry chicks should try harder to obtain food at the lowest possible cost. To separate the effects of chick positioning and parental sex on pay-offs of begging would require an experiment where the nestlings' choice between sites is constrained.

Ultimate Factors Favouring Flexible Communication

The following three ultimate reasons may explain why each parent should be interested in individual communication with its offspring, for example by feeding from different locations. First, the two sexes may differ in the trade-off between feeding nestlings and other activities (Stamps et al. 1985). Male birds may invest time and energy in attracting extra-pair mates (e.g. Wright & Cotton 1994) or defending the nest and/or territory (Clutton-Brock 1991), and females may be more involved in nest cleaning (Christe et al. 1996) and brooding (Stamps et al. 1985; personal observation). Second, male and female parents may, under some conditions, be in conflict over the offspring sex ratio (Gowaty & Droge 1991). Third, socially monogamous birds, including great tits, engage in extra-pair copulations that result in relatedness asymmetries between nestlings and their female and male feeding parent, respectively (Birkhead & Møller 1992; Westneat & Sargent 1996). Male parents therefore often have lower fitness returns on investment in current offspring than females, which may make females a more reliable food source to 'needy' chicks (Slagsvold et al. 1994; Keller 1997).

Which of these three, not mutually exclusive, hypotheses could explain variation in parental feeding location and nestling 'begging patch' choice will have to be investigated in the future. Theoretical and further empirical studies of begging signals in relation to factors that affect sexual conflict over investment (e.g. time constraints, conflict over sex ratio, extra-pair paternity) may therefore help us to understand the adaptive significance of flexible parent–offspring communication.

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REFERENCES

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

Birkhead, T. R. & Møller, A. P. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences.* London: Academic Press.

Christe, P., Richner, H. & Oppliger, A. 1996. Of great tits and fleas: sleep baby sleep . . .. *Anim. Behav.*, **52,** 1087–1092.

Clutton-Brock, T. H. 1991. *The Evolution of Parental Care.* Princeton: Princeton University Press.

Cotton, P. A., Kacelnik, A. & Wright, J. 1996. Chick begging as a signal: are nestlings honest? *Behav. Ecol.*, **7,** 178–182.

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

Godfray, H. C. J. 1995a. Evolutionary theory of parent–offspring conflict. *Nature, Lond.*, **376,** 133–138.

Godfray, H. C. J. 1995b. Signalling of need between parents and young: parent–offspring conflict and sibling rivalry. *Am. Nat.*, **146,** 1–24.

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

Gowaty, P. A. & Droge, D. L. 1991. Sex ratio conflict and the evolution of sex-biased provisioning in birds. *Acta Congr. Int. Ornithol.*, **XX,** 932–945.

Haskell, D. 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. *Proc. R. Soc. Lond. Ser. B*, **257,** 161–164.

Kacelnik, A., Cotton, P. A., Stirling, L. & Wright, J. 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. *Proc. R. Soc. Lond. Ser. B*, **259,** 259–263.

Keller, L. 1997. Indiscriminate altruism: unduly nice parents and siblings. *Trends Ecol. Evol.*, **12,** 99–103.

Kilner, R. 1995. When do canary parents respond to nestling signals of need? *Proc. R. Soc. Lond. Ser. B*, **260,** 343–348.

Kilner, R. & Johnstone, R. A. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.*, **12,** 11–15.

Leech, S. M. & Leonard, M. L. 1996. Is there an energetic cost to begging in nestling tree swallows (*Tachycineta bicolor*)? *Proc. R. Soc. Lond. Ser. B*, **263,** 983–987.

Leonard, M. & Horn, A. 1996. Provisioning rules in tree swallows. *Behav. Ecol. Sociobiol.*, **38,** 341–347.

McCarty, J. P. 1996. The energetic cost of begging in nestling passerines. *Auk*, **113,** 178–188.

McRae, S., Weatherhead, P. J. & Montgomerie, R. 1993. American robin nestlings compete by jockeying for position. *Behav. Ecol. Sociobiol.*, **33,** 101–106.

Milinski, M. & Parker, G. A. 1991. Competition for resources. In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 137–168. Oxford: Blackwell Scientific Publications.

Parker, G. A. 1985. Models of parent–offspring conflict. V. Effects of the behaviour of the two parents. *Anim. Behav.*, **33,** 519–533.

Parker, G. A. & Macnair, M. R. 1979. Models of parent–offspring conflict. IV. Suppression: evolutionary retaliation by the parent. *Anim. Behav.*, **27,** 1210–1235.

Rodríguez-Gironés, M. A., Cotton, P. A. & Kacelnik, A. 1996. The evolution of begging: signaling and sibling competition. *Proc. natn. Acad. Sci. U.S.A.*, **93,** 14 637–14 641.

Sasvári, L. 1990. Feeding response of mated and widowed bird parents to fledglings: an experimental study. *Ornis Scand.*, **21,** 287–292.

Slagsvold, T., Amundsen, T. & Dale, S. 1994. Selection by sexual conflict for evenly spaced offspring in blue tits. *Nature, Lond.*, **370,** 136–138.

Smith, H. G. & Montgomerie, R. 1991. Nestling American robins compete with siblings by begging. *Behav. Ecol. Sociobiol.*, **29,** 307–312.

Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*. 3rd edn. New York: W. H. Freeman.

Stamps, J., Clark, A., Arrowood, P. & Kus, B. 1985. Parent–offspring conflict in budgerigars. *Behaviour*, **94,** 1–40.

Trivers, R. L. 1974. Parent–offspring conflict. *Am. Zool.*, **14,** 249–264.

Westneat, D. F. & Sargent, R. C. 1996. Sex and parenting: the effects of sexual conflict and parentage on parental strategies. *Trends Ecol. Evol.*, **11,** 87–91.

Westneat, D. F., Clark, A. B. & Rambo, K. C. 1995. Within-brood patterns of paternity and paternal behavior in red-winged blackbirds. *Behav. Ecol. Sociobiol.*, **37,** 349–356.

Wilkinson, L. 1989. *SYSTAT: The System for Statistics.* Evanston, Illinois: SYSTAT.

Wright, J. & Cotton, P. A. 1994. Experimentally induced sex differences in parental care: an effect of certainty of paternity? *Anim. Behav.*, **47,** 1311–1322.