Differences in parental food allocation rules: evidence for sexual conflict in the blue tit?

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Evolutionary conflicts of interest between family members are expected to influence patterns of parental investment. In altricial birds, despite providing the same kind of parental care, patterns of investment in different offspring can differ between parents, a situation termed parentally biased favoritism. Previous explanations for parentally biased favoritism have received mixed theoretical and empirical support. Here, we test the prediction that in blue tits, *Cyanistes caeruleus*, females bias their food allocation rules to favor the smallest offspring during the nestling stage. By doing so, females could increase the subsequent amount of paternal care supplied by their partner during the fledging period, as a previous study showed that males feed the largest fledglings. When size differences within the brood are less pronounced, all offspring will require similar amounts of postfledging care, and thus, the male parent will lose the advantage of caring for the largest offspring that are closest to independence. In this study, we controlled the hunger of the smallest and largest nestlings in the brood and compared the food allocation rules of the 2 parents. We found that the male parent had a stronger preference than the female to feed the closest nestlings and made no distinction between nestlings based on size, whereas the female provisioned small hungry nestlings more when they were at intermediate distances from her. These differences in parental food allocation rules are consistent with predictions based on sexual conflict over postfledging parental investment. *Key words:* begging, biparental care, *Cyanistes caeruleus*, parental investment, *Behav Ecol* 18:674–679 (2007)]

In breeding systems with biparental care, male and female parents work together to raise offspring. However, this joint effort does not mean that each parent necessarily supports the evolutionary interests of its partner. In fact, Trivers (1972) recognized that conflicts of interest within the family, between parents and offspring, between individual offspring, and between the 2 parents, are expected to influence patterns of parental investment (reviewed in Parker et al. 2002). Parents invest in offspring in order to maximize their own lifetime reproductive success, trading off the costs and benefits of providing parental care (Clutton-Brock 1991). Each parent will prefer their partner to invest more than they do themselves because the costs of investment by one parent will not usually affect the other (Lessells 1999). Similarly, offspring have different interests from their parents over investment and also compete with each other over the division of investment (Trivers 1974; Mock and Parker 1997). As a result of these conflicts, parents are expected to respond to the behavior of other family members and negotiate patterns of parental investment (Hinde 2006; Hinde and Kilner 2007).

These evolutionary conflicts of interest may be expressed in differences in how the 2 parents allocate the same form of parental care to individual offspring, a situation termed "parentally biased favoritism" by Lessells (2002). Although several studies have found evidence for parentally biased favoritism in altricial birds during the nestling period (reviewed in Lessells 2002), there has been no consensus on the reasons for its occurrence. Generally, explanations for empirical observations of parentally biased favoritism have been centered around 3 themes: 1) male and female parents differ in the cost of reproduction and their overall investment into offspring, which leads to the parent investing least biasing investment into the most valuable offspring (Slagsvold 1997; Kölliker et al. 1998), 2) males and females differ in the benefits they receive from investment in different offspring, for instance, if some of the offspring are unrelated to one of the carers (Gottlander 1987; Westneat et al. 1995; Slagsvold 1997), and 3) parent–offspring conflict selects for parents to each feed a subset of their young to prevent dominant offspring from monopolizing parental resources (Slagsvold 1997; Kölliker et al. 1998; Kilner 2002). However, mathematical models investigating various possible explanations for parentally biased favoritism found support only for explanations (2) and (3) (Lessells 2002).

Parentally biased favoritism is most likely mediated by each parent's response to offspring solicitation behavior, and there is evidence that parents can differ in their response to the begging displays of their nestlings (Kölliker et al. 1998; Kilner 2002). Nestling position in the nest relative to the provisioning adult can influence food allocation, with nestlings that are closer to the parent receiving more food (Kilner 1995; Leonard and Horn 1996), but the strength of this effect may differ between the sexes (Porkert and Spinka 2004), and the 2 parents may also feed from different locations (Kölliker et al. 1998). In several species, females provide more food to the smallest offspring than males (reviewed in Slagsvold 1997; Lessells 2002), although whether parents respond directly to size is not clear in most studies. Parents can also differ in how they respond to the combination of begging and nonbegging cues such as size (Krebs 2001). Differences in the food allocation rules of the 2 parents may therefore be the mechanism behind parentally biased favoritism (Lessells 2002).

In this study, we experimentally test whether parentally biased favoritism occurs in broods of blue tits, *Cyanistes caeruleus*, during the nestling period, following a previous study that demonstrated its occurrence during postfledging parental care (Slagsvold et al. 1994). In blue tits, nestlings hatch asynchronously, with the female parent controlling this hatching spread and thus initial size differences between offspring. Slagsvold et al. (1994) showed that during postfledging care,

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male blue tits are more likely than females to feed the largest offspring. In asynchronous broods, the largest offspring will reach independence quicker than their smaller siblings, which will result in males investing less postfledging care than females in asynchronous broods. This may have an adverse affect on the females' postbreeding survival, as females in asynchronous broods had an 18% lower survival rate than females in synchronous broods (Slagsvold et al. 1994). This sexual conflict between the parents may drive females to produce broods that hatch more synchronously, thus manipulating males to provide more care to the brood after fledging (Slagsvold et al. 1994, 1995). Here, we test the prediction that females also bias their investment into the smallest offspring during the nestling stage in order to minimize size differences between offspring so that all offspring require similar amounts of postfledging care. By doing so, females could potentially increase the subsequent amount of paternal care supplied by their partner during the fledging period. Therefore, we predicted differences between the food allocation rules of males and females that relate to nestling size and sibling competition.

METHODS

Fieldwork

We studied the breeding population of blue tits in 2 small deciduous woods near Lancaster University, UK, during the spring of 2003. All birds in the study nested in wooden nestboxes of a standard size. All nests (n = 45) were regularly monitored from the start of the breeding season to establish laying date of the first egg, clutch size, hatch date, and hatching success and checked at the end of the breeding season to establish fledging success. Brood size at hatching was $8.37 \pm$ 2.12 (mean \pm standard deviation [SD]) nestlings (n = 45nests). Nestlings were ringed with numbered, metal British Trust for Ornithology rings at 6 days posthatching. Breeding adults were caught at the nest during the second half of the nestling period and fitted with a metal and color ring combination if they were not already ringed. Adults were sexed in the hand according to the presence of a brood patch, as only females incubate eggs and brood nestlings. Sex identification was also checked according to brooding behavior from videotapes of the nest (see below).

Ten days after hatching, feeding interactions between parents and nestlings were filmed for 1 h at each focal nest (n = 25). Due to technical problems with videotaping, data from 3 of these nests could not be used. In addition, in one of the remaining 22 nests, only the female parent provisioned nestlings during the observation hour.

Prior to filming, the hunger of 4 focal nestlings in each nest was manipulated by removing nestlings from the nest, taking them to warmed dummy nests nearby, and carrying out a treatment of either food deprivation or hand feeding. The 2 largest and 2 smallest nestlings (according to mass) in each nest were chosen as focal nestlings. The mean mass of focal nestlings was 9.7 g (SD = 0.72) for "large" nestlings and 8.0 g (SD = 0.95) for "small" nestlings. As nestlings at this age gain, on average, under 1 g per day (Perrins 1979), the mass difference between large and small nestling categories represents between 1 and 2 days growth. The 4 focal nestlings were randomly allocated to either a "fed" or "food-deprived" experimental treatment, so that each of the 2 treatments was carried out on both the large and small nestlings. This manipulation increased the mass of nestlings, but differences in mass between large and small nestlings were retained in both the deprived treatment (paired *t*-test: $t_{20} = 9.49$, P < 0.01) and the fed treatment (paired *t*-test: $t_{20} = 8.45, P < 0.01$). At the start of the procedure, all the focal nestlings were fed, until satiation, with Nectarblend chick rearing softfood (Haiths, Cleethorpes, UK). Nestlings were fed until they would no longer gape in response to a standardized stimulus of a light tap on the bill and the sound of a "squeak" made by the experimenter (which mimicked the parental feeding call). Nestlings in the deprived treatment were not fed again during the hour they were kept away from the nest. Nestlings in the fed treatment were kept warm in a separate dummy nest and were offered food every 10 min for 1 h; each time they were fed until they did not gape to the stimulus. At 60 min, after feeding the nestlings in the fed treatment, nestling mass was recorded for all 4 focal nestlings, and they were then returned to the nest. Nestlings were marked individually with small head patterns using white Tippex to allow identification on video recordings. Activity within the nest was then filmed for 1 h using an infrared camera inside the nest-box linked to a Sony digital camera (DCR-TRV330E). A second video camera was placed on a tripod approximately 5-10 m from the nest-box, recording the parents entering and leaving the nest to assist with the identification of individual parents. Dummy cameras were placed at the nest 1 day before recording to allow adult birds to become used to their presence. Filming took place between 0730 and 1800 h. Across nests, provisioning rate does not appear to vary predictably within these hours either in this study (Dickens M, Hartley IR, personal observation) or in previous work on blue tits (Cowie and Hinsley 1988). Mean parental provisioning rate in focal nests was 38.96 feeds per hour (range 18-62), and within nests, the 2 parents did not feed at significantly different rates during the observation hour (paired *t*-test: $t_{20} = 0.23$, P = 0.823). After 1 h of filming, nestling mass was recorded again and the cameras removed.

All procedures were carried out under license from English Nature, The British Trust for Ornithology, and the Home Office as appropriate.

Data collection from videotapes

Nestlings were successfully identified on the screen using the Tippex head markings. Parents were identified using color rings, although in 2 nests, there were several feeds (9/51 and 1/53) where it was not possible to identify the parent. During each parental provisioning visit over the 1-h observation period, the behavior of nestlings (begging and position in the nest) and the position of the adult was recorded directly before each feed—at the point between the adult landing on the nest and reaching toward a particular nestling to feed for the first time, together with the identity of the fed nestling. All time variables were recorded to 1/25th of a second (one frame on the video).

To record the positioning of parents and offspring, the nest area was divided into 9 equal areas on the screen (following McRae et al. 1993) with 1 central area and 8 areas in a circle adjacent to the center. Nestling and adult locations were then assigned to 1 of the 9 areas at each beg event immediately before a feed occurred (adults could not occupy the area in the middle of the nest). The distance between each nestling and the provisioning adult was quantified by transforming the 2 locations into a position score ranging from 1 (nestling and parent were in the same area of the nest) to 6 (nestling and parent were opposite each other).

For each nestling, observations were made of visual begging signals at each food delivery event directly before the adult allocated a food item to a chick. Postural begging intensity was categorized into 6 levels (adapted from Redondo and Castro 1992): (0) no begging, (1) gape open, head flat (2) gape open, head raised, (3) gape open, head raised, neck fully stretched, (4) gape open, head raised, front of body raised, (5) gape open, head raised, whole body raised.

Figure 1

The feeding locations of female and male parents at the nest. Bars inside the circles represent histograms of the circular distribution of feeding locations around the nest cup; data are the mean feeding locations of each parent (in degrees). Filled circles represent the mean feeding location across nests. The entrance hole is indicated with an arrow.



Statistical analysis

As parents may have been disturbed at the start of the filming period, when focal nestlings were placed back into the nest, analysis was carried out on the last 45 min of data only.

Parental feeding locations were analyzed using circular statistics (Mardia and Jupp 2000). Feeding locations in each of the 8 divisions around the circumference of the nest cup were converted to the midpoint in degrees covered by that segment (with the nest entrance taken as 0°). As data on feeding location did not follow the von Mises distribution (which may be thought of as a circular version of the normal distribution), parametric tests were not appropriate and the nonparametric Watson's 2-sample U^2 test, which can be regarded as analogous to the Mann-Whitney test on linear data, was used to compare male and female feeding locations within nests. The test ranks data according to the combined data set, therefore ties in the data set were broken in favor of the null hypothesis that there was no difference between male and female feeding locations (following Mardia and Jupp 2000). The variability of feeding locations across nests was tested using the Rayleigh test of uniformity. Tests were carried out using the CircStat package (Agostinelli 2005) in R 2.1.1.

The provisioning behavior of male and female parents was compared within nests using parametric or nonparametric paired tests as appropriate. For comparisons of how the 2 parents fed according to nestling hunger and size, and how they integrated different cues, only data from the focal nestlings used in the experimental treatment were used in analysis. For other comparisons (examining nestling begging and position), data from all nestlings were used. A model was created to examine how parents integrate different cues, with the following explanatory factors assessed for their ability to predict the allocation of food items to individual nestlings; nestling begging posture, nestling position relative to the provisioning adult, nestling size, and the sex of the provisioning adult. A multilevel model (Goldstein 2003) with binomial errors and a logit link was used to retain information from individual feeds while guarding against pseudoreplication due to multiple observations occurring for each individual nestling. Therefore, the model was structured to contain random effects from both the nest and the particular feed from which observations on individual nestlings originated. The dependent variable was whether each individual nestling was fed at a particular feeding event (0/1) to identify nestlings that received (1) or did not receive (0) food during a provisioning event. Only the first nestling to be offered a food item was considered to be allocated food by the adult, whether or not the adult then went on to give the food item to another nestling, as this decision is the parent's primary choice of which offspring to invest in at each feed. The model considered all 2- and 3-way interactions between explanatory variables. Explanatory variables were assessed for significance when they were the last terms in the model, within 3-way, 2-way, and main effects, to control for any influence of the order of terms. Nonsignificant terms were removed from the final model. Mixed models were created in S-PLUS 7.0 and all other tests carried out using SPSS 11.5.

RESULTS

Parental feeding positions

Parents usually chose to feed between $45-90^{\circ}$ from the entrance hole (Figure 1). This pattern held for both male and female parents (Rayleigh test of uniformity: females r = 0.96, n = 22, P < 0.001; males r = 0.97, n = 21, P < 0.001). Males and females did not differ in their feeding locations across nests (Figure 1). However, the feeding locations of the 2 parents did differ within 52.4% of nests (11 of 21 nests: Watson's U^2 test, in all P < 0.05). Where there was a significant difference between the positions of parents, this was either because they fed from different sides of the nest (n = 6 nests, mean angular distance between parents = 137.8° , SD = 13.1°) or because, although on the same side, the female fed from further back in the nest than the male (n = 5 nests, mean angular distance between parents = 25.5° , SD = 12.9°).

Parental feeding locations appear to be very predictable, at least within the time scale of the experiment. Within individuals of both sexes, there was little variation in feeding location, on average parents fed from their most frequently used position in 85.7% of feeds. Only females used a third or fourth feeding position.

Food allocation rules

Both parents provisioned deprived nestlings more than fed nestlings (Wilcoxon signed-ranks test: females Z = -3.74, n = 22, P < 0.001; males Z = -3.62, n = 21, P < 0.001; Figure 2). However, there was a nonsignificant trend for deprived nestlings to gain a higher mean proportion of male than female feeds (paired *t*-test: $t_{20} = -1.979$, P = 0.06), whereas nestlings in the fed treatment gained a similar mean proportion of feeds from each parent (Wilcoxon signed-ranks test: Z = -0.420, n = 21, P = 0.675).

When food-deprived, large nestlings received more food than small nestlings (Wilcoxon signed-ranks test: Z = -2.34, n = 22, P = 0.019), despite there being no difference in the intensity of begging posture with nestling size (Wilcoxon signed-ranks test: Z = -1.19, n = 22, P = 0.236). Large deprived nestlings did not gain a significantly higher proportion of male than female feeds (Wilcoxon signed-ranks test: Z = -1.53, n = 21, P = 0.125).



Figure 2

The proportion of food items (mean \pm standard error) allocated to focal nestlings by the male and female parents according to nestling relative size and experimental manipulation of nestling hunger.

Parents provided food more often to nestlings that begged more intensely (Wilcoxon signed-ranks test: Z = -4.08, n =22, P < 0.001), and there was no difference between the parents in the begging level of nestlings that were provisioned (Wilcoxon signed-ranks test: Z = 0.00, n = 21, P > 0.100). Parents also provisioned according to nestling position in the nest, preferentially feeding those nestlings that were closest to them (Wilcoxon signed-ranks test: Z = -3.75, n = 22, P <0.001; Figure 3). The male parent had a stronger preference to feed nestlings that were close to the provisioning adult than did the female (mean distance of adult from fed nestling: male = 2.76 (SD = 0.14), female = 3.17 (SD = 0.17), paired *t*-test: $t_{20} = -3.50$, P = 0.021; Figure 3).

How do parents integrate begging and nonbegging cues?

Nestling begging intensity was the most important factor influencing parents in the allocation of food items to individual nestlings (Table 1). However, the influence of begging intensity depended on how close nestlings were to the provisioning adult (begging posture \times nestling position: Table 1). In con-



Figure 3

The proportion of nestlings fed (mean \pm standard error) by the provisioning male and female parents according to the distance of the nestling from the adult. As distance score increases, nestlings are further away from the provisioning adult.

Table 1

Summary of mixed effects model examining how begging (begging posture and nestling position) and nonbegging cues (nestling size) influence how the male and female parents allocate food to individual focal nestlings

Model term	df	F	Р
Nestling begging posture	1,2179	549.25	< 0.001
Nestling position	1,2179	130.16	< 0.001
Parental sex	1,708	0.44	0.506
Nestling size	1,2179	10.51	0.001
Begging posture \times nestling position	1,2173	27.22	< 0.001
Begging posture \times nestling size	1,2173	15.21	0.001
Nestling position \times parental sex	1,2173	9.27	0.002
Nestling position \times nestling size	1,2173	7.13	0.008
Nestling position \times parental sex \times			
nestling size	1,2169	6.00	0.014

The dependent variable is fed (0/1) to identify nestlings that received (1) or that did not receive (0) food at each provisioning event. Each provisioning event is "nested" within brood as a random effect, and the model has binomial errors with a logit link. Explanatory variables were assessed for significance when they were the last terms in the model, within 3-way, 2-way, and main effects, to control for any influence of the order of terms. Nonsignificant interactions were removed from the final model. df, degrees of freedom.

trast to nestlings that were close to the provisioning adult, when nestlings were further away from the adult, begging posture did not strongly influence the allocation of food. This meant that for a similar level of begging intensity, a nestling begging close to the provisioning adult was more likely to receive food than one begging further away.

Male and female parents differed in how they responded to the combination of nestling position and nestling size (nestling position \times parental sex \times nestling size: Table 1). Male parents allocated less food to both small and large nestlings that were further away (Figure 4a). Female parents also allocated less food to large nestlings as they were further away but showed a different pattern of allocation toward small nestlings (Figure 4b). Small nestlings that were close were fed less than those at intermediate distances, whereas small nestlings at intermediate distances were given more food by the female than large nestlings in the same position.

DISCUSSION

Male and female parents responded similarly to begging intensity, allocating more food to nestlings begging at higher intensities, but they differed in how they responded to positional cues. By feeding nestlings that are further away, female parents may be ensuring that allocation patterns are more egalitarian, whereas the male parent, with a stronger preference to feed according to nestling proximity, potentially allows offspring to control food allocation. This result concurs with several other studies comparing male and female allocation rules. Porkert and Spinka (2004) found that male common redstarts, Phoenicurus phoenicurus, had a stronger preference for feeding nestlings that were in the front positions in the nest than did the female parent. In a study on tree swallows, Tachycineta bicolor, Whittingham et al. (2003) also found that males had a stronger preference than females to feed the nestling that was closest to the entrance of the nest. In addition, our study suggests that in blue tits, the female responds differently to nestling position according to the relative size of offspring. Male parents followed the general rule of feeding nestlings less as they get further away, regardless of nestling size. Females, however, preferentially fed smaller



Figure 4

The proportion of large and small hungry focal nestlings fed (mean \pm standard error) and the distance between the nestling and the provisioning adult for (a) the male parent and (b) the female parent. As the distance score increases, nestlings are further away from the provisioning adult.

nestlings when they were at intermediate distances from the parent. This difference in how the female allocated food with respect to nestling size may ensure that sibling competition does not eliminate feeds to the most needy offspring—those that cannot obtain positions close to the provisioning adult.

Despite these differences in parental allocation rules, we found no evidence for parentally biased favoritism according to nestling size in terms of the number of feeds nestlings received. Specifically, we found no evidence that the female parent provided more food to the smallest nestlings in the brood.

Why do male and female parents differ in their allocation rules?

These differences in provisioning rules could lead to parents optimizing investment in each individual offspring in the face of sibling competition (Kölliker et al. 1998). Parents are constrained when making allocation decisions by high provisioning rates, which means that they must make the assessment of nestling need as efficient as possible. Under these circumstances, it may be possible for competitive offspring to dominate positions close to the provisioning adult, especially where the 2 adults feed from the same area of the nest, which occurred in around half of the blue tit nests in this study. If the parents differ in their allocation rules, it would enable them to each feed a different subset of the brood, thus ensuring that the most competitive offspring do not monopolize parental feeds (Kölliker et al. 1998; Kilner 2002). In this case, differences in allocation rules would represent cooperation, not conflict between parents (Lessells 1999). This would not explain, however, why parents do not feed from separate locations in all nests.

Alternatively, differences in allocation rules may represent differences between parents in adaptive patterns of investment in particular types of offspring (Lessells 2002). There are several possible causes for this occurring in blue tits. Higher mortality rates of adult female birds during the breeding season (Owens and Bennett 1994) may cause females to place a higher value on the current reproductive attempt than do males and thus invest more than the male in lower quality offspring (Slagsvold et al. 1994). However, recent theoretical models have not provided any support for this explanation (Lessells 2002). The presence of extrapair young within broods may be an important factor (Slagsvold et al. 1994). A previous study on this population of blue tits has shown that extrapair young occurs in 39.8% of broods (Leech et al. 2001); accordingly, males in this population will often find themselves providing parental care for nestlings that they are not related to. It is possible that small nestlings may be more likely to be extrapair offspring (Gottlander 1987; Westneat and Sherman 1993) although data are lacking for this population. Alternatively, the presence of extrapair offspring might reduce the value of the brood as a whole to the male, and so he might invest less than the female in low-quality offspring (Lessells 2002). Theoretical models support this explanation, and although they predict that parentally biased favoritism should be extreme (some types of offspring are cared for by only one parent), the costs of discriminating between offspring may result in a more moderate bias against extrapair young (Lessells 2002).

Do differences in allocation rules represent the outcome of sexual conflict?

In blue tits, female parents have a strong influence over competitive interactions between their offspring even before hatching, as they decide when to commence incubation. The timing of incubation, and specifically whether females start incubation before they have finished laying the clutch, dictates the initial size differences between siblings and thus the degree of competitive equality in the brood. Slagsvold et al. (1994) have shown that by minimizing the hatching asynchrony in the brood, female blue tits can manipulate their partner's contribution, as the male parent contributes more to postfledging parental care when the brood is more competitively equal. When hatching asynchrony is greater, males bias their investment into the largest offspring who need parental investment for a shorter time after fledging. The female's food allocation rules during the nestling period may also be a tactic by the female to ensure substantial male investment into offspring. By partially compensating for the lower competitive ability of the smallest offspring in the brood, females may be attempting to keep size differences between offspring to a minimum, and by doing so, they gain more paternal care for the brood and reduce their own investment costs.

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REFERENCES

- Agostinelli C. 2005. CircStats: Circular Statistics. R package version 0.1-9 (S-plus original by Ulric Lund). Vienna (Austria): R Foundation for Statistical Computing.
- Clutton-Brock TH. 1991. The evolution of parental care. Princeton (NJ): Princeton University Press.
- Cowie RA, Hinsley SJ. 1988. Feeding ecology of great tits (*Parus major*) and blue tits (*Parus caeruleus*), breeding in suburban gardens. J Anim Ecol. 57:611–626.
- Goldstein H. 2003. Multilevel statistical models. 3rd ed. London: Arnold. Gottlander K. 1987. Parental feeding behaviour and sibling competition
- in the pied flycatcher *Ficedula hypoleuca*. Ornis Scand. 18:269–276. Hinde CA. 2006. Negotiation over offspring care?—a positive response
- to partner-provisioning rate in great tits. Behav Ecol. 17:6–12. Hinde CA, Kilner RM. 2007. Negotiations within the family over the
- supply of parental care. Proc R Soc Lond B Biol Sci. 274:53–60. Kilner R. 1995. When do canary parents respond to nestling signals of
- need? Proc R Soc Lond B Biol Sci. 260:343–348.
 Kilner RM. 2002. Sex differences in canary (*Serinus canaria*) provisioning rules. Behav Ecol Sociobiol. 52:400–407.
- Kölliker M, Richner H, Werner I, Heeb P. 1998. Begging signals and biparental care: nestling choice between parental feeding locations. Anim Behav. 55:215–222.
- Krebs EA. 2001. Begging and food distribution in crimson rosella (*Platycercus elegans*) broods: why don't hungry chicks beg more? Behav Ecol Sociobiol. 50:20–30.
- Leech DI, Hartley IR, Stewart IRK, Griffith SC, Burke T. 2001. No effect of parental quality or extrapair paternity on brood sex ratio in the blue tit (*Parus caeruleus*). Behav Ecol. 12:674–680.
- Leonard M, Horn A. 1996. Provisioning rules in tree swallows. Behav Ecol Sociobiol. 38:341–347.
- Lessells CM. 1999. Sexual conflict. In: Keller L, editor. Levels of selection in evolution (monographs in behaviour and ecology). Princeton (NJ): Princeton University Press. p. 75–99.
- Lessells CM. 2002. Parentally biased favouritism: why should parents specialize in caring for different offspring? Philos Trans R Soc Lond B Biol Sci. 357:381–403.

- Mardia KV, Jupp PE. 2000. Directional statistics. Chichester (UK): John Wiley and Sons.
- McRae SB, Weatherhead PJ, Montgomerie R. 1993. American robin nestlings compete by jockeying for position. Behav Ecol Sociobiol. 33:101–106.
- Mock DW, Parker GA. 1997. The evolution of sibling rivalry. Oxford: Oxford University Press.
- Owens IPF, Bennett PM. 1994. Mortality costs of parental care and sexual dimorphism in birds. Proc R Soc Lond B Biol Sci. 257:1-8.
- Parker GA, Royle NJ, Hartley IR. 2002. Intra-familial conflict and parental investment: a synthesis. Philos Trans R Soc Lond B Biol Sci. 357:295–307.
- Perrins CM. 1979. British tits. London: Collins.
- Porkert J, Spinka M. 2004. Provisioning behaviour at the nest in singleparent versus biparental nests and male versus female parents in the common redstart (*Phoenicurus phoenicurus*). Acta Ethol. 7:29–36.
- Redondo T, Castro F. 1992. Signalling of nutritional need by magpie nestlings. Ethology. 92:193–204.
- Slagsvold T. 1997. Brood division in birds in relation to offspring size: sibling rivalry and parental control. Anim Behav. 54:1357–1368.
- Slagsvold T, Amundsen T, Dale S. 1994. Selection by sexual conflict for evenly spaced offspring in blue tits. Nature. 370:136–138.
- Slagsvold T, Amundsen T, Dale S. 1995. Costs and benefits of hatching asynchrony in blue tits *Parus caeruleus*. J Anim Ecol. 64: 563–578.
- Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the decent of man 1871–1971. Chicago: Aldine. p. 136–179.
- Trivers RL. 1974. Parent-offspring conflict. Am Zool. 14:249-264.
- Westneat DF, Clark AB, Rambo KC. 1995. Within brood patterns of paternity and paternal behavior in red winged blackbirds. Behav Ecol Sociobiol. 37:349–356.
- Westneat DF, Sherman PW. 1993. Parentage and the evolution of parental behaviour. Behav Ecol. 4:66–77.
- Whittingham LA, Dunn PO, Clotfelter ED. 2003. Parental allocation of food to nestling tree swallows: the influence of nestling behaviour, sex and paternity. Anim Behav. 65:1203–1210.