Brood size, sibling competition, and the cost of begging in great tits (*Parus major*)

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Evolutionary theory of parent-offspring conflict explains begging displays of nestling birds as selfish attempts to influence parental food allocation. Models predict that this conflict may be resolved by honest signaling of offspring need to parents, or by competition among nestmates, leading to escalated begging scrambles. Although the former type of models has been qualitatively supported by experimental studies, the potential for a begging component driven by scramble competition cannot be excluded by the evidence. In a brood-size manipulation experiment with great tits, *Parus major*, we explored the scramble component in the begging activity of great tit nestlings by investigating the mechanisms of sibling competition in relation to brood size. While under full parental compensation, the feeding rate per nestling will remain constant over all brood sizes for both types of models; the scramble begging models alone predict an increase in begging intensity with brood size, if begging costs do not arise exclusively through predation. Great tit parents adjusted feeding rates to brood size and fed nestlings at similar rates and with similar prey sizes in all three brood-size categories. Despite full parental compensation, the begging and food solicitation activities increased with experimental brood size, whereas nestling body condition deteriorated. These findings support a scramble component in begging and suggest that the competition-induced costs of food solicitation behavior play an important role in the evolution of parent-offspring communication. *Key words:* brood size, cost of begging, *Parus major*, parent-offspring communication, scramble competition. *[Behav Ecol 14:457–462 (2003)]*

Food distribution by parents among offspring is a key element in the parent-offspring conflict. Nestlings are potential competitors and attempt to skew parental food allocation in their favor; in birds, this is most often by conspicuous begging displays. Several models have been proposed to explain the evolution of conspicuous offspring solicitation (for a review, see Godfray, 1995; Mock and Parker, 1997). One type of models predicts that begging intensity reflects the true condition of the individual, that parents adjust their feeding efforts to begging intensity, and that the cost of the signal imposes honesty (Godfray, 1995). An effect of nestling hunger level on begging intensity has been experimentally demonstrated in a large range of bird species (Budden and Wright, 2001; Kilner and Johnstone, 1997), including the great tit (Kölliker et al., 1998, 2000). Although this evidence qualitatively supports the honest signaling models, it does not exclude the potential for a begging component driven by scramble competition, at least in respect to species rearing multichick broods. This component refers to a second nonexclusive type of models.

These scramble models (Harper, 1986; MacNair and Parker, 1979) for the evolution of offspring begging assume that begging strategies are driven by escalated scramble competition among brood members for parental resources (Harper, 1986; MacNair and Parker, 1979). Under the assumption that begging costs do not arise exclusively through predation, these models predict an increase in begging intensity of each nestling with brood size, even if parents keep the feeding rate per nestling constant over all brood sizes (Harper, 1986).

The aim of the present study is to explore whether variation in the begging intensity of great tit nestlings entails a scramble component by investigating the mechanisms and consequences of sibling competition in relation to experimentally altered brood size. The conditions under which our experimental design is able to detect a scramble component are listed in Table 1. Although under full parental compensation, the feeding rate per nestling will remain constant over all brood sizes for both types of models, the scramble begging models alone predict an increase in begging intensity with brood size owing to the intensified scramble competition in larger broods. In contrast, honest signaling models predict that under the same condition, the begging intensity per nestling will remain constant, or may even decrease (Johnstone, 1999), over all brood sizes.

We manipulated brood size and compared, among treatment groups, the parental feeding rates, the sizes of the provisioned food items, and offspring begging intensity, and we evaluated the effect on nestling body condition. We assume that enhanced begging scrambles in larger broods are costly and affect nestling condition. Nestling body condition is well correlated with first-year survival (see Heeb et al., 1999; Perrins and Moss, 1975; Tinbergen and Boerlijst, 1990) and can therefore be used as a measure of offspring fitness. Brood size influences parental feeding rates (Smith et al., 1988; Verhulst and Tinbergen, 1997) and the begging intensity of nestlings (Leonard et al., 2000). In birds, the nestlings vocalize, stretch their bodies, flap their wings, and jockey for favorable feeding positions in the nest. The availability of such favorable feeding positions may be more limited in larger broods, the competition for access to them may be more intense (Kölliker et al., 1998; Ostreiher, 1997), and the mobility of nestlings will potentially increase with brood size.

MATERIALS AND METHODS

The study was performed in spring 1999 in a natural great tit (*Parus major*) population, breeding in nest-boxes in a forest near Bern, Switzerland. From early April onward, nest-boxes were visited regularly to record the date of egg laying, clutch size, and dates of hatching (defined as day 0) and fledging (the day the last young left the nest). To eliminate nest-based ectoparasites early in the nesting period, nests were

Table 1

Predictions for honest signaling and scramble competition models for reduced, control, and enlarged broods with and without parental compensation, assuming that the begging costs do not arise purely through predation

Brood-size manipulation:	Honest signaling–type models			Scramble-type models		
	Reduced	Control	Enlarged	Reduced	Control	Enlarged
Parents compensate						
Feeding rate/brood	<	<		<	<	
Feeding rate/nestling	=	=		=	=	
Begging/nestling	=	=		<	<	
Condition of nestling	=	=		>	>	
Parents do not compensate						
Feeding rate/brood	=	=		=	=	
Feeding rate/nestling	>	>		>	>	
Begging/nestling	<	<		≪	≪	
Condition of nestling	>	>		≫	≫	

heat-treated in a microwave appliance when the birds started building their nest (Richner et al., 1993). Nine days after hatching, all nestlings were marked with numbered aluminum leg rings. Body mass was taken to the nearest 0.1 g by using a Sartorius electronic balance, and tarsus length was determined to the nearest 0.1 mm by using dial calipers.

Experimental procedures

Two days after hatching, we cross-fostered nestlings that hatched the same day within a group of three nests of similar brood size (±one chick). We randomly assigned these nests to serve as a reduced (original brood size minus two nestlings), control (same number of nestlings), or enlarged (plus two nestlings) experimental nest. Within a cross-foster group, broods of different origin were ordered according to mean body mass, whereas individual nestlings were ranked according to body mass within their brood of origin. To keep variance in body weight similar among the three nests and to ensure that each nest of a group contained nestlings of all three origins, nestlings of the same origin were sequentially distributed over the foster broods according to their rank within their brood of origin and the rank between potential foster broods. For a detailed description of similar designs in other years, see Brinkhof et al. (1999) and Kölliker et al. (2000). Clutch size did not differ between brood-size treatments, indicating that broods were randomly allocated to experimental groups (Table 2). On the day of filming the nests, that is, 11 days after hatching, brood size differed significantly between experimental groups (Table 2), demonstrating that the brood-size manipulation was successful and affected brood size throughout the nestling period.

Some nests were experimentally infested with hen fleas (*Ceratophyllus gallinae*). Flea infestation, however, had no effect

on the variance (Levene test: $F_{1,56} = 0.06$, $p = .81$) or the mean condition of nestlings (ANOVA: $F_{1,56} = 0.75$, $p = .39$). Furthermore, there was no indication for an interaction between the brood-size manipulation and the flea treatment on nestling condition (ANOVA: $F_{2,55} = 0.29$, $p = .75$). Moreover, flea infestation had no effect on the other analysed variables (all ANOVA; feeding rate: $F_{1,56} = 1.07$, $p = .30$; feeding rate per nestling: $F_{1,56} = 0.90$, $p = .35$; food size: $F_{1,56} = 0.01$, $p = .92$; begging intensity: $F_{1,56} = 0.15$, $p = .70$; mobility: $F_{1,54} = 0.23$, $p = .63$) or on their interactions with parental sex or brood size manipulation (all, $p > .09$). In addition, the main results reported here are not altered when the flea treatment is considered in the analysis. We therefore excluded the flea treatment from further analyses.

Analysis of video recordings

For observations of activities within nest-boxes, we videotaped nests for 3 h at 11 days after hatching by use of a weak infrared light source and an infrared-sensitive camera, installed in the upper part of the nest-box. This allowed close-up recording of feeding bouts from a position vertically above the nest cup (Christe et al., 1996a,b; Kölliker et al., 1998). To accustom the birds to the presence of the camera, a dummy camera was installed 1 day before filming. All nestlings were weighed and marked individually on their heads with an individualized pattern of small spots of acrylic paint (Kölliker et al., 1998) that was visible to the infrared-sensitive camera. All three broods of a cross-foster group were filmed simultaneously. Great tits usually resume normal provisioning about 30 min after a human's visit to the nest (Neuenschwander S, personal observation). We therefore discarded the first 30 min of filming and analyzed the subsequent 2 h. To control for potential observer-bias, films were randomly renumbered

Table 2

Brood size of reduced, control and enlarged broods, before cross-fostering (clutch size), and after cross-fostering 2 and 11 days posthatching

Factor	Reduced	Control	Enlarged	χ^{2} [a]	P
Before cross-fostering	8.6 ± 0.98 (21)	8.5 ± 0.80 (17)	8.2 ± 0.81 (20)	1.40	.25
After cross-fostering	6.0 ± 1.02 (21)	7.9 ± 0.93 (17)	9.5 ± 0.95 (20)	68.8	<.0001
11 days after hatching	5.7 ± 1.01 (21)	7.2 ± 0.83 (17)	8.7 ± 1.09 (20)	45.1	<.0001

Values are mean (± SD) with sample size of nests in parentheses.
[a] Kruskal-Wallis test.

Table 3
Feeding rate per hour, feeding rate per nestling and hour, food size, nestling body mass in g, begging intensity, and nestling mobility in reduced, control, and enlarged broods at peak demand 11 days after hatching

Variable	Reduced	Control	Enlarged	F	p
Parental food provisioning (MANOVA)					
Feeding rate	20.1 ± 9.91 (21)	29.4 ± 8.57 (17)	30.1 ± 8.54 (20)	9.36	<.0001[a]
Feeding rate/nestling	3.5 ± 1.59 (21)	4.1 ± 1.38 (17)	3.5 ± 0.97 (20)	1.17	.32
Food size	2.0 ± 0.23 (21)	2.0 ± 0.16 (17)	2.1 ± 0.18 (20)	0.26	.77
Nestling mass and behavior (ANOVA)					
Body mass	15.3 ± 1.54 (21)	15.0 ± 1.35 (17)	14.0 ± 1.17 (20)	5.45	.0011[a]
Begging intensity	2.4 ± 0.64 (21)	2.6 ± 0.64 (17)	2.8 ± 0.54 (20)	2.47	.016[a]
Mobility	0.58 ± 0.127 (21)	0.63 ± 0.095 (16)	0.70 ± 0.098 (19)	5.05	.0098

Values are mean (±SD) with sample size of nests in parentheses.
[a] Ordered heterogeneity test.

before film analysis. Following the method of Kölliker et al. (1998), for every feeding event we recorded the sex of the feeding parent, prey size (1, small; 2, medium; 3, large), position of each nestling just before a parent entered the nestbox, and the begging intensity (posture) of each nestling when the parent was at its usual feeding location (0, calm; 1, weak gaping; 2, persistent gaping; 3, gaping with neck fully stretched; 4, gaping with neck fully stretched and wing flapping). To define the position of adults and nestlings we divided, on the video screen, the surface of the nest cup into nine equal sectors, i.e., one circle in the center plus eight adjacent sectors around this circle (McRae et al., 1993). The mobility of a nestling was defined as the average probability of changing the sector between the end of the current and the start of the subsequent feeding visit.

Statistical analysis

Sixty-three nests with video recordings were available. In five nests, the male did not participate in brood provisioning during the recorded period. These five nests were evenly distributed over the three brood-size categories (likelihood ratio: $\chi^2 = 1.48$, $p = .48$) and were excluded from the analyses. In two nests, some nestlings were not individually distinguishable on the film, and the nests could not be used for the analyses of nestling begging behavior. Final sample size for the analyses of nestling behavior was 56 broods; in all other analyses, 58.

For the analysis, the brood-size manipulation was included as a fixed factor in an ANOVA model. Parental variables are not independent and were thus analyzed by repeated-measure analysis (MANOVA). Data were transformed if the assumptions of parametric tests (normality and homogeneity of variances) were not fulfilled (Shapiro-Wilk W test; Levene test). Significance levels are two-tailed, except when there was a clear a priori prediction for the direction of effects, in which case the ordered heterogeneity test was used (Rice and Gaines, 1994). Probability values from ordered heterogeneity test are denoted by p_{OHT}.

An important distinction arising from Table 1 concerns the question of whether parents fully compensate, with their rates of food provisioning, for the effect of brood-size manipulation. Thus, we performed both a power analysis (Cohen, 1988) and an analysis based on the Bayesian information criterion (BIC) (see Raftery, 1995). For the latter analysis, the competing hypotheses are reformulated in terms of statistical models. The hypothesis that parents fully compensate for brood size implies, in modelling terms, that brood size does not improve the model when included as a factor. On the

other hand, the hypothesis that parents only partially compensate for brood size means that the inclusion of brood size improves the model fit. BIC can be used as an approximative measure of support for one or the other model and, therefore, allows estimating the evidence in favor of one or the other hypothesis. In the case of models with normal errors, BIC is computed as follows:

$$BIC = n \times \log(1 - R^2) + p_k \times \log(n),$$

where n is the number of observations (sample size), log the natural logarithm, R^2 the unadjusted R^2 of the ANOVA, and p_k the number of degrees of freedom for the model (excluding the df for the intercept) (Raftery, 1995).

BIC is calculated for both models (with and without brood size as a factor) and the model with smaller BIC is favored. The statistical "significance" of the evidence in favor of one or the other hypothesis can be judged from the extent of the BIC difference between the two models. Raftery (1995) suggested that a BIC-difference in the range of two to six can be interpreted as "positive," and a difference in the range of six to ten as "strong evidence" in favor of a given model (hypothesis).

Statistical analyses were performed by using the JMPIN statistical package (Sall and Lehmann, 1996). Power analyses were performed with G·Power (Buchner et al., 1997).

RESULTS

Parental food provisioning behavior

To assess the effect of brood size on parental food provisioning, we analysed both feeding rate and food item size. Mean rate of food provisioning increased significantly with experimental brood size (Table 3). Females and males did not differ in their overall feeding rate (MANOVA; factor parental sex: $F_{1,55} = 1.14$, $p = .29$), and the feeding response to the brood size manipulation did not differ significantly between males and females (MANOVA; interaction brood size × parental sex: $F_{2,55} = 2.04$, $p = .14$).

Feeding frequency per nestling (Table 3, Figure 1) was not significantly different between brood size manipulation categories. Males and females fed nestlings at similar rates (MANOVA; factor parental sex: $F_{1,55} = 1.62$, $p = .21$) and did not differ significantly in their response to the brood-size manipulation (MANOVA; interaction brood size × parental sex: $F_{2,55} = 2.05$, $p = .14$). The mean size of food items brought by the parents to the nestlings did not differ between the three experimental groups (Table 3). The two parents
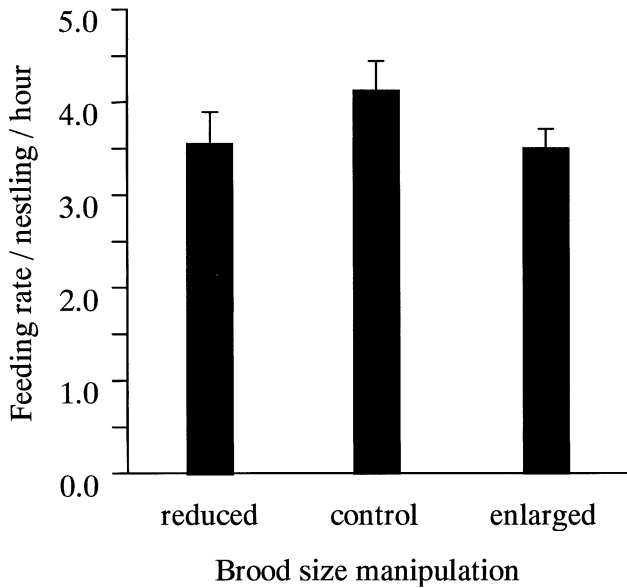
Figure 1
Mean number of feeding visits per chick per hour (±SE) for breeding pairs of reduced, control, and enlarged broods.

brought food items of similar size (MANOVA; factor parental sex: $F_{1,55} = 0.23$, $p = .64$) and showed a similar response to brood-size manipulation (MANOVA; interaction brood size × parental sex: $F_{2,55} = 0.013$, $p = .99$).

We performed two analyses to evaluate the null hypothesis of no difference between brood-size categories. First, we did a power analysis with an estimation of effect size taken from the study by Smith et al. (1988). Smith et al., in a similar experimental design, showed a significant negative association between feeding rate per nestling and brood size. In the present study, the corresponding power of 81% (sample size of 58, critical α-level of 0.05, effect size f of 0.42, following the method of Cohen, 1988) suggests that the probability of detecting a significant effect as large as the one observed by Smith et al. (1988), if present, was high. Second, we performed an analysis based on BIC (following the method of Raftery, 1995; see above). Both the analysis of food item size and per capita feeding rate supported the full-parental compensation hypothesis. BIC for the intercept-only model (BIC0) was smaller than was BIC for the model containing brood size as a factor (BIC1) (per capita feeding rate: BIC0 = 0, BIC1 = 5.70; food item size: BIC0 = 0, BIC1 = 7.57). The evidence for full parental compensation in our study is therefore "positive to strong" with respect to per capita feeding rate, and "strong" with respect to food item size (see above). In summary, the two analyses suggest that individual nestlings in reduced, control, and enlarged broods were on average fed at similar frequencies and with items of similar size.

Nestling behavior

Despite a similar per capita feeding rate, the nestlings increased their begging intensity significantly from reduced to enlarged broods (Table 3). Nestlings also significantly changed their position more frequently between parental visits from reduced to enlarged broods (Table 3). Because begging intensity and nestling mobility were positively correlated (Pearson correlation coefficient: $N = 56$; $r = .817$; $p < .0001$), we combined the parameters into a single measure
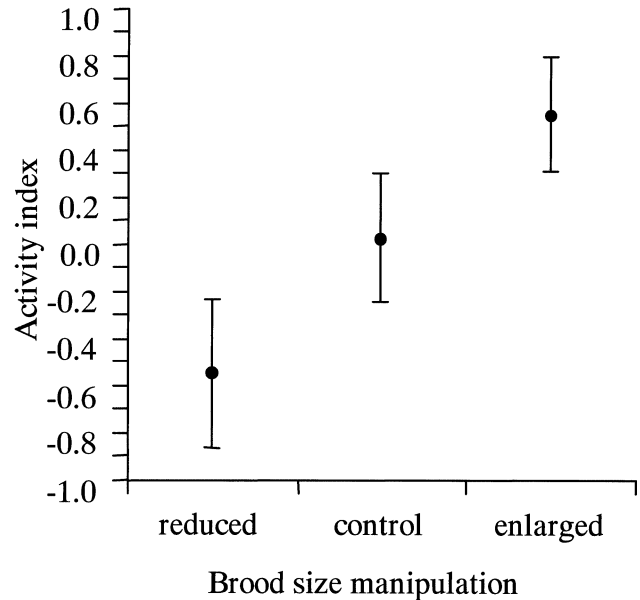

Figure 2
Overall mean begging activity (±SE), defined as the first principle component of begging and mobility intensity in reduced, control, and enlarged broods.

of begging activity by using principle component analysis. The first principal component (defined as activity) explained 90.8 % of the total variance in begging intensity and nestling mobility. Both activity (ANOVA: $F_{2,53} = 4.65$, $p_{OHT} = .0023$; Figure 2) and activity per feeding visit (ANOVA: $F_{2,53} = 4.23$, $p_{OHT} = .0033$) increased significantly from reduced to enlarged broods.

Condition of nestlings

Mean body mass of nestlings 11 days after hatching was significantly lower in enlarged than in reduced broods (Table 3). Their mean tarsus length 9 days after hatching was not influenced by brood-size manipulation (ANOVA: $F_{2,55} = 0.34$, $p = .71$). Mean condition of nestlings, calculated as the residuals from a regression of body mass on tarsus length, decreased significantly from reduced to enlarged broods (ANOVA: $F_{2,55} = 17.27$, $p_{OHT} < .0001$; Figure 3).

DISCUSSION

The experimental manipulation of brood size shows an increase in mean begging rates from reduced to enlarged broods even though parents adjusted to the manipulation and maintained similar feeding rates per nestling over all three brood-size categories. Although nestlings were fed at similar rates, body condition decreased with an increase in experimental brood size, suggesting that the decrease in body condition was at least partly owing to the increased energetic costs of begging and food solicitation behaviors in enlarged broods.

Together the findings support a role for the scramble-type model of the parent-offspring conflict (Godfray, 1995; Harper, 1986; MacNair and Parker, 1979; Rodríguez-Gironés, 1999) that predicts an increase in begging intensity with brood size. It has previously been shown that the begging intensity of great tit nestlings does depend on hunger level (Kölliker et al., 1998, 2000), just as the honest signalling of "need" models would predict (Godfray, 1991). The results of the present
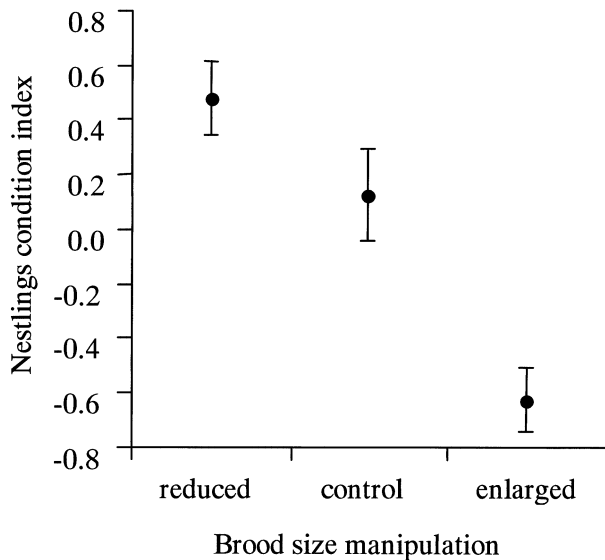
Figure 3
Mean condition of chicks (±SE), defined as the residual body mass of the regression of the body mass on the tarsus length in reduced, control, and enlarged broods.

study do not contradict these previous results, however. They rather suggest that in addition to an "honest," "need"-based aspect of great tit begging, a component of the begging strategy has evolved in response to the intensified competition in larger broods following the scramble-type models.

In addition to the suggested link between brood size and body condition owing to enhanced begging activity (and the associated metabolic costs) in larger broods, the brood-size manipulation probably had additional effects on nestling body condition that were not quantified here. For example, metabolic costs to the individual nestling associated with thermoregulation may be smaller in larger broods, because in large broods, the tight squeezing of nestlings also has a strong insulating effect. But it could also be larger if this isolating effect leads to overheating, and thus, nestlings have to dissipate heat.

Although great tits in our population fully increased their food provisioning frequency and compensated for the increased number of nestlings, in another study on the same species, the feeding rate per nestling decreased from reduced to enlarged broods (Smith et al., 1988). Because parent birds may face a trade-off between size and number of food items provided, we also included, in contrast to the study above, food item size in our analysis. We found no evidence for poorer per capita feeding rates in enlarged broods, although we cannot fully exclude that food was of similar size but of lower nutritional value. The interpretation that the poorer body condition of nestlings in enlarged broods is owing to the increased begging and food solicitation behaviors rests on the assumption that these behaviors are costly. Such costs are themselves a basic assumption of both the honest signaling– and scramble-type begging models, and there seems no reason to believe that scramble begging as observed here carries lower cost than the one assumed in honest signaling–type models.

Begging costs are a central assumption of theoretical models of parent-offspring interactions. Predation costs of begging vocalizations have been demonstrated relatively unambiguously (Haskell, 1994; Leech and Leonard, 1997). On the contrary, the costs arising to the individual performing the begging display ("energetic costs") have proven difficult

to assess. This has resulted in a currently ongoing debate on whether begging actually carries any such costs or not.

Studies measuring the energetic cost of begging by assessing oxygen consumption of individual nestlings (Bachman and Chappell, 1998; Leech and Leonard, 1996; McCarty, 1996) generally found low metabolic costs of begging, which led some authors to suggest that begging may be very cheap (Bachman and Chappell, 1998; McCarty, 1996). However, these studies neglect the anaerobic component of energy metabolism (Budden and Wright, 2001; Weathers et al., 1997). Even more importantly, not energy expenditure as such, but rather effects of begging on fitness-related traits (e.g., growth, survival) are expected to be of ultimate importance in the evolution of begging strategies (Verhulst and Wiersma, 1997). Depending on the trade-offs involved, even small changes in energy expenditure may significantly affect nestling fitness through their effects on growth, immune function, and other life-history parameters. In support of this argument, two recent and currently single studies on the growth cost of begging reported significantly negative effects of experimentally increased begging on chick growth (Kilner, 2001; Rodríguez-Gironés et al., 2001). In this line of evidence, our study indirectly suggests begging costs through a relationship between begging activity and reduced nestling condition owing to brood size in the great tit.

Even when assuming that metabolic costs refer to fitness costs of begging, our study suggests a reason why the measurement of energy metabolism of individual nestlings tested in isolation may be insufficient to quantify natural metabolic begging costs: Nestlings of most species do not beg for food in isolation but have to struggle with equally active competitors, i.e., siblings. This component has not been measured in the energetic studies. On the one hand, the intensified competition in larger broods may signify to individual nestlings additional costs because of the higher levels of vigilance required to be among the first beggars when parents arrive at the nest (Roulin, 2001). On the other hand, the maintenance of a given begging level may be more costly in larger broods in which competition is intense. As an example, one aspect of the begging display of many altricial nestlings is the spreading and flapping of the wings. This behavior can effectively disrupt the begging attempts of nestmates (Kölliker M, personal observation) and make it hard to maintain a given intended begging level. In addition, and as already mentioned, it may physically well be more expensive to reach a favorable position close to the fixed parents' feeding location (Kölliker et al., 1998; McRae et al., 1993) in larger broods, in which space is more limited and competition for favorable positions more intense.

REFERENCES

Bachman GC, Chappell MA, 1998. The energetic cost of begging behaviour in nestling house wrens. Anim Behav 55:1607–1618.

Brinkhof MWG, Heeb P, Kölliker M, Richner H, 1999. Immunocompetence of nestling great tits in relation to rearing environment and parentage. Proc R Soc Lond B 266:2315–2322.

Buchner A, Faul F, Erfelder E, 1997. G·Power: a priori, post-hoc, and compromise power analyses for the Macintosh. Trier, Germany: University of Trier.

Budden AE, Wright J, 2001. Begging in nestling birds. Curr Ornithol 16:83–118.

Christe P, Richner H, Oppliger A, 1996a. Begging, food provisioning,

and nestling competition in great tit broods infested with ectoparasites. Behav Ecol 7:127–131.

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

Cohen J, 1988. Statistical power analysis for the behavioral sciences, second edition. Mahwah, New Jersey: Lawrence Erlbaum Associates.

Godfray HCJ, 1991. Signalling of need by offspring to their parents. Nature 352:328–330.

Godfray HCJ, 1995. Evolutionary theory of parent-offspring conflict. Nature 376:133–138.

Harper AB, 1986. The Evolution of begging sibling competition and parent-offspring conflict. Am Nat 128:99–114.

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

Heeb P, Werner I, Mateman AC, Kölliker M, Brinkhof MWG, Lessells CM, Richner H, 1999. Ectoparasite infestation and sex-biased local recruitment of hosts. Nature 400:63–65.

Johnstone RA, 1999. Signaling of need, sibling competition, and the cost of honesty. Proc Natl Acad Sci USA 96:12644–12649.

Kilner R, 2001. A growth cost of begging in captive canary chicks. Proc Natl Acad Sci USA 98:11394–11398.

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

Kölliker M, Brinkhof MWG, Heeb P, Fitze PS, Richner H, 2000. The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. Proc R Soc Lond B 267:2127–2132

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.

Leech SM, Leonard ML, 1996. Is there an energetic cost to begging in nestling tree swallows (*Tachycineta bicolor*)? Proc R Soc Lond B 263:983–987.

Leech SM, Leonard ML, 1997. Begging and the risk of predation in nestling birds. Behav Ecol 8:644–646.

Leonard ML, Horn AG, Gozna A, Ramen S, 2000. Brood size and begging intensity in nestling birds. Behav Ecol 11:196–201.

MacNair MR, Parker GA, 1979. Models of parent-offspring conflict, III: intra-brood conflict. Anim Behav 27:1202–1209.

McCarty JP, 1996. The energetic cost of begging in nestling passerines. Auk 113:178–188.

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

Ostreiher R, 1997. Food devision in the Arabian babbler nest: adult choice or nestling competition? Behav Ecol 8:233–238.

Perrins CM, Moss D, 1975. Reproductive rates in the great tit. J Anim Ecol 44:695–706.

Raftery AE, 1995. Bayesian model selection in social research. In: Sociological methodology (Marsden PV, ed). Cambridge: Blackwells; 111–196.

Rice WR, Gaines SD, 1994. Extending nondirectional heterogeneity tests to evaluate simply ordered alternative hypotheses. Proc Natl Acad Sci USA 91:225–226.

Richner H, Oppliger A, Christe P, 1993. Effect of an ectoparasite on reproduction in great tits. J Anim Ecol 62:703–710.

Rodríguez-Gironés MA, 1999. Sibling competition stabilizes signalling resolution models of parent-offspring conflict. Proc R Soc Lond B 266:2399–2402.

Rodríguez-Gironés MA, Zúñiga JM, Redondo T, 2001. Effects of begging on growth rates of nestling chicks. Behav Ecol 12:269–274.

Roulin A, 2001. On the cost of begging vocalization: implications of vigilance. Behav Ecol 12:506–511.

Sall J, Lehmann A, 1996. JMPIN start statistics. Cary, North Carolina: SAS Institute.

Smith HG, Källander H, Fontell K, Ljungström M, 1988. Feeding frequency and parental division of labour in the double-brooded great tit *Parus major*. Behav Ecol Sociobiol 22:447–453.

Tinbergen JM, Boerlijst MC, 1990. Nestling weight and survival in individual great tits (*Parus major*). J Anim Ecol 59:1113–1127.

Verhulst S, Tinbergen JM, 1997. Clutch size and parental effort in the great tit Parus major. Ardea 85:111–126.

Verhulst S, Wiersma P, 1997. Is begging cheap? Auk 114:134.

Weathers WW, Hodum PJ, Anderson DJ, 1997. Is the energy cost of begging by nestling passerines surprisingly low? Auk 114:133.