The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care

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The coevolution of parental investment and offspring solicitation is driven by partly different evolutionary interests of genes expressed in parents and their offspring. In species with biparental care, the outcome of this conflict may be influenced by the sexual conflict over parental investment. Models for the resolution of such family conflicts have made so far untested assumptions about genetic variation and covariation in the parental resource provisioning response and the level of offspring solicitation. Using a combination of cross-fostering and begging playback experiments, we show that, in the great tit (*Parus major*), (i) the begging call intensity of nestlings depends on their common origin, suggesting genetic variation for this begging display, (ii) only mothers respond to begging calls by increased food provisioning, and (iii) the size of the parental response is positively related to the begging call intensity of nestlings in the maternal but not paternal line. This study indicates that genetic covariation, its differential expression in the maternal and paternal lines and/or early environmental and parental effects need to be taken into account when predicting the phenotypic outcome of the conflict over investment between genes expressed in each parent and the offspring.

Keywords: parent–offspring conflict; conflict resolution; begging; quantitative genetics; *Parus major*

1. INTRODUCTION

Offspring solicitation displays and the resulting increase in parental resource provisioning (parental response) are commonly modelled as the phenotypic outcome of an evolutionary conflict over investment among genes expressed in offspring and their parents (Trivers 1974; Parker & Macnair 1979; Harper 1986; Godfray 1991, 1995*a,b*; Mock & Parker 1997). The models are founded on the presence of genetic variation for both offspring solicitation and parental response allowing the traits to coevolve (Mock & Parker 1997). To date, empirical research has mainly concentrated on the phenotypic predictions of these models (Kilner & Johnstone 1996; Mock & Parker 1997) while very little is known about the quantitative genetic bases of the behaviours involved in parent–offspring conflict, particularly in natural systems. Specifically, evolutionary resolution of parent–offspring conflict may be influenced by genetic covariation between offspring begging intensity and parental response (West-Eberhard 1983; Lynch 1987; Eshel & Feldman 1991; Cheverud & Moore 1994), for example due to a runaway process (West-Eberhard 1983).

It is the norm in birds that both parents feed their offspring (Clutton-Brock 1991). Thus, the coevolution of offspring solicitation and parental response may not only be influenced by parent–offspring conflict, but also by sexual conflict over parental investment (Houston & Davies 1985; Parker 1985; Mock & Parker 1997). The sexes commonly differ in their respective roles during

reproduction (Clutton-Brock 1991; Birkhead & Møller 1992; Hrdy 1999), including their feeding behaviours (Stamps *et al*. 1985; Kölliker *et al*. 1998; Kölliker 1999). Therefore, one may often expect different dynamics in the coevolution of genes expressed in mothers and offspring (i.e. in the 'maternal line') and genes expressed in fathers and offspring (i.e. in the 'paternal line'). For example, the presence of extra-pair nestlings (Birkhead & Møller 1992) reduces the average relatedness among successive brood mates in the paternal versus the maternal line, which potentially favours higher equilibrium solicitation (Parker 1985; Godfray 1995*b*; Kölliker *et al*. 1998) and lower parental response levels (Parker 1985; Godfray 1995*b*) in the paternal line.

The aim of this study was to investigate the quantitative genetic basis of offspring solicitation and parental food provisioning responses experimentally in natural populations of the great tit, a passerine bird where both parents provide food to their offspring (e.g. Perrins 1979; Kölliker *et al*. 1998). We assessed the importance of a common origin in the expression of begging call intensity of nestlings using a cross-fostering experiment while randomizing for the rearing environment. The rearing environment in this experiment may reflect a nutritional component in the begging calls (Kilner & Johnstone 1996) and the effect of a common origin indicates genetic variation, including environmental and parental effects before hatching. We combined the cross-fostering with a begging playback experiment in one population. This combined experiment allowed us to (i) test the parental responses of the two sexes to offspring begging call intensity (in terms of food provisioning), and (ii) investigate the presence of origin-related covariation between

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offspring begging call intensity and parental response. Such origin-related covariation would suggest genetic covariation and/or environmental and parental effects before hatching.

2. MATERIAL AND METHODS

(a) *Study area and general methods*

The experiments were carried out in the Bremgartenwald (1997) and the Forst (1998), two forests near Bern (Switzerland) where great tits have been breeding in nest-boxes for several years. In order to minimize potential variation in environmental parental effects induced by nest-based ectoparasites (Heeb *et al.* 1998), we sterilized the nests by heat treatments before the first egg was laid (Heeb *et al.* 1998).

As soon as a clutch was completed, we measured the total mass of the clutch to the nearest 0.1 g using a Sartorius balance (in 1998 only). The mean egg mass was calculated by dividing the clutch mass by the number of eggs. We caught parent birds on the nest when the nestlings were 14–15 days old and measured their body mass (to the nearest 0.1 g) and tarsus length (to the nearest 0.1 mm). Age was determined as first-year or older birds from the colour of the wing coverts (Perrins 1979). A body condition index was taken as the residuals from a linear regression of body mass on tarsus length.

(b) *Experimental methods: cross-fostering experiment*

Hatchlings of each brood from a group of three broods with the same hatching date were transferred to each of the other two broods. Thus, all nestlings used for begging recordings (see § 2(c)) were raised by foster-parents. Before the cross-fostering, all hatchlings of a cross-foster group were weighed and ranked within their nest of origin according to their body mass. Hatchlings from the same origin were then sequentially divided among the two other broods according to their weight rank and the average body mass of the three broods. For example, a hatchling with rank 1 from a given origin was placed in the heavier of the two foster nests and the hatchling ranked 2 in the lighter one, the one ranked 3 again in the heavier nest and so on for the other two origins until all the hatchlings were distributed (for more details, see Brinkhof *et al.* 1999). Because of environmental variation in hatchling body mass among broods, this procedure results in body mass matching of nestlings from different origins raised in the same nest of rearing. We carried out a second body mass matching of nestlings from different origins raised in the same nest when selecting the nestlings for the begging recordings. Nestlings were ranked according to body mass within their nest of rearing and the two (1997) or four (1998) nestlings from the two origins with ranks as similar as possible were chosen. As intended, no significant similarity in body mass relative to the brood mean, i.e. in the position in the weight hierarchy, among nestlings from the same origin was detectable (nested analysis of variance (ANOVA), common origin (group) in 1997 $F_{36,17} = 1.777$ and $p = 0.103$ and common origin (group) in 1998 $F_{18,62} = 1.263$ and $p = 0.244$). Given our focus on the effect of a common genetic origin on begging call intensity, the steps described in body mass matching are important. Nestlings from a given origin would otherwise not only have their origin in common but also tend to occupy similar positions in the weight hierarchy of their own foster broods. Thus, the effect of the common origin would be confounded with position in the weight hierarchy. A potential alternative

design with random distribution of hatchlings among broods of a cross-foster group would maintain this problem and, thus, tend to lead to an overestimation of the origin effect.

(c) *Experimental methods: recording of begging calls*

Two nestlings per family originating from 54 families (1997) and four nestlings per family originating from 27 families (1998) were transferred to the laboratory at the age of ten days for recording of begging calls. The nestlings from the same cross-foster group were taken simultaneously in the laboratory and the recording sessions were randomly ordered with respect to the nestlings' origin. They were individually housed in warmed artificial nests to which they were randomly allocated by drawing lots. Begging was elicited by first tapping on the nest-box with a wooden stick and then gently on the nestling's beak. The begging calls of each nestling were recorded in two sessions, i.e. 60 and 150 min after removal from the nests, with three repetitions per nestling and per session. The three repetitions were averaged resulting in two measures of begging call intensity per nestling. The mean of these two measures is referred to in the following as the 'absolute' begging call intensity and reflects the overall begging level of a nestling, while the change from the first to the second session is referred to as the 'relative' begging call intensity and reflects the effect of hunger level. The begging vocalizations were digitized (at 8 bit and 22.05 kHz) using a microphone and the sound analysis software Canary 1.2 (Charif *et al.* 1995). We calibrated the recording set-up and then measured the acoustic energy (energy flux density) (Charif *et al.* 1995) between 1 and 10 kHz during the first 3 s of the begging bouts before making acoustic analyses.

(d) *Experimental methods: begging playback experiments*

The parental responses to begging call intensity in terms of food provisioning were investigated experimentally in the Forst population (1998) by means of begging playbacks at the natural nests. We broadcast two computer-manipulated levels of begging call intensity at each nest successively on day 9 after hatching and determined the parental feeding responses from video recordings (Kölliker *et al.* 1998). The template for the computer-modulated begging sequences used in all playback experiments consisted of a bout of begging vocalizations from a natural brood not used in the experiments. The vocalizations were elicited by tapping on the nest-box, recorded using a microphone and a digital audiotape recorder and then transferred to a computer. We manipulated this begging sequence in the computer using Canary 1.2 in order to obtain high- and low-energy begging level sequences by simultaneously varying both the length and amplitude of the sequence. One begging sequence per 90 s was then played on tapes of 45 min (at 16 bit and 44.1 kHz), resulting in high- and low-energy begging level tapes of 45 min each. We broadcast the calls from the high- and low-energy begging tapes successively in the field from a speaker on the side of the nest-box connected to a Walkman after a control period of 1 h without playback. The order in which the two tapes were played was alternated between and kept constant within cross-foster groups. In order to avoid time-effects, we ran the playback experiments of the three broods from the same cross-foster group at approximately the same time, i.e. within 1 h. Because great tits usually resume normal feeding within 15 min of disturbance at the nest (Kölliker *et al.* 1998), we counted the number of visits by each parent from the videos during 30 min of each playback level (discarding the first

Table 1. *Analysis of origin-related variation in begging call intensity*

(Random effects, nested ANOVA with the cross-foster group as main nesting factor and both the nest of rearing and the nest of origin as factors nested within the group. Due to non-normality of the data in population 1, the effect of the nest of origin was tested using the jackknife method; see § 2.)

source	test statistics (d.f.)	p
population 1 (1997)		
nest of origin (group)	$t_{17} = 2.718$	0.0150
population 2 (1998)		
between subjects (absolute intensity)		
group	$F_{8,62} = 5.933$	< 0.0001
nest of rearing (group)	$F_{18,62} = 2.320$	0.0080
nest of origin (group)	$F_{18,62} = 2.173$	0.0130
within subjects (relative intensity)		
hunger	$F_{1,62} = 135.05$	< 0.0001
hunger × group	$F_{8,62} = 1.929$	0.0710
hunger × nest of rearing (group)	$F_{18,62} = 1.913$	0.0310
hunger × nest of origin (group)	$F_{18,62} = 1.367$	0.1810

Table 2. *Analysis of origin-related covariation between parental responses and offspring begging call intensity*

(Repeated-measures analysis of covariance with the mother's and father's responses as repeated measures, the cross-foster group as random factor and the begging call intensity of biological offspring as the covariate.)

source	test statistics (d.f.)	p
between nests		
group	$F_{7,13} = 2.503$	0.0730
begging call intensity	$F_{1,13} = 6.923$	0.0210
within nests		
parent sex	$F_{1,13} = 6.549$	0.0240
parent sex × group	$F_{7,13} = 3.652$	0.0210
parent sex × begging call intensity	$F_{1,13} = 19.258$	0.0007

15 min) and classified the sizes of the food items as small (rank 1), medium (rank 2) or large (rank 3) (Kölliker *et al.* 1998). The product of the number of visits and the average food size is used as an index of the food quantity brought to the nest. The parental response is defined as the proportional change in the food index from the low- to the high-intensity playback. In addition, we counted the number of gaping nestlings at each parental feeding visit. The frequency of gaping nestlings was not influenced by the change in intensity of the begging calls broadcast (χ^2-test, $\chi^2_1 = 1.202$ and $p = 0.273$), suggesting that the parental feeding responses in the playback experiment were not influenced by an interaction between the begging calls broadcast and the begging behaviour of the nestlings.

(e) *Statistical methods*

The origin-related variation in begging call intensity was analysed using a random effects, nested, ANOVA model where both the nest of rearing and the nest of origin were nested factors within the cross-foster group. The data on nestling begging call intensity were positively skewed and could only be transformed to a normal distribution in the 1998 sample. We tested the effect of the nest of origin for the untransformed 1997 data by use of the jackknife method (see Sokal & Rohlf 1995, pp. 821–823). The variance component due to the common origin (σ_o) was first calculated from the nested ANOVA including the full sample and then by excluding each cross-foster group in turn. A pseudovalue of $\phi_i = n\sigma_o - (n-1)\sigma_{o(-i)}$ was calculated for each turn, where n corresponds to the number of cross-foster groups and $\sigma_{o(-i)}$ to the variance component when the ith group was excluded (Sokal & Rolf 1995). The jackknifed estimate of the variance component due to the common origin was the mean of these pseudovalues. A t-test with d.f. $= n-1$ could then be used to test whether this variance component differed significantly from zero, provided that the pseudovalues (not the original measures) were normally distributed (Sokal & Rolf 1995). This was the case in our sample (Shapiro–Wilk W-test, $W = 0.945$ and $p = 0.382$). A transformation to the power of 0.4 for the 1998 data yielded approximately normal distributions and homogeneous variances across groups. Therefore, a

random effects, nested, ANOVA model with the first and second recording sessions as repeated measures, the group as the main nesting factor and both the nest of rearing and the nest of origin as nested factors could be applied directly.

Directed statistical tests (Rice & Gaines 1994) were used in the analyses of parental responses in the begging playback experiments due to the *a priori* expectation of higher parental feeding efforts at higher begging call intensities. The corresponding p-values are denoted as p_{dir}. The cross-foster group was entered in the model as a (random) factor in the analysis of the origin-related covariation between begging call intensity and parental response in order to control for between-group variation statistically. Statistical analyses were carried out using JMPIN statistical software (Sall & Lehman 1996).

3. RESULTS

(a) *Origin-related variation in begging call intensity*

The common origin of nestlings explained a significant part of the variation in the absolute begging call intensity (i.e. the mean of the two recording sessions) in both populations (table 1) and accounted for 25.8 and 20.0% of the total variation in the two populations, respectively. The average begging call intensity of nestlings from the same origin was not significantly related to their native clutch size or average native egg mass (p-values > 0.8). When controlling for variation in hatchling body mass statistically by including it as a covariate in the model ($p = 0.065$), the effect of the common origin on begging call intensity remained significant ($F_{18,61} = 1.914$ and $p = 0.031$). Further, the origin-related variation in begging call intensity was independent of nestling body mass on the day of begging recordings since it remained significant ($F_{18,61} = 2.125$ and $p = 0.015$) when body mass was included in the model as a covariate ($p = 0.877$). Thus, the origin-related variation in begging call intensity was independent of egg mass, clutch size, body mass at hatching or body mass when begging calls were recorded. The relative begging call intensity (i.e. the difference between the two recording sessions) was not significantly related to the common origin (table 1). The common nest of rearing had significant effects on both the absolute and relative begging call intensities (table 1).
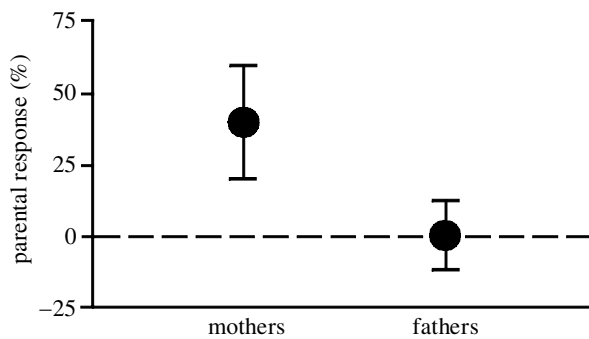
Figure 1. Responses of great tit mothers and fathers to an increase in begging call intensity (mean ± s.e.) in the playback experiment. Parental response was defined as the proportional change in the amount of food brought to the nest from the low- to the high-intensity playbacks. The dashed line indicates the null expectation, i.e. no response. The variances in parental responses were not significantly different between mothers and fathers (Levene test, $F_{1,48} = 2.071$ and $p = 0.157$).

(b) Parental response to vocal begging and origin-related covariation with offspring begging call intensity

Male and female parents brought similar amounts of food to the brood during the initial control period without begging playbacks (paired t-test, $t_{21} = 0.848$ and $p = 0.406$) (Kölliker *et al.* 1998). In the playback experiment, on average mothers responded to an increase in begging call intensity with a 40.6% (± 19.2% s.e.) augmentation in their food provisioning, while fathers did not respond significantly (one-sample t-test, mothers $t_{25} = 2.117$ and $p_{dir} = 0.028$; fathers $t_{23} = 0.092$ and $p_{dir} = 0.580$) (figure 1).

The size of the response of the mothers (but not of the fathers) was positively related to the begging call intensity of their biological offspring (mothers $r^2 = 0.457$, $n = 24$ and $p = 0.0003$; fathers $r^2 = 0.041$, $n = 22$ and $p = 0.368$) (figure 2).

The full model for the analysis of the sex difference in parental response and the origin-related covariation between parental response and nestling begging call intensity is presented in table 2. The difference between mothers and fathers in the parental response to vocal begging was significant (parent sex effect) and the slopes of the origin-related covariations between parental response and offspring begging call intensity (figure 2) differed significantly between the two parental lines (parent sex × begging call intensity interaction).

The conditions and ages of mothers and fathers were not significantly related to maternal response or the begging call intensity of biological offspring (p-values > 0.12). The statistical power for detecting an effect of the size obtained for the origin-related covariation between maternal response and offspring begging call intensity was in all cases larger than 0.81. Thus, the covariation in the maternal line was not mediated by the age or condition of the parents. In addition, the covariation was similar for first-year and older mothers, which is demonstrated by the non-significant interaction between female age and offspring begging call intensity ($F_{1,10} = 0.001$ and $p = 0.978$) when female age was included as a factor in the model (table 2). This indicates that the
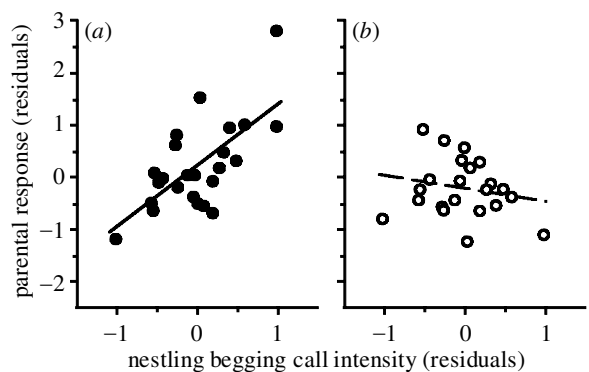

Figure 2. Origin-related covariation between the parental response and begging call intensity of offspring in (*a*) the maternal line and (*b*) the paternal line. Parental response is defined as the proportional change in food provisioning due to higher begging call intensity during the playback experiment at the natural nests. The intensity of the begging calls of the nestlings was measured from recordings made under controlled laboratory conditions. For illustration, parental responses are standardized for between-group variation (by taking residuals) and the begging call intensity of nestlings is standardized for between-group and between-nest-of-rearing variation (by taking residuals). Each point represents the mean of these residuals per family.

origin-related covariation between parental response and offspring begging call intensity in the maternal line did not arise from maternal adjustments of the response to begging due to experience with offspring in previous breeding attempts.

4. DISCUSSION

It is well-documented that the intensities of various begging displays are influenced by the amount of food that nestlings obtain (i.e. their 'need') (Kilner & Johnstone 1996; Kölliker *et al.* 1998). The observed effects of both hunger level and a common rearing environment on the acoustic begging level of nestlings were in concordance with such a nutritional component. By demonstrating significant origin-related variation in begging call intensity, we have provided experimental evidence suggesting genetic variation in the acoustic begging level of great tit nestlings. To our knowledge, this is the first study in a wild-living animal species supporting the fundamental assumption in all-resolution models of parent–offspring conflict that levels of solicitation are genetically variable (Godfray 1995*a*; Mock & Parker 1997). Unfortunately, no direct test for genetic variation in the parental responses could be made because less than 10% of the nestlings in the populations studied were recaptured locally as adult breeders (Heeb *et al.* 1999). However, the origin-related covariation between the maternal response and offspring begging call intensity indirectly suggests its presence, at least with respect to the response of females. This is because a genetic correlation between two traits requires a genetic component in both (e.g. Roff 1997, p. 77).

Only mothers responded significantly to variation in begging call intensity in the playback experiment. This finding is in agreement with an earlier study where

female great tits allocated a higher proportion of feeds to hungry nestlings than males (Kölliker *et al*. 1998). Great tit fathers possibly respond to other, non-vocal aspects of the begging display which were not experimentally manipulated here. If true, differences between the sexes in their relative preferences for aspects of the begging display may be one reason for the evolution of multiple begging signals in great tits.

Our finding of origin-related covariation between the response of mothers and the begging call intensity of nestlings may reflect a genetic correlation between the two traits which is expressed in the maternal line only. This would imply that different (sets of) genes affecting the parental response are expressed in mothers and fathers and that the maternally expressed loci may be linked to the genes expressed in the offspring. The evolution of such a differentially expressed genetic covariation may be a consequence of the sex difference in parental responses. If so, no difference in the origin-related covariations among the maternal and paternal lines would be expected in species with similar responses to begging calls by the two parents (Ottosson *et al*. 1997; Price 1998; Wright 1998).

Genetic covariation between begging intensity and parental response may have a strong impact on the predicted outcome of parent–offspring conflict (West-Eberhard 1983; Harper 1986; Lynch 1987; Eshel & Feldman 1991; Cheverud & Moore 1994). In the case of positive covariation, as in the maternal line of great tits, a runaway process may result in more escalated begging and a stronger parental response than predicted from selection alone (Lynch 1987; West-Eberhard 1983; Cheverud & Moore 1994). Alternatively, both offspring begging call intensity and the maternal response may be genetically associated with quality which will lead to indirect coevolution via associated variation in genetic quality (Lyon *et al*. 1994; Queller 1994). However, we could not detect any significant origin-related association between measures of parental quality (e.g. parental age or condition, clutch size and egg mass) and the begging call intensity of nestlings.

An alternative to the purely genetic interpretation of our findings is an environmental/parental effect before the exchange of the newly hatched nestlings. While cross-fostering experiments separate the effects of the common environment and common origin during the chick-rearing period, environmental variation before the exchange of young may confound the estimate of a genetic component (Brinkhof *et al*. 1999). Candidates for correlates of such early environmental and parental effects are, for example, egg mass, clutch size, hatchling body mass and age or condition of the parents. However, none of these factors could explain the relationship between the maternal response and begging call intensity. Alternatively, hormones transferred from the mother to the yolk during egg formation (Schwabl 1993) could explain our results, provided that the allocation of maternal hormones to the eggs is related to the mother's subsequent response to vocal begging and that the hormones affect nestling begging not only shortly after hatching, but up to ten days of age (Schwabl 1996). Further research is required in order to disentangle genetic variation from environmental and parental effects unequivocally.

Asymmetries between the sexes in their reproductive roles (Clutton-Brock 1991; Hrdy 1999) and the sexual conflict over parental investment (Houston & Davies 1985; Mock & Parker 1997) may promote the differentiation of the parent–offspring signalling system among parental lines. Our study indicates, for the first time, that origin-related covariation and interactions between the maternal and paternal lines may affect the coevolution of nestling begging call intensity and the parental food provisioning response. Future models for the resolution of parent–offspring conflict should try to take these factors into account.

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