The evolution of multicomponent begging display in gull chicks: sibling competition and genetic variability

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The evolution of begging display may be influenced by gene–environment interaction, through the mechanisms that adjust begging behaviour to environmental conditions of offspring, including intensity of sibling competition within broods. We decomposed the complex begging display of yellow-legged gull, *Larus michahellis*, chicks into two different functional components: begging for food (pecks) and drawing the attention of parents (chatter calls). We examined these begging components in 2-day-old chicks that hatched and grew up in foster nests, by performing a begging test for each chick alone without the hindrance of its foster siblings. Male chicks and those with poorer body condition begged for food at higher rates than females and those with better body condition, respectively. Chicks from larger broods begged for food more frequently, but chicks from male-biased broods begged less frequently. If begging is costly, chicks may adjust their begging efforts to the intensity of sibling competition. Frequency of chatter calls varied with sex, chick order within broods and body condition: females, the third chicks and those with poorer condition produced chatter calls more frequently. Genetic origin had a significant effect on frequency of chatter calls but not on begging for food, while foster nest effect was null in both traits. Therefore, chatter calls (but not pecks) can be subject to evolution under directional selection. Different begging components may have evolved through different evolutionary pathways.

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In animals in which parents distribute food and care among more than one offspring, broodmates are potential competitors and attempt to skew parental allocation in their favour through begging displays (i.e. solicitation display for food and care). The evolution of begging behaviours has been modelled to explain evolutionary conflicts between family members (Trivers 1974; Kilner & Johnstone 1997). Empirical evidence often provides support for the honest-signalling models of begging (Godfray 1991) by showing that begging intensity reflects condition and cryptic need of offspring, that parents adjust their provisioning to offspring begging intensity and that begging is costly (reviewed in Godfray 1995; Kilner & Johnstone 1997). In theory, this cost should be solely imposed to prevent other competitors adopting the highest signal levels. However, scramble models also predict that parents provision offspring in relation to intensity of begging, which is costly. Begging may be honest only when the potential for intra-family conflicts is low and food is not limiting (Royle et al. 2002).

The scramble models for the evolution of begging explain that begging strategies are driven by escalated sibling competition within broods for parental provisioning and care (MacNair & Parker 1979; Harper 1986). These models predict that begging intensity and duration should increase under severe sibling competition (e.g. Neuenschwander et al. 2003). Therefore, begging behaviours may evolve through the mechanisms that adjust begging behaviour to environmental conditions of offspring (Dor & Lotem 2009), including intensity of sibling competition within broods.

Factors associated with intensity of sibling competition, which could influence begging behaviour of offspring, include number of competitors within the brood (Neuenschwander et al. 2003), brood hierarchy (Cotton et al. 1999) and possibly brood sex composition. In species in which male offspring grow faster than female offspring, male-biased brood sex composition can negatively influence growth and survival of male and female offspring owing to increased parental rearing costs (e.g. Nager et al. 2000; Müller et al. 2005; Kim & Monaghan 2006). However, effects of brood sex composition on behaviours of offspring in the contexts of familial communication remain unexplored, although previous studies suggested a sex difference in begging display in birds (Teather 1992; Saino et al. 2003; von Engelhardt et al. 2006; Müller et al. 2007). Optimal begging strategy is expected to depend on

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brood sex composition if male and female offspring adjust their begging strategy to the level of competition.

Evolutionary models of parent–offspring conflict resolution are based on the assumption that begging behaviours are genetically variable and therefore have the potential to (co)evolve. However, little is known about genetic variation in begging behaviours, particularly in natural systems (Kölliker et al. 2000; Kölliker & Richner 2001; Dor & Lotem 2009), while a number of empirical studies have tested for predictions of conflict resolution models of begging at the phenotypic level (e.g. Morales et al. 2009; Hinde et al. 2010; Noguera et al. 2010). To explore genetic variation of offspring behaviours and ultimately seek the probable evolutionary scenario, it is necessary to decompose the complex begging display. The individual elements of begging display may function collectively, and the multiple elements increase the information content of the display (Kilner 2002). For example, in a number of passerine species, nestlings display a range of begging postures accompanied by loud begging calls and jostle for position in the nest (Kilner 2002 and references therein). However, whether the individual elements have coevolved through selection pressure on the combined function of different behaviours or evolved individually through selection on discrete function is unknown.

In the present study, we explored whether the frequency of begging display is influenced by body condition, brood hierarchy (laying order) and brood sex composition in nestlings of the yellow-legged gull, *Larus michahellis*, using a cross-fostering design and begging test. Tinbergen & Perdeck (1950) described the begging display of gull chicks directed to the red patch on the parent's bill, and this became a model system for behavioural studies (Morales et al. 2009; ten Cate et al. 2009). In the study species, parents and young communicate intensively during the nestling period. Parents produce 'mew calls' to call their chicks for feeding when they return to the territories after foraging (Tinbergen 1953) or for other parental care after an antipredatory alert (personal observation). Nestlings display a series of begging calls and behaviours, which presumably function differently in parent–offspring communication. While nestlings produce 'chatter calls' to draw the attention of their parents for care, for instance immediately after 'mew calls' by their parents, they simultaneously produce 'pee calls' and peck the red patch of the parent's mandible to stimulate the parent to feed them (Noguera et al. 2010).

Study chicks were reared in experimental broods with foster siblings other than their original siblings, thus disrupting the natural covariance between primary sex ratio and parental quality. We explored key predictions of conflict resolution models of begging: (1) that more demanding chicks or those in poor condition should display more frequent begging and (2) that chicks that suffer severe sibling competition because of large brood size or male-biased brood sex composition should increase begging intensity if they adjust their behaviour to increased competition against rivals, respectively. We also examined whether intrinsic attributes of chicks, such as sex and laying order, affect the begging strategy. Additionally, our experimental design allowed us to disentangle genetic and environmental influences (i.e. effects of nest of origin and foster nest, respectively) on the phenotypic variations in components of begging display.

METHODS

General Field Procedures

We studied begging behaviour of gull chicks from May to June 2009 at a colony of yellow-legged gulls in the Parque Nacional das Illas Atlánticas, Sálvora Island, Galicia, Spain (42°28′N, 09°00′W). In the study species, incubation and parental care for chicks are shared by both parents and the semiprecocial young hatch asynchronously, with the third chick hatching normally 1–3 days after the other two (Hillström et al. 2000).

We studied 72 nests with a clutch of three eggs (modal clutch size; see Kim et al. 2010a, b for sampling details). To disentangle genetic and environmental variances of chicks in begging behaviours, all three eggs were swapped 1 day after clutch completion within a group of four nests, the minimum number that allows interchange of all the eggs without manipulating their laying order within the clutch. We selected four nests in which the second and third eggs were laid on the same days (at a 2-day interval) because gulls usually start incubation after laying the second egg. The laying date of the first eggs did not differ by more than 1 day between the four nests. This resulted in all three eggs from the same original nest being incubated, then the hatchlings being raised in three different foster nests other than the original nest, but conserving their original order within the clutch and brood (Kim et al. 2010a, b for details).

A total of 191 chicks hatched among the 72 study nests (one-chick brood: $N = 3$ nests; two-chick brood: $N = 19$ nests; three-chick brood: $N = 50$ nests). The overall hatching rate of eggs in the study nests was 88.4%, which is higher than that of noncross-fostered eggs in other colonies of the same species (e.g. 78%: Rubolini et al. 2005; 79.6%: Pérez et al. 2006). All hatchlings were marked with leg flags made with coloured Velcro for their identification and blood sampled for sexing on the day of hatching. The study was done with permission of the Parque Nacional das Illas Atlánticas and Xunta de Galicia, and all the field procedures we performed complied with the current laws of Spain.

Sex Identification of Chicks and Brood Sex Ratio

To identify the sex of the chicks, we collected a droplet of blood from the brachial vein of each chick on the day of hatching, using a sterile needle and a capillary tube. This was mixed with alcohol and stored at room temperature until molecular sexing at a laboratory (IREC-CSIC, Spain). Chick sex was identified from blood cell DNA by detecting two CHD genes (*CHD1W* and *CHD1Z*), using a pair of primers (2550F and 2718R; Fridolfsson & Ellegren 1999). The sex ratio of original and foster broods was calculated as the proportion of males in the brood (means ± SE sex ratio: original broods: 0.512 ± 0.034; foster broods: 0.516 ± 0.040, $N = 72$) to test whether brood sex ratio influences the begging display of individual chicks.

Begging Test and Parameters

We tested for frequency of begging behaviours in all chicks that survived until 2 days old ($N = 179$). Gull chicks' begging behaviours to stimulate parents to regurgitate food can be elicited by the presentation of dummies that simulate the head of a parent (Tinbergen & Perdeck 1950; Tinbergen 1953). We tested for intensity of begging components using the standard protocol from Tinbergen & Perdeck (1950) with minor modifications (see also Noguera et al. 2010 and supplementary videos therein). A begging test was performed for each chick individually (in the absence of sibling competition) in a hide placed outside the dense gull colony to avoid disturbance to the chick's performance by adult gulls' alarm calls. We transported 2-day-old chicks (hatching day = day 0) from their nests to the hide in textile bags. We first placed each chick on the ground and covered it with a cloth until it stayed calm and quiet. The chick received a playback of three mew calls, which were previously recorded at the same colony, to simulate a natural feeding event immediately before we removed the cloth and presented a dummy, mimicking an adult gull's head. The dummy was made of white plaster and the bill was painted yellow; a red spot

made of a sticker of a natural size and colour (the population mean) was added onto the lower mandible (see also Noguera et al. 2010 for details). The visual stimulation was performed by nodding the dummy head close to the chick 30 times during a minute. To standardize the visual stimulation across all study chicks, a researcher nodded the dummy head while listening to 30 mechanical sounds, recorded in an mp3 player, through an earphone. Another researcher recorded the number of pecks delivered to the red spot and begging calls of chicks during the test. We recorded two easily distinguishable begging calls, 'chatter' and 'pee' calls (Tinbergen & Perdeck 1950).

All chicks were weighed and measured immediately after the begging behaviour test (before we returned them to their nests) to estimate body condition, because handling stress before the test can influence behaviours of chicks. We weighed chicks to the nearest 0.01 g using electronic balances, and measured tarsus length to the nearest 0.01 mm using electronic callipers. All chicks were returned to their nests of origin after the begging test and measurement, usually within 1 h after having been collected. Each chick was protected from wind and strong sunlight by keeping it inside a textile bag and under thick vegetation while away from the nest (Kim & Monaghan 2005). No begging test was performed when it was raining.

Chatter calls were produced by chicks mostly during and immediately after the playback of mew calls, and they were not related to the other two begging elements (peck: $r = 0.126$, $P = 0.093$; pee call: $r = 0.013$, $P = 0.862$). However, most chicks displayed pecking and pee calls simultaneously during the visual stimulation with the dummy head, and these two elements were highly correlated ($r = 0.559$, $P < 0.001$). Therefore, we used only numbers of pecks and chatter calls for data analyses.

Body condition of each chick on the day of begging test (i.e. age 2 days) was calculated as the residual from a linear regression of body mass against tarsus length ($r = 0.691$, $P < 0.001$; see Schulte-Hostedde et al. 2005).

Statistical Analyses

We explored factors associated with number of pecks and number of chatter calls of gull chicks using standard generalized linear mixed-effect models (GLMMs) with a Poisson error distribution and a log link, including original and foster nests (nested within the cross-foster group) as random effects, to account for the nonindependence of chicks from the same original and foster broods. Sex and order (i.e. egg-laying order within clutch) of chicks were included in the models as factors because physiological status and maternal input, which influence personality and behaviour of chicks, often differ between the sexes and laying orders (Badyaev et al. 2006). Brood size calculated for each chick as total number of chicks hatched in the foster nest until the day of the begging test was also included as a fixed effect in the models. In six study nests, brood size of the first chicks was smaller than that of their foster siblings because the last chicks hatched 3−4 days later than the first chicks in these nests. Chicks without any broodmate on the day of the begging test were excluded in the analyses that examine the effects of brood sex ratio on begging behaviours of the focal chicks. When brood size without considering hatching date of foster siblings (i.e. the same brood size for foster siblings) was used as a fixed effect and chicks with no broodmate were included in the analyses, the results did not change (results are presented in the Appendix, Table A1). Initially a GLMM with all explanatory variables and two-way interactions of interest were fitted for numbers of pecks and chatter calls (full model: begging = sex + chick order + sex ratio of original brood + sex ratio of foster brood + brood size + chick condition + hatching date + egg volume + time + sex*sex ratio of original brood + sex*sex ratio of foster brood + sex*brood

size + order*sex ratio + order*brood size). Then nonsignificant interactions and main terms were dropped sequentially to simplify the model. This model simplification method proceeded until we obtained a minimum adequate GLMM that included only terms significant at the $P < 0.05$ level. The final models were confirmed using a forward procedure. Statistical significance of terms was assessed using type III tests (Littell et al. 1996). Analyses were carried out using PROC GLIMMIX in SAS (SAS Institute 1999).

We estimated genetic and environmental variations in begging components of gull chicks using a cross-fostering design and robust quantitative genetic analysis. Genetic and common environmental components (V_{Origin} and V_{Foster}) of total phenotypic variances (V_P) for the two begging components were estimated using restricted maximum likelihood (REML) univariate linear mixed-effect models, with original and foster nests (nested within the cross-foster group) fitted as random effects. Only essential fixed effects (i.e. sex, order and chick condition) were included in the quantitative genetic models to protect against bias in heritability estimates of begging behaviours and avoid overparameterizing (Wilson 2008). Genetic variances (V_G) were calculated as twice the variance component of the original nest (V_{Origin}) because full siblings share on average 50% of their genes (Lynch & Walsh 1998). Note that mechanisms of paternity assurance (Velando 2004) prevent extrapair paternity in gulls (Bukacinska et al. 1998; Gilbert et al. 1998). Common environmental variances (V_E) were equal to the foster nest component (V_{Foster}), and phenotypic (co)variances were calculated as the sum of the original nest, foster nest and residual variance components ($V_P = V_{Origin} + V_{Foster} + V_R$). Heritability ($H^2$, original nest effect) and common environmental effect (c^2, foster nest effect) were estimated as $H^2 = V_G/V_P$ and $c^2 = V_E/V_P$ for each trait.

The statistical significance of each variance component was assessed using likelihood ratio tests that compare models based on −2 times the difference in REML log-likelihood scores distributed as χ^2 where the degree of freedom equalled the number of variance terms removed. The significance of each variance component function (H^2 and c^2) was assessed using a t test. ASReml v3 (VSN International, Hemel Hempstead, U.K.; Gilmour et al. 2006) was used for quantitative genetic analyses. Prior to the quantitative genetic analyses, numbers of pecks and chatter calls were log transformed to make the distribution of the data and model error terms close to normal because generalized linear mixed-effect modelling is not recommended for the quantitative genetic analyses owing to estimation biases of variance components (Gilmour et al. 2006).

RESULTS

Effects of Growing Conditions on Begging Intensity

On average, a chick produced 6.8 pecks, 11.8 pee calls and 1.3 chatter calls during the begging test. Male chicks pecked more frequently than females (Table 1). Sex ratio of the foster brood, calculated as proportion of males in the brood, and brood size at hatching showed significant effects on number of pecks (Tables 1, A1, Figs 1, 2). Chicks from a larger brood and those from less male-biased broods pecked more frequently. Chicks with better body condition pecked less frequently (Table 1). Chick order (egg-laying order), hatching date, egg volume, time of day, sex ratio of original brood and two-way interactions of interest (see Table 1 legend) were nonsignificant ($P > 0.248$) for number of pecks.

Sex, chick order, body condition and time of day were significantly related to number of chatter calls (Table 1). Female chicks and the third chicks produced more chatter calls than males and the first and second chicks (Fig. 3). Body condition and time of day were negatively related to number of chatter calls. All other factors and interactions were nonsignificant ($P > 0.077$).

Table 1
Summary of minimum adequate generalized linear mixed-effect (GLMMs) with a Poisson error distribution and a log link for intensity of begging displays, number of pecks and number of chatter calls, at age 2 days in yellow-legged gull chicks

Terms	Estimate±SE	F	df	P
Number of pecks				
(Intercept)	0.386±0.610			
Sex				
Male	0.584±0.193	9.16	1, 170	0.003
Female	0			
Brood sex ratio	−1.020±0.297	11.75	1, 170	<0.001
Brood size	0.615±0.211	8.50	1, 170	0.004
Chick condition	−0.025±0.011	5.69	1, 170	0.018
Number of chatter calls				
(Intercept)	2.828±1.045			
Sex				
Male	−0.451±0.214	4.44	1, 145.4	0.037
Female	0			
Chick order				
First	−0.605±0.211	6.72	2, 113.3	0.002
Second	−0.757±0.227			
Third	0			
Chick condition	−0.034±0.016	4.85	1, 164.4	0.029
Time of day	−3.521±1.676	4.41	1, 154.5	0.037

$N = 175$ chicks. Full model: begging intensity = sex + chick order + sex ratio of original brood + sex ratio of foster brood + brood size + chick condition + hatching date + egg volume + time + sex*sex ratio of original brood + sex*sex ratio of foster brood + sex*brood size + order*sex ratio + order*brood size, random effects: original nest (group) + foster nest (group).

Quantitative Genetics of Begging Intensity

Both original and foster nest effects were very low or null for log-transformed number of pecks (Table 2) in the REML univariate model, which included sex and chick condition as fixed effects (see Table 1). Log-transformed number of chatter calls showed significant heritability, but the common environment shared by the foster broodmates did not influence the variation in frequency of chatter calls (Table 2) in the model, which included sex, chick order and body condition as fixed effects (see Table 1).

DISCUSSION

We decomposed the complex begging display of gull chicks into two different components, begging for food (pecks) and drawing the attention of parents (chat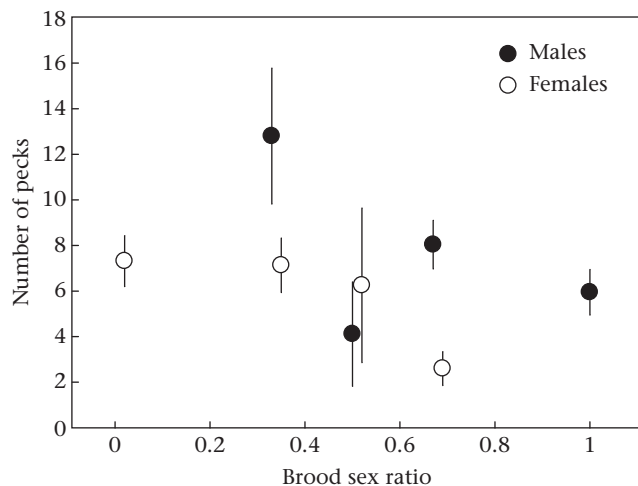ter calls), although they often function collectively (Noguera et al. 2010). The two begging components varied with respect to different intrinsic attributes of individual chicks and factors related to brood competition. Genetic origin had a significant effect on number of chatter calls ($H^2 = 0.33$), but not on number of pecks.

Our results on begging rate for food in relation to chick condition and sex may be consistent with Godfray's (1991) signalling model of begging, which predicts an increase in begging frequency with cryptic need of offspring, because male chicks and hungrier chicks possibly need more food. However, our study cannot test whether the evolutionary process that has driven the observed patterns is scramble competition or honest signalling. These results agree with a previous experimental study, showing that begging for food increased in gull chicks whose diet was experimentally restricted (Noguera et al. 2010). Increased food solicitation behaviours in hungrier chicks with poorer body condition have also been shown in other empirical studies (e.g. Cotton et al. 1996; Leonard & Horn 1998). In the present study, sexual differences in begging behaviour appeared before sexual dimorphism in body mass and skeletal size occurred (linear mixed-effect models for sexual difference in 2-day-old chicks, $N = 179$: body mass: $P = 0.838$;

Figure 2. Number of pecks per individual in yellow-legged gull chicks (means ± SE) according to brood size.

Figure 1. Number of pecks per individual in male and female yellow-legged gull chicks (means ± SE) according to sex ratio of foster brood (proportion of males).
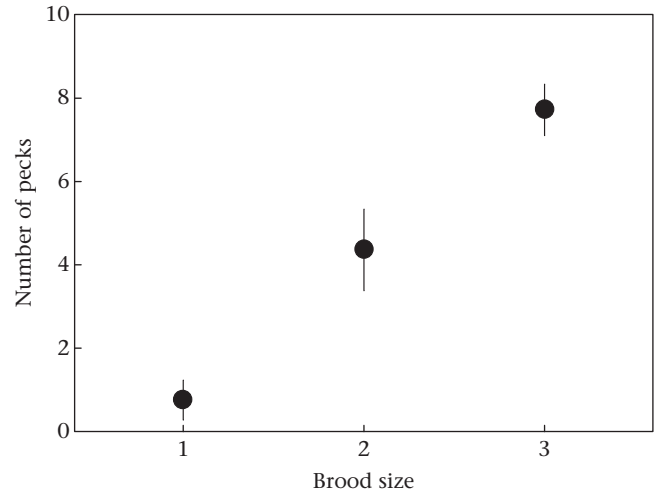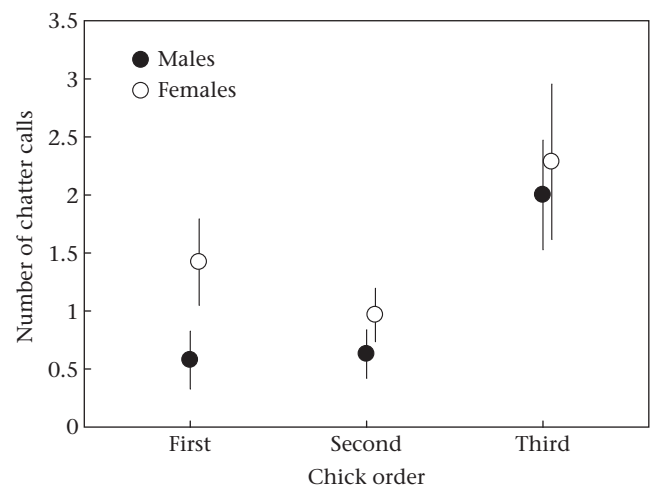

Figure 3. Number of chatter calls per individual (means ± SE) according to the chick sex and order (egg-laying order).

Table 2
Quantitative genetics for log-transformed numbers of pecks and chatter calls

	Pecks		Chatter calls	
	Estimate±SE	P	Estimate±SE	P
V_{Origin} ($\times 10^{-2}$)	0.142±1.785	0.469	1.488±0.859	0.046
V_{Foster} ($\times 10^{-2}$)	0	1	0	1
V_{P} ($\times 10^{-2}$)	20.694±2.200		9.026±0.988	
H^2	0.014±0.173	0.469	0.330±0.180	0.034
c^2	0	1	0	1

$N = 179$ chicks. Results from REML univariate linear mixed-effect models.

tarsus: $P = 0.539$). The sex difference in food solicitation behaviour during the very early nestling period when the two sexes do not yet differ in mass and size is rare evidence showing how an intrinsic attribute related to offspring need for resources influences begging. In birds with sexual size dimorphism, male chicks require more food than females to grow faster and bigger during the nestling period (Clutton-Brock 1991; Griffiths 1992) and the food demand is likely to be different between the two sexes before the actual differences in body mass and size appear. Therefore, male chicks may display more frequent food solicitation behaviours because they are needier than female chicks.

We found that food solicitation behaviours increased with brood size, suggesting that increased sibling competition resulted in escalated begging scramble, as also shown in other empirical studies (e.g. Leonard et al. 2000; Neuenschwander et al. 2003). The scramble-type models of begging predict that offspring should enhance begging to adjust their behaviour to increased competition for parental provisioning against more demanding competitors (MacNair & Parker 1979; Harper 1986). In the yellow-legged gull, male broodmates are potentially more demanding competitors and they begged for food more frequently. Therefore, it is puzzling that male and female chicks from male-biased broods, which presumably suffer more severe sibling competition against demanding broodmates than those from female-biased broods, displayed less frequent food solicitation behaviours. It may be that chicks under severe sibling competition decrease begging rate because they refrain from begging ('sibling negotiation hypothesis': Roulin et al. 2000) or because they try to reduce the costs of begging display (Mathevon & Charrier 2004). Intensive begging of gull chicks incurs oxidative costs (Noguera et al. 2010), although it is unknown whether their begging incurs costs in energy expenditure and predation risk. Costs of begging generally function to limit chick behaviour (Godfray 1991), thereby paving the way for stable resolution of intrafamily conflicts (Kilner 2001). When competition is severe because of demanding and outcompeting broodmates, chicks may reduce costs of begging to compensate for the disadvantages in parental provisioning. The begging strategy of chicks was tested in our study when their broodmates were absent (our begging test), but after experiencing natural sibling competition for 2 days in the foster nest. Overall, these results highlight that begging for food in gull chicks is a plastic response influenced by their early experience.

Number of chatter calls decreased with body condition, similarly to number of pecks. However, female chicks showed more frequent chatter calls than males, which demand more food to grow faster. Number of chatter calls also varied with respect to chick position within broods, which is often related to differential hatching size and maternal effect. In large gull species, the third chicks are generally smaller than the first and second chicks at hatching, but receive higher levels of maternal androgens (Royle et al. 2001; Eising & Groothuis 2003). Maternal androgens deposited in eggs affect offspring behaviour by enhancing begging intensity and prolonging begging duration (Schwabl 1996; Eising & Groothuis

2003; von Engelhardt et al. 2006). Therefore, the within-brood variation in number of chatter calls may be caused by differential yolk deposition of maternal hormones. The third chicks and female chicks presumably have disadvantages in scramble competition for parental provisioning against their elder (and bigger) siblings and more demanding broodmates. However, increased chatter calls may help them to draw the attention of their parents returning from foraging trips, although chatter calls have oxidative costs (Noguera et al. 2010) and the third chicks have the lowest amount of antioxidants (Rubolini et al. 2006).

One may think that the multicomponent begging behaviour has (co)evolved to function optimally to the extent that the cost of begging does not exceed the gain of chicks (Kilner 2002). Our results probably support this idea by showing that phenotypic patterns of begging components vary with respect to intrinsic attributes of chicks and intensity of sibling competition in gull chicks. However, it is necessary to examine sources of phenotypic variation in begging components (Kölliker & Richner 2001; Smiseth et al. 2008) to infer how they have evolved and predict their evolutionary potentials. In the present study, the frequency of chatter calls depended on their origin, suggesting genetic variation for this begging component (see also Kölliker et al. 2000), although our estimate of genetic variation may partly include maternal effects, which could not be teased apart by our cross-fostering design (Dor & Lotem 2009). Whereas chatter calls can be subject to evolution under directional selection, the other begging component, pecks, showed nonsignificant genetic variance. One possible explanation for this is that if parent–offspring conflict underlying parental provisioning and food solicitation behaviour of offspring is resolved and the population is at evolutionary equilibrium, these parental and offspring behaviours may not be genetically variable (Dor & Lotem 2009). This food solicitation behaviour of gull chicks could have evolved to the present form under strong selection pressure. However, low genetic variability will not allow further evolutionary change in frequency of pecks.

Our findings on phenotypic patterns and quantitative genetics of multicomponent begging behaviour together provide an insight into the evolution of complex begging behaviour. Different begging components may have evolved through different evolutionary pathways, but collectively function to draw the attention of parents and beg for food. Most importantly, chicks adjust their costly begging efforts to the intensity of sibling competition.

Acknowledgments

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APPENDIX

Table A1
Summary of minimum adequate GLMMs with a Poisson error distribution and a log link for number of pecks ($N = 179$) when brood size calculated as total number of chicks hatched in the foster nest (without considering hatching date of foster siblings) was included as a fixed effect and chicks with no broodmate were included in the analyses

Terms	Estimate±SE	F	df	P
(Intercept)	0.254±0.611			
Sex				
Male	0.596±0.192	9.68	1, 174	0.002
Female	0			
Brood sex ratio	−1.028±0.296	12.03	1, 174	<0.001
Brood size	0.654±0.209	9.82	1, 174	0.002
Chick condition	−0.025±0.011	5.58	1, 174	0.019