



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 \pm 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

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