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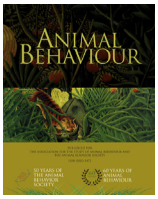

Begging response of gull chicks to the red spot on the parental bill

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In some animals, offspring begging is elicited by parents through behavioural or morphological signals. The red spot on the lower mandible in adult gulls is one of the best-known examples of a signal triggering chick begging. We examined whether the begging response of chicks (pecking for food and the chatter call for drawing parental attention) was affected by the spot size within the natural range of variation on a dummy head. Using a cross-fostering experiment, we examined whether these responses covary with the size of the genetic or social parent's spot. We found that the natural variation in size of this parental signal strongly influenced intensity of chick begging. Pecking increased when chicks were stimulated by a larger red spot. Additionally, pecking intensity increased in chicks reared by mothers with a large red spot, suggesting that this begging component is influenced by previous experience. In contrast, chick hatching order affected the number of chatter calls produced in relation to the size of the red spot on the dummy, suggesting the presence of different begging strategies according to brood hierarchy. The differential call response to a small/large red spot on the dummy was positively correlated with the original mothers' red spot size and negatively with that of the original fathers. These results suggest a genetic correlation between biased chick response for a large spot and parental signal in contrasting patterns for mothers and fathers. Our results suggest that the parental red spot and offspring begging are traits subject to coevolution.

In species with parental care, conflicts of interest are expected over the amount of parental investment that family members receive because they are not equally related to one another (Hamilton 1964; Trivers 1985). Communication between parents and offspring is one possible outcome to have evolved for the resolution of these conflicts (Godfray 1991). Empirical research has mainly focused on how offspring traits influence parental behaviour (see Royle et al. 2002). Thus, for example, extravagant behaviours performed by offspring to solicit food and care from their parents are thought to be an outcome of parent–offspring conflict (Trivers 1974; Kilner & Johnstone 1997; Royle et al. 2002; Kilner & Hinde 2012). Additionally, other studies have examined how offspring traits that represent their quality, such as coloration or chemical stimuli, affect parental provisioning (e.g. Lyon et al. 1994; Mas et al. 2009). Although often neglected, parental traits may also influence offspring behaviour in many different taxa. In the burying beetle *Nicrophorus vespilloides*, parental chemical cues act as stimuli for larval begging (Smiseth et al. 2010). In some bird species, parental calls also trigger nestling begging (e.g. Madden et al. 2005).

The red spot on the lower mandible of adults in large gull species is probably the earliest example ever studied of parental signals influencing offspring behaviour. In 1947, Niko Tinbergen studied whether the red patch in both sexes of the herring gull, *Larus argentatus*, induces begging behaviour of gull chicks (Tinbergen 1948) based on previous observations that naïve gull chicks have a strong tendency to peck red objects (Heinroth & Heinroth 1928; Goethe 1937). From detailed observations and experiments, he showed that the red spot stimulates hatchlings to peck at the parents' bills (Tinbergen 1948; Tinbergen & Perdeck 1950; see also ten Cate 2009 for a detailed review of Tinbergen's work), and this begging behaviour induces the parent to regurgitate food (Weidmann 1956; Beer 1966). These studies, as recently confirmed (see ten Cate et al. 2009), have become a model of an 'innate releasing mechanism' (i.e. fixed patterns of action released by an external stimulus) in the analysis of instinctive behaviour. Nevertheless, nothing is known about whether natural variation in the red spot affects this mechanism.

The red spot size in adult gulls is highly variable among individuals; this variability is related to carotenoid deposition (Blount et al. 2002; Pérez et al. 2008) and mirrors the bearer's condition and health (Kristiansen et al. 2006; Pérez et al. 2008, 2010a, b). It is known that parents adjust their chick provisioning effort according to their partner's red spot size (Morales et al.

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2009). Therefore, this signal may play a role in communication between all family members by providing a network environment for signallers and receivers (Horn & Leonard 2005). It is necessary to determine whether the natural variability of this coloured signal also influences chick begging, and hence parent–offspring conflict, to confirm a unique case of a signal that plays a simultaneous role in different conflicts among family members over care.

The evolution of parental traits and the evolution of offspring begging are not independent from each other (Cheverud & Moore 1994) because both simultaneously influence the social environment in which both phenotypes are expressed (i.e. indirect genetic effects, Wolf et al. 1998). Therefore, genetic covariation between the parental and offspring traits may be expected. Additionally, offspring begging signals can be manipulated by mothers (e.g. by adding hormones to the egg) to match parental conditions that offspring will encounter (e.g. Hinde et al. 2009, 2010), thereby producing covariation between parental trait and offspring begging. Both indirect genetic and maternal effects may produce coadaptation of traits expressed by parents and offspring (Moore et al. 1997; Wolf et al. 1998; Kölliker et al. 2005). In gulls, parents respond to offspring demand (Morales et al. 2009); thus coadaptation of the parental red spot and offspring begging may occur if the red spot influences offspring solicitation within the range over which parents are sensitive.

In the present study, we explored whether the frequency of the begging display is influenced by the size (within the natural range of variation) of the parent's red spot in chicks of the yellow-legged gull, *Larus michahellis*. This study species nests on the ground, where parents and the semialtricial young communicate intensively during the nestling period. Chicks display a series of begging calls and behaviours, which presumably have different functions in parent–offspring communication (Impekoven 1971; Noguera et al. 2010; Kim et al. 2011). First, chicks produce 'chatter calls' from a distance to attract the parents' attention, for example immediately after the parents return to the territory (Impekoven 1971; Beer 1979). The chatter call, which is characterized by rapidly repeated sound elements with a wide frequency range, is a costly signal that probably induces oxidative stress (Noguera et al. 2010). Fathers, more than mothers, feed their offspring in response to chatter calls (J. C. Noguera, S.-Y. Kim & A. Velando, unpublished data). Parents approach chicks with their head down, then the chicks, in a hunched posture, peck at the red spot on the parent's bill (Impekoven 1971). Pecking seems to stimulate parental provisioning, since the number of pecks and feeding rates of both parents are highly correlated (Morales et al. 2009; J. C. Noguera, S.-Y. Kim & A. Velando, unpublished data). We first examined the effect of the size of the red spot on these complex begging components by performing two sequential begging tests with small and large spots and 1-day-old chicks, an age at which the red spot is especially important for triggering offspring behaviour (Tinbergen & Perdeck 1950). We predicted more intense begging when chicks were stimulated with a larger red spot.

In our study, chicks were reared in foster nests, thus disrupting the natural covariance between begging response to parental signal and parental traits. Thus, we also studied the relationship between the red spot size of the original and foster parents and the chicks' response to red spots of different sizes. During the first few days of life, gull chicks are intensively brooded by their parents. If experience with foster parents during the first day of life influences the chicks' begging response to red spot size, a relationship between chick response and spot size of foster parents is predicted (see Hailman 1967; ten Cate et al. 2009). In contrast, a relationship between begging response to red spot size and the spot size of the original parents is predicted if there is either a genetic correlation between chick begging biases and parental signals (e.g. by conflict and coadaptation; Smiseth et al. 2008; Kilner & Hinde 2012; Kölliker et al. 2012) or prehatching maternal influences on begging behaviours (e.g. coadaptation by maternal effects, Hinde et al. 2009, 2010).

METHODS

General Field Procedures

This study was carried out from April to June 2011 at a large colony of yellow-legged gulls in the Parque Nacional das Illas Atlánticas, Sálvora Island, Galicia, Spain (42°28′N, 09°00′W). Yellow-legged gulls are socially monogamous colonial breeders that defend a small breeding territory (Alonso-Alvarez & Velando 2001). Clutches typically contain three eggs (modal clutch size) and eggs are laid at intervals of 1–3 days (Kim et al. 2011). In large gull species, the first two chicks hatch with little difference in time but third chicks hatch later and have a disadvantage in competition with their broodmates (Kim & Monaghan 2006). During egg laying, we selected 21 nests with a clutch of two or three eggs. We captured 26 adults from these nests with nest traps (R60 special tilting cage; www.moudry.cz). A nest trap was placed over each nest for less than 20 min, avoiding the midday hours to reduce heat stress, and a maximum of three attempts per nest were made on nonconsecutive days. Thus, in 16 nests we captured only one adult per nest, and in the rest (five nests) we captured both incubating parents. No nest was abandoned by birds in the days following capture attempts. Birds were weighed (±10 g) and head length, bill depth, wing length and tarsus length were measured (±0.05 mm). Birds were sexed (17 females and nine males) by a discriminant function including these morphometric variables (Bosch 1996), known to be 100% consistent with sex determined by copulatory behaviour (Alonso-Alvarez & Velando 2003). We photographed the whole bill of each bird (Nikon Coolpix 5200) against a white standard together with a red standard and a millimetre scale in a dark box with controlled light, keeping a constant distance (15 cm) from the lens to the bill (see Pérez et al. 2008). The sharply defined red spot area visible in photographs (in mm^2) was measured by the same person (J.C.N.) with image analysis software (Adobe Photoshop CS3). The measures of six randomly selected photographs in triplicate indicated that this method was highly repeatable ($r = 0.98$, $F_{5,12} = 161.01$, $P < 0.001$).

To tease apart genetic or maternal and early environmental effects on begging behaviours, we swapped all clutches close to hatching, when at least one egg showed a crack in the shell (expected to hatch 3 days later). The whole clutches were interchanged between two or three nests of similar clutch size and stage. To identify hatching order, we marked the tip of the chick's bill through the egg hole made by the fully developed chick and hatchlings using leg flags made with coloured Velcro. On the day of hatching, chicks were weighed (±1 g) and, to identify the sex of the chicks, we collected a droplet of blood from the brachial vein of each chick using a sterile needle and a capillary tube. Chick sex was identified from blood cell DNA by detecting two CHD genes (CHD1W and CHD1Z; Fridolfsson & Ellegren 1999). The study was done with permission of the Parque Nacional das Illas Atlánticas (permit number 161/2011) and Xunta de Galicia (permit number 57/2011), and all the field procedures that we performed complied with the current laws of Spain.

Begging Test

We tested for frequency of begging behaviours in all hatchlings that survived until 1 day old ($N = 41$ chicks from 18 broods). In