



Maternal testosterone influences a begging component that makes fathers work harder in chick provisioning



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ABSTRACT

In species with biparental care, parents disagree evolutionarily over the amount of care that each of them is willing to provide to offspring. It has recently been hypothesised that females may try to manipulate their mates by modifying offspring begging behaviour through yolk hormone deposition, shifting the division of labour in their own favour. To test this hypothesis we first investigated how yellow-legged gull (*Larus michaellis*) parents feed offspring in relation to each component of complex begging behaviour and if feeding behaviour varies between sexes. Then we investigated the effect of yolk testosterone on chicks' begging by experimentally increasing yolk testosterone levels. Our results revealed that yolk testosterone has a component-specific effect on chicks' begging, specifically increasing the number of chatter calls. Parental feeding effort was influenced by the number of chatter calls emitted by chicks, but most importantly, the influence was stronger in male than in female parents. Moreover, chick body mass increased with the number of paternal feeds. In conclusion, these results show that female gulls may use yolk testosterone deposition to exploit their partners as predicted by the 'Manipulating Androgen Hypothesis (MAH)'.

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Introduction

A family is a small society in which family members have shared but not identical interests (Lessells, 1999; Trivers, 1974). These evolutionary conflicts of interest are of special importance in the evolution of parental care (Parker et al., 2002). For instance, a conflict between parents occurs because both benefit from care provided by either of the parents but the cost for each parent depends only on its own effort (sexual conflict; Lessells, 1999). Thus, each parent has increased fitness if the other gives more care. How these conflicts of interest among family members are resolved is a current issue in evolutionary biology (Royle et al., 2012).

In a number of bird species, allocation of maternal hormones to egg yolks varies within and between clutches (review in Gil, 2008; Groothuis et al., 2005; Smiseth et al., 2011). This variation may be a strategy mediating adaptive transgenerational phenotypic plasticity (Groothuis et al., 2005; Mousseau and Fox, 1998) in which molecular (neuroendocrine) signals promote programmed responses in physiology and behaviour that favour the young during development (Alonso-Alvarez and Velando, 2012; Lessells, 2008). However, it has recently been hypothesised that such hormonal variation may also be a female strategy to manipulate the male's contribution to parental

care ('Manipulating Androgens Hypothesis; MAH': Groothuis et al., 2005; Lessells, 2006; Moreno-Rueda, 2007; Müller et al., 2007). This hypothesis is based on the effects that yolk hormones exert on offspring signals (i.e. begging behaviour; reviewed in Smiseth et al., 2011) that are used by the partner to adjust their level of parental care (Kilner and Johnstone, 1997 and references therein). A key assumption and prediction of this hypothesis is that maternal hormones increase offspring begging and that the male parent responds to offspring begging affected by maternally-derived hormones (Moreno-Rueda, 2007). Although this hypothesis seems theoretically plausible, yet there is no empirical evidence supporting this hypothesis (but see Barnett et al., 2011; Laaksonen et al., 2011; Ruuskanen et al., 2009; Tschirren and Richner, 2008 for similar experiments).

The yellow-legged gull (*Larus michaellis*) is a suitable model to study the effects of maternal hormones on complex begging displays and the assumptions and predictions of the MAH. In this species, parental care is provided by both parents over a long period (more than three months), so there is potentially severe sexual conflict over parental care. Nestlings perform complex begging displays involving calls (chatter calls) and pecking at the parents' bills. Although chatter calls and pecks may function collectively, the two begging components not only appear to have evolved through different evolutionary-pathways but also encode different information during parent-offspring communication (Kim et al., 2011; Noguera et al., 2010). Importantly, maternal hormones may differentially affect different components involved in complex begging displays (Smiseth et al., 2011 and references therein). Moreover, analyses of within-clutch variation of yolk testosterone have revealed that in

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the yellow-legged gull and other closely related gull species mothers may allocate a higher level of testosterone to the third egg (Royle et al., 2001; Rubolini et al., 2011), the chicks from which also appear to show a higher rate of chatter calls after hatching (Kim et al., 2011).

Another important aspect of this species is that both sexes have a conspicuous carotenoid-based sexual signal during adulthood, the red-spot on the lower mandible. This trait depends on carotenoid deposition and reliably reflects the bearer's antioxidant status, body condition and health (Pérez et al., 2008, 2010, 2012). Furthermore, the red spot in gulls has been a classic model in the study of signalling between parents and young because it elicits begging responses in hatchlings (i.e. Tinbergen and Perdeck, 1950; Velando et al., 2013). A recent study indicates that this trait is used by both sexes to adjust their level of parental care during the chick rearing period (Morales et al., 2009). Thus, all members in a gull family use this signal to adjust their behavioural strategies during conflict.

It has been suggested that carotenoid-based signals, such as the red spot on the lower mandible of the yellow-legged gull, may mirror the provisioning ability of the signalers (Endler, 1980; Hill, 1991; McGraw et al., 2003; Velando et al., 2005). In this case, it would be advantageous for both parents and offspring to utilize this information in their own favour. For instance, gull mothers and offspring would benefit if yolk testosterone particularly promotes begging behaviour toward better caregivers. Although several studies have shown that females allocated more testosterone to eggs when mated with more attractive or colourful males (Gil, 2003; Groothuis et al., 2005 and reference therein), how maternal testosterone and sexual signals may interact and affect offspring begging behaviour and fitness-related traits is unknown.

In the present study, we first observed whether parents adjust food provisioning according to the begging behaviour of their offspring. Then we performed an experiment to investigate whether maternal testosterone and the sexual signals exhibited by parents influence the intensity of complex begging displays. We experimentally manipulated the testosterone level in the last laid egg of three-egg clutches and also the size of the red spot on a dummy head used to elicit begging responses in the gull chicks. If females can manipulate male contribution to parental care through testosterone deposition into the eggs, we expect that, (1) chicks hatched from testosterone-treated eggs will perform more intense begging behaviour and (2) in our observational study, males but not females will increase their feeding effort according to chick's begging. Additionally, if sexual signals displayed by adult parents encode reliable information about their provisioning capacity, we expect an interactive effect of yolk testosterone and red spot size on begging intensity.

Materials and methods

All field procedures used in this study were performed with permission by the Xunta de Galicia, permit numbers 2008/190 and 2009/232.

Field procedures

The study was conducted during the breeding season of 2008 and 2009 in a large yellow-legged gull colony at Sálvora Island (Parque Nacional das illas Atlánticas de Galicia, NW Spain). Yellow-legged gulls generally lay clutches of three eggs at one to three day intervals (modal clutch size; 85% of breeding pairs lay a clutch of three eggs in the study population; our unpublished data), and incubation and parental care of the chicks are shared by both parents. They are socially monogamous colonial breeders that defend a small breeding territory (Alonso-Alvarez and Velando, 2001) where chicks are fed. The semi-precocial young hatch asynchronously, with the third chick hatching normally one to three days after the other two chicks (Hillström et al., 2000).

Observational study of begging behaviour and parental feeding

In May–June 2008, we conducted an observational study to see how parents respond to chick begging. We searched for nests with three eggs close to hatching, which is usually detectable by a small hole in the shell. We captured one adult per nest with nest traps (TRB60-tent string trap; www.moundry.cz). Captured birds were marked with a numbered coloured PVC ring and a black spot on the neck to facilitate identification from distance. All captured birds ($n = 14$) were sexed by means of the following discriminant function (Bosch, 1996): $D = 1.430 * HL + 5.135 * BD + 0.114 * W + 0.262 * T - 366.988$, where 'HL' is head length, 'BD' is bill depth, 'W' wing length and 'T' is tarsus length. By using this function, values under zero correspond to females and over zero to males. Sexes determined by using this function are known to be 100% consistent with sex determined by copulatory behaviour (Alonso-Alvarez and Velando, 2003). On the day of hatching, all chicks within a clutch were individually marked with a small coloured spot on the head (black, blue or green) and leg flags made with Velcro strip. Different colour marks did not influence feeding by either parental sex (generalized linear mixed model; sex: $F_{1,35} = 0.68$, $p = 0.42$; chick's colour: $F_{2,36} = 1.82$, $p = 0.18$; sex \times chick's colour: $F_{2,33} = 0.43$, $p = 0.65$). Two days after the first chick hatched, we continuously observed each pair from 09.00 to 13.00 h. Each observer simultaneously recorded the behaviour of two to three focal pairs from a hide that had been put in place the previous day. During the 4 h of observation, we recorded the number of chatter calls and pecks to the parents' bill performed by each individual chick and the number of regurgitates that each chick received from each parent (male and female). During the first days after hatching parents often feed the chicks one by one and therefore, sibling competition for regurgitates among siblings rarely occurs. All chicks were weighed immediately before and after the observation period.

Testosterone experiment

From May to June 2009, we performed an experiment where testosterone levels were increased in the last laid eggs and the begging behaviour of chicks measured after hatching. We visited each nest in the study area daily during the egg laying period until clutch completion to mark eggs and register laying dates. The third eggs from 92 three-egg clutches were randomly assigned to either the testosterone or control treatment. Only the third eggs were used for the experiment because we expected that female manipulation would have stronger effects on the third chicks due to their initial disadvantages in sibling competition (Kim et al., 2011).

Eggs were collected from the nest and weighed (± 0.01 g) on the day of laying and immediately transported to a hide located outside the colony (within 10 min walking distance from all the study areas). Egg mass and laying date did not differ between experimental treatments (General Linear Model, GLM; egg mass: $F_{1,90} = 0.348$, $p = 0.56$; laying date: $F_{1,90} = 0.239$, $p = 0.63$). The eggshell over the acute pole of the egg was carefully cleaned, sterilized with ethanol and the egg left in a vertical position (acute pole upward) for 30 min until the egg yolk stabilized. A hole was then drilled close to the acute pole with a sterilized needle of the same diameter as the needle used for injection. In the testosterone-injected group (T), the egg yolk was injected with 261 ng of testosterone (Sigma, Germany) dissolved in 20 μ l of sterile sesame oil, using a 100 μ l Hamilton syringe mounting 23-gauge needle (51 mm-long). The same amount of testosterone was previously used in other studies on the same species (Boncoraglio et al., 2006; Rubolini et al., 2006), which reported an increase of the total content of the hormone equal (12.6 ng/g yolk \pm 5.44 SD in 38 freshly laid eggs) to two standard deviations of the population mean (see details in Rubolini et al., 2006). Control eggs (C) were injected with 20 μ l of sterile sesame oil using the same procedure as for T eggs. The hole in the shell was sealed with a patch of previously-sterilized hen eggshell. The patch was glued with a very small

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