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The hormonal control of begging and early aggressive behavior: Experiments in black-headed gull chicks

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Abstract

The hormonal control of begging and sibling competition is largely unknown, but recent evidence suggests a role for steroid hormones. We tested the influence of the aromatizable androgen testosterone (T), the non-aromatizable androgen 5α-dihydrotestosterone (DHT), and 17β-estradiol (E) on both begging behavior and aggressive behavior in black-headed gull chicks (*Larus ridibundus*). Chicks of this species have a conspicuous begging display, while their frequently performed early aggressive behavior is facilitated by testosterone and important for territorial defense. Hormone treatment was applied by implants between days 6 and 16 after hatching. Behavior was tested by means of standard stimulus tests. The results were validated in a second experiment under semi-natural conditions. Begging was suppressed by T and DHT and not affected by E. Aggressive Pecking was strongly facilitated by T. The erect threat posture, characteristic for older chicks, was facilitated by T, DHT, and E and the nest-oriented threat display, typical for young chicks, only by T and DHT. Growth was suppressed in the T group. The results indicate that androgen production, needed for territorial defense, has costs in terms of a suppression of begging and growth. It is discussed to what extent older chicks may avoid these costs by converting testosterone to estrogen and why pre-natal and post-natal exposure to androgens differ in their effect on begging behavior.

Keywords: Testosterone; Androgens; Estrogen; Begging; Development; Aggression; Sibling competition

Introduction

Much is known about the role of gonadal steroids on the organization and activation of adult social behavior. However, despite the fact that early social behavior can be of great importance for survival (Mock and Parker, 1997), not much is known about the influence of gonadal hormones on social behavior early in ontogeny. In avian species, early treatment with testosterone can induce precocial social display and copulatory behavior (for a review, see Groothuis, 1993), but the function of gonadal hormones in the regulation of social behavior of young birds under natural condition is still largely unexplored. Recently, the hormonal basis of sibling competition has attracted some attention, but the data do not yet show a coherent picture. In white storks (*Ciconia ciconia*), first hatched chicks are more aggressive, receive more food, and have higher plasma levels of testosterone than their siblings. The number of younger siblings that die is higher when the difference in testosterone levels between first and later hatched chicks is greater (Sasvári et al., 1999). Although the data are not based on experimental evidence, they suggest a role for testosterone in sibling competition and/or begging behavior. In the blue-footed booby (*Sula nebouxii*), a facultative siblicidal species, dominant chicks did not show higher testosterone levels than subdominant chicks (Nuñez-de la Mora et al., 1996; Ramos-Fernandez et al., 2000). However, in the closely related Nazca booby (*Sula granti*), plasma levels of testosterone, but not those of DHEA and cortisol, were elevated immediately after actual fights between siblings

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(Ferree et al., 2004). Finally, Groothuis and Meeuwissen (1992) reported that testosterone treatment of black-headed gull chicks (*Larus ridibundus*) strongly facilitated territorial defense but inhibited the begging display. Although they did not quantify the latter, it is to our knowledge the only published experimental study on the influence of post-natal exposure to androgens on a begging display in a bird species.

The possible suppressing effect of testosterone on begging behavior is, however, not supported by two other studies. Androgen injections into the yolk of eggs before incubation induced a higher frequency of begging behavior after hatching, not only in chicks of the canary (*Serinus canaria*, Schwabl, 1993), but also in the black-headed gull (Eising and Groothuis, 2003). This contradiction suggests that pre-hatching and post-hatching treatment with testosterone have different effects on begging behavior.

A suppressive effect of post-natal testosterone exposure on begging behavior would make the case of the black-headed gull chick especially interesting. These chicks frequently perform both conspicuous begging displays and aggressive behavior, including threat displays. In this colonial breeding species, chicks defend small territories around the nest and young chicks produce testosterone contingent on the level of aggressive challenges (Ros et al., 2002). Furthermore, within individuals, these testosterone levels correlate with the frequency of aggressive behaviors, while testosterone treatment strongly facilitates aggressive behavior (Groothuis and Meeuwissen, 1992; Ros et al., 2002). Together, the available information suggests that the gull chicks face the problem that androgens, required for territorial defense, at the same time inhibit begging behavior, which is needed for obtaining food from the parents. In that case, the suppression of begging is a possible cost of producing testosterone that is needed for territorial defense, in addition to other costs of the hormone such as reduced growth (Ros, 1999), the development of a less cryptic plumage (Ros, 1999), and malformation of the syrinx (Groothuis and Meeuwissen, 1992). To reduce these costs, territorial behavior becomes increasingly sensitive to relatively low levels of androgens in the course of the first 4 weeks after hatching (Groothuis and Meeuwissen, 1992; Ros et al., 2002). One mechanism underlying this increase in sensitivity and avoiding the costs of testosterone exposure might be to increase aromatase activity that converts testosterone into estrogen. This hormone has been shown to facilitate aggressive behavior in many species, including adult laughing gulls (*Larus atricilla*), a closely related species of the black-headed gull (Terkel et al., 1976), while it might not influence the syrinx or suppress growth and the frequency of begging behavior.

In order to test the hormonal background of both begging and aggressive behavior, we implanted chicks of the black-headed gull with testosterone, estrogen, or 5α-dihydrotestosterone, a non-aromatizable androgen. Controls received sham surgery. The effect of treatment on begging, aggressive behavior, and growth was assessed in standard tests in hand-reared birds (experiment 1). In addition, the effect of testosterone and estrogen on begging and aggressive behavior was validated under semi-natural conditions (experiment 2, in a breeding colony housed in a large aviary). Based on the available literature of black-headed gulls, we expected that the androgens would suppress begging behavior and growth and stimulate aggressive behavior. In addition, we tested whether estrogen would stimulate aggressive behavior typical for older chicks while it would, in contrast to the androgens, not suppress begging behavior and growth.

Materials and methods

Experiment 1: hormonal specificity of social behaviors in standard tests

Rearing conditions

Black-headed gull chicks of 2–3 days of age were collected in June from a large gull colony in the north of The Netherlands and hand reared at the laboratory where they were housed in groups of three or four peers. Groups were held in adjacent cages measuring 85 × 75 × 85 cm and could not see each other. The floors of the cages were covered with straw. Each cage contained a thermal lamp providing constant dimmed light and a temperature of approximately 37°C in the middle of the cage. Additional tube lighting had a 16L:8D schedule. The chicks were individually marked (on the head or back) with rhodamine or picrine (ICN Biochemicals, Cleveland, Ohio; chemicals were dissolved in acetone). Food and water were available ad libitum. During the first 2 weeks, chicks were fed with a moistened mixture of pellets used in trout farming (Trouvit, Trouw, Gent) and a mixture used for growing chicks (Sivo start, Bogena, Waalwijk). This basic diet was supplemented daily with smelt (*Osmerus eperlanus*) and mashed hard-boiled chicken eggs. At 2 weeks of age, the diet gradually shifted to dry trout pellets, with egg added twice a week. A vitamin supplement (Calviet, UTD, Meppel) was added weekly.

Design

Forty-six animals were housed in ten groups of four animals and two groups of three animals. Groothuis and Meeuwissen (1992) showed that such groups are excellent for conducting hormonal studies. Endogenous testosterone production of chicks reared in such groups is retarded due to the lack of social stimulation by conspecifics from other groups. Such chicks behave towards each other as they normally do in sibling groups, showing no aggression and threat display behavior while frequently give begging displays. At 6 days post-hatching in every group, chicks were assigned randomly to one of the four treatments: no hormonal treatment: C: $n = 11$; testosterone implants: T: $n =$