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Commentaries

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The Interaction between Organizational and Activational Effects of Testosterone in the Control of Early Aggression in Birds: A Comment on Sasvári, Hegyi & Péczely

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Recently, Sasvári et al. (1999) published a paper in this journal on the relationship between brood reduction and testosterone levels in the asynchronously hatching chicks of the white stork (*Ciconia ciconia*) in which they showed that levels of testosterone in plasma, drawn at 5 and 15 d after hatching, decreased with laying order. They compared nests in which one or more chicks died at between the age of 5 and 15 d after hatching with nests in which no chick died in this period. In correlation with the mortality, parents of the first group were in lower physical condition and delivered less food to the chicks than parents of the second group. Interestingly, in the first group relative to the second group, levels of testosterone were increased nearly twofold in chicks that hatched first and decreased about twofold in chicks that hatched last. Furthermore, chicks that hatched first were twice as likely to be the first to be fed in the first group as compared with the second group. They did not observe overt aggression between siblings between the age of 5 and 15 d after hatching.

The authors argued that the mortality difference in nests was affected by testosterone-dependent competition between the chicks, which in turn was a result of maternal transmission of hormones to the egg yolk. However, they did not take measurements of androgen concentrations in yolk samples to substantiate this rather complicated mechanism. Since testosterone levels were still elevated at day 5 after hatching and increased from day 5 to day 15 after hatching, a maternal source for these hormones is highly unlikely. They did not give a mechanism to explain how endogenous production of testosterone could be organized by exposure to testosterone in the yolk. We fear that Sasvári et al.'s discussion overshadows the importance of the data collected because research into the endocrinology of early competitive behaviour is extremely rare.

Early regulation of aggressive behaviour by steroid hormones is especially interesting because both organizational and activational effects of hormones closely interact at this stage. Schwabl (1993) showed that steroid hormones in the egg yolk, possibly of maternal origin, correlated with competitive behaviour between chicks in the nest. Organizational effects of the exposure of the embryo to the steroid environment are probably mainly responsible for this effect since absorption of hormones from the yolk stops within days after hatching. Activational effects of steroids may play an additional role to fine-tune aggressive behaviour to the social challenges of the chick's environment. This has been proposed for early territorial behaviour in black-headed gull chicks (Ros 1999).

In siblicidal species an increase in aggressive behaviour between chicks occurs especially in times of food shortage and this social instability may result in an increased androgen release in a similar way to that described for adult birds in the framework of the 'challenge hypothesis' (Wingfield et al. 1990). Nevertheless, in an experiment designed to test this mechanism in the blue-footed booby, no testosterone was detectable in experimentally food-deprived chicks (Nuñez-de la Mora et al. 1996). In contrast to this finding, measurable testosterone levels were found in the two species of Ciconiformes that have been studied. Tuckova (1999) manipulated nests of the bald ibis (*Geronticus eremita*) so that they were either synchronously or asynchronously hatching. Aggression was increased in the synchronously hatched chicks compared to the asynchronously hatched chicks. This aggression was however, not significantly correlated with testosterone levels measured from faeces. On the other hand, Sasvári et al. (1999) found increased levels of testosterone in chicks of the white stork. Interestingly, this was correlated with mortality in the nest. These chicks show aggression during food shortage like booby chicks, but this aggression is only apparent from the age of 60 d onwards. Nonetheless, competition for food must have been fierce between 5 and 15 d after hatching since many chicks died in this period.

Currently there is insufficient data available to draw conclusions about the hormonal control of aggressive behaviour during early ontogeny. It can be hypothesized that androgens have an activating role as derived from the study of Sasvári, but causality needs to be verified in this study since the presented data were correlative. Moreover, the premise that all types of aggressive competition are under influence of androgens is at odds with the results of experiments on blue footed-boobies and bald ibis (Nunez-de la Mora et al. 1996; Tuckova 1999). Still, several factors might have confounded the results of these studies. Plasma levels of androgens may be low early in ontogeny since gonads are often in an immature state, and hormones released from other organs, like the adrenals, may play a role in the regulation of early aggression. Furthermore, the active hormone may not be testosterone but a precursor or metabolite of testosterone. Finally, the timing of taking the blood sample may be crucial for finding relations between hormones and aggressive behaviour since hormone release is subject to both daily rhythms and temporal fluctuations. Taking into account the importance of such factors, future studies are necessary to unravel the interaction between organizational and activational effects of steroid hormones during early regulation of aggressive behaviour.

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