A hormonal mechanism for parental favouritism

In many taxa, parents compensate for the overproduction of young by conferring vital advantages on certain offspring, enabling them to out-compete their siblings when resources are scarce[1,2]. With birds, the competitive advantage is usually related to the age of chicks, which varies because of earlier hatching and incubation[2–4]. Recent studies of canaries (*Serinus canaria*) show that hen birds may influence competitiveness directly by depositing increasing amounts of testosterone in the yolks of successively laid eggs[5–7]. We have observed a contrasting phenomenon in cattle egrets (*Bubulcus ibis*), where egret mothers deposit more androgens in the first eggs of their clutches, adding a potential hormonal boost to the advantage caused by earlier hatching. This may help senior siblings eliminate junior nest-mates.

The higher doses of testosterone bestowed by canary mothers on later-laid chicks[5,6] increases their begging vigour[7]. This confers growth advantages when chicks hatch at the same time, but does not fully compensate for the disadvantages of hatching late in asynchronous broods. The effects of incubation onset and testosterone dosage work in opposition, so canary mothers can favour either their early-egg offspring (by early hatching) or those from later-laid eggs (by testosterone in tandem with synchronous hatching)[7]. Comparative studies were needed to assess the generality of such hormonal influences on sibling competition[8].

Cattle egrets offer an ideal contrast to canaries. The separation of hatching times produces large differences in the size and strength of siblings, reducing the number of fights between nestlings and aiding the elimination of junior brood members during food shortages (siblicide)[9]. It would be surprising if senior egret chicks were empowered by the earlier hatching, at the same time as being hormonally handicapped by low yolk androgen levels.

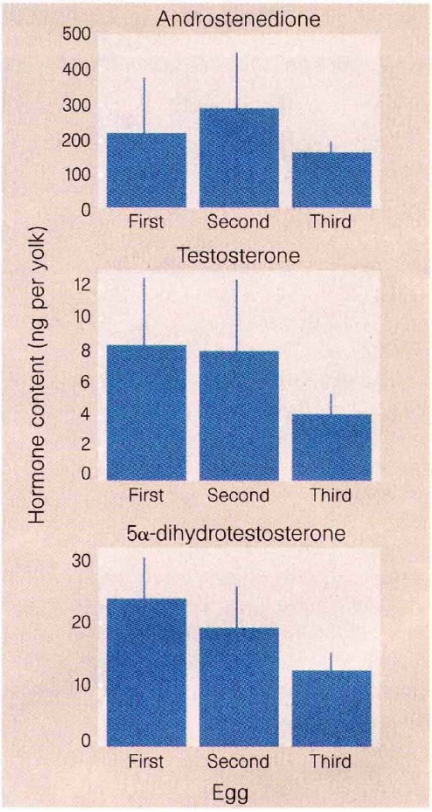

Figure 1 **Mean yolk contents (error bars show 95% confidence limits) of maternal androgens androstenedione, testosterone and 5α-dihydrotestosterone for first-, second- and third-laid cattle egret eggs in a clutch. Repeated-measures ANOVA showed significant differences in all three hormone levels between chicks (androstenedione, $P = 0.0359$; testosterone, $P = 0.0022$; 5α-dihydrotestosterone, $P = 0.008$).**

Our studies of eight three-egg cattle egret clutches (the modal clutch size), each egg collected on the day it was laid, show that the two first-laid eggs contain more androgens than the third egg (Fig. 1). This suggests that, in contrast to canaries, cattle egret androgens act in concert with hatching asynchrony to favour senior siblings. We do not know whether these hormones influence the aggression or begging of egret chicks, but experimental manipulations of yolk testosterone levels in canaries show that androgens enhance begging behaviour[7], growth rate[7] and aggression[5]. Our results suggest that hormonal favouritism may be a common mechanism for bird mothers to influence sibling competitiveness. They also support the view that parents are not in evolutionary conflict with siblicidal offspring, but may be subtle participants in the process of orderly brood reduction[10].

These findings underscore the need for cross-taxonomic surveys of yolk androgens in relation to laying order, sibling rivalry and reproductive strategy[8], and for within-species studies of broods facing different conditions[6], to elucidate the function of maternal hormones in reproductive optimization. In turn, this should illuminate how 'trans-generational' hormone effects[11] and the evolutionary interests of parents[2] have helped to shape the endocrine control of reproductive systems.

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1. Kozlowski, J. & Stearns, S. C. *Evolution* **43,** 1369–1377 (1989).
2. Mock, D. W. & Parker, G. A. *The Evolution of Sibling Rivalry* (Oxford Univ. Press, in the press).
3. Lack, D. *Ibis* **89,** 302–352 (1947).
4. Magrath, R. D. *Nature* **339,** 536–538 (1989).
5. Schwabl, H. *Proc. Natl Acad. Sci. USA* **90,** 11446–11450 (1993).
6. Schwabl, H. *J. Exp. Zool.* **276,** 157–163 (1996).
7. Schwabl, H. *Comp. Physiol. Biochem. A* **114,** 271–276 (1996).
8. Winckler, D. W. *Proc. Natl Acad. Sci. USA* **90,** 11439–11441 (1993).
9. Mock, D. W. & Ploger, B. J. *Anim. Behav.* **35,** 150–160 (1987).
10. Mock, D. W. & Forbes, L. S. *Auk* **111,** 115–123 (1995).
11. Bern, H. *Am. Zool.* **30,** 877–885 (1990).

Self-recognition by proteoglycans

During the emergence of multicellular organisms, molecular mechanisms have arisen to allow self-recognition and discrimination against 'non-self'. We suggest that cell-surface proteoglycans might have provided these key recognition and adhesion functions. If so, the simplest Metazoans alive today, such as Porifera (sponges), should retain, at least in part, proteoglycan adhesion and recognition mechanisms. We have shown, using atomic force microscopy, that proteoglycan-to-proteoglycan binding produces fundamental cell cohesion forces in the sponge *Microciona prolifera*[1], as previously implied by functional investigations[2,3]. Early work on cell adhesion of dissociated marine sponge cells provided evidence for cell sorting by species[2–4]. Here we show that proteoglycans underlie the molecular mechanism of this self-recognition.

We mixed metabolically attenuated cells (at 0 °C) of three marine sponge species, *Microciona prolifera, Halichondria panicea* and *Cliona celata,* bearing surface proteoglycans, in artificial sea water. Within 5–15 min species-specific recognition and adhesion occurred, but only when the sea water contained a physiological concentration of Ca^{2+} (Fig. 1a). After selective washing of proteoglycans from the cell surface, none of the three species displayed aggregation. Replacing the purified proteoglycans (again at 0 °C) completely restored species-