



Maternal testosterone in tree swallow eggs varies with female aggression

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Variation in the investment of maternal resources in eggs, such as proteins and lipids, can have a profound influence on the growth and development of young. Maternal resources transferred to eggs also include androgens found in the yolk. In several species of birds the concentration of testosterone in the yolk either increases or decreases with laying order. Yolk testosterone has been shown to have various effects on the young including enhanced growth and dominance as well as reduced survival. Previous work suggested that the concentration of testosterone in the yolk may be influenced by the female's social conditions, specifically the frequency of aggressive interactions. In tree swallows, *Tachycineta bicolor*, we found that yolk testosterone was correlated with the aggressive interactions of the female before and during egg laying. In contrast to other species, yolk testosterone did not vary with laying order in tree swallows. Thus, patterns of yolk testosterone are more variable than thought previously and may be influenced by the social conditions experienced by the female during laying.

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Parent birds can influence the quality of their offspring and confer advantages to particular individuals in several ways. For example, by varying the start of incubation relative to the completion of egg laying, females can produce asynchronously hatching broods that may confer a competitive advantage to the earlier hatching young (Ricklefs 1993). Variation in the investment of maternal resources in eggs has also been a focus of interest. Larger eggs can provide embryos with more protein and lipids, which can increase the growth rate and survival prospects of newly hatched young (reviewed in Williams 1994). The discovery of maternal androgens in eggs, in particular testosterone (Schwabl 1993), has stimulated much interest in the factors that influence yolk testosterone (T) deposition and its effect on offspring fitness.

In canaries, *Serinus canaria*, the concentration of yolk T increases with laying order and positively influences nestling growth and dominance behaviour in juveniles (Schwabl 1993, 1996a). This pattern of yolk T deposition works in opposition to hatching asynchrony, which confers a size advantage to the earlier hatching young (Schwabl 1996a). Variation in the amount of yolk T appears to be correlated with the level of T circulating in the female during yolk formation, which in turn may be

influenced by the female's social conditions such as breeding density (Schwabl 1996b, 1997a, b).

The canary has been the focus of much of the original work (Schwabl 1993, 1996a, b), which has stimulated widespread interest in examining the general occurrence of intraclutch patterns of yolk T concentrations as well as the functions of yolk androgens. Increasing levels of yolk T with laying order occur also in red-winged blackbirds, *Agelaius phoeniceus* (Lipar et al. 1999a), American kestrels, *Falco sparverius* (Sockman & Schwabl 2000), lesser black-backed gulls, *Larus fuscus* (Royle et al. 2001), common terns, *Sterna hirundo* (French et al. 2001) and black-headed gulls, *Larus ridibundus* (Eising et al. 2001). In contrast, decreasing levels of yolk T with laying order occur in cattle egrets, *Bubulcus ibis* (Schwabl et al. 1997) and zebra finches, *Taeniopygia guttata* (Gil et al. 1999). Benefits from increased levels of yolk T for nestling growth, as initially found in canaries (Schwabl 1996a), apply also to black-headed gulls (Eising et al. 2001) and are likely for red-winged blackbirds in which yolk T increases the mass of the hatching and begging muscle (Lipar & Ketterson 2000). However, benefits are not universal as recently pointed out in a study of American kestrels in which high yolk androgens had a negative influence on nestling growth and survival (Sockman & Schwabl 2000).

In contrast to the relationship between yolk T and laying order, the influence of female aggressive interactions on yolk hormone deposition has received

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