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Using life-histories to predict and interpret variability in yolk hormones

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ABSTRACT

Variation in yolk hormones is assumed to provide the plasticity necessary for mothers to individually optimize reproductive decisions via changes in offspring phenotype, the benefit being to maximise fitness. However, rather than routinely expecting adaptive variation within all species, the pattern and magnitude of yolk hormone deposition should theoretically relate to variation in life-histories. Here we present data on intra-clutch variation in yolk corticosterone in three species along a developmental continuum (European starling (*Sturnus vulgaris*): fully altricial; black guillemot (*Cepphus grylle*): semi-precocial; common eider (*Somateria mollissima*): fully precocial) to examine how and why variation in life-histories might relate to the evolution of variation in yolk steroids. Starlings and guillemots showed a significant increase in yolk corticosterone across the laying sequence; however, we found no pattern within eider clutches. Moreover, starlings showed the largest difference (94.6%) in yolk corticosterone between first- and last-laid eggs, whereas guillemots showed a moderate difference (58.9%). Despite these general species-specific patterns, individuals showed marked variation in the intra-clutch patterns of yolk corticosterone within each species indicating potential differences in intra-clutch flexibility among females. It is well documented that exposure to elevated yolk glucocorticoids reduces offspring quality at birth/hatching in many taxa and it has therefore been proposed that elevated yolk levels may modulate offspring competition and/or facilitate brood reduction under harsh conditions in birds. Our data suggests that intra-clutch variation in yolk corticosterone has the potential to act as an adaptive maternal effect in species where modulation of competition between nest-bound offspring would benefit mothers (starlings and guillemots). However, in precocial species where mothers would not benefit from a modulation of offspring quality, intra-clutch variation in yolk hormones may play little or no adaptive role. While future phylogenetically-controlled studies will be helpful in examining questions of adaptive mechanisms once more data on yolk corticosterone becomes available, our results nonetheless suggest that research on the evolutionary role of yolk hormones can benefit by *a priori* incorporating species-specific life-history-driven hypotheses.

1. Introduction

Maternal effects are widely recognized as one of the most important factors influencing offspring phenotype (Mousseau and Fox, 1998; Marshall and Uller, 2007). Maternally-derived yolk steroids are considered potent maternal effects by providing adaptive flexibility to mothers via influences on offspring quality (reviewed in Groothuis et al., 2005a,b). However, despite over a decade of research and an abundance of reported phenotypic responses in offspring following exposure to maternally-derived yolk hormones (Schwabl, 1993; Groothuis et al., 2005a), the field is only beginning to examine effects within an evolutionary context (Groothuis et al., 2005a; Love et al., 2005; Love and Williams, 2008a). Without an evolutionary framework from which to work, it is difficult to interpret how variation between and within individuals acts in different species to shape the role (if any) of yolk hormones as adaptive maternal effects. For example, while many researchers in this field would readily recognize that not all species should exhibit the same within-clutch patterns in yolk hormones (Groothuis et al., 2005a), there has been a general under-appreciation of the underlying role of life-history in driving intra-clutch patterns and inter-individual variation in hormones (Williams, 2008). Indeed with specific regard to yolk hormones, given that species vary considerably in their life-histories (i.e., clutch size, degree of offspring competition, degree of parental care) we would predict that different species should vary markedly in the extent to which this type of hormonally-mediated maternal effect would contribute to variation in offspring phenotype.

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