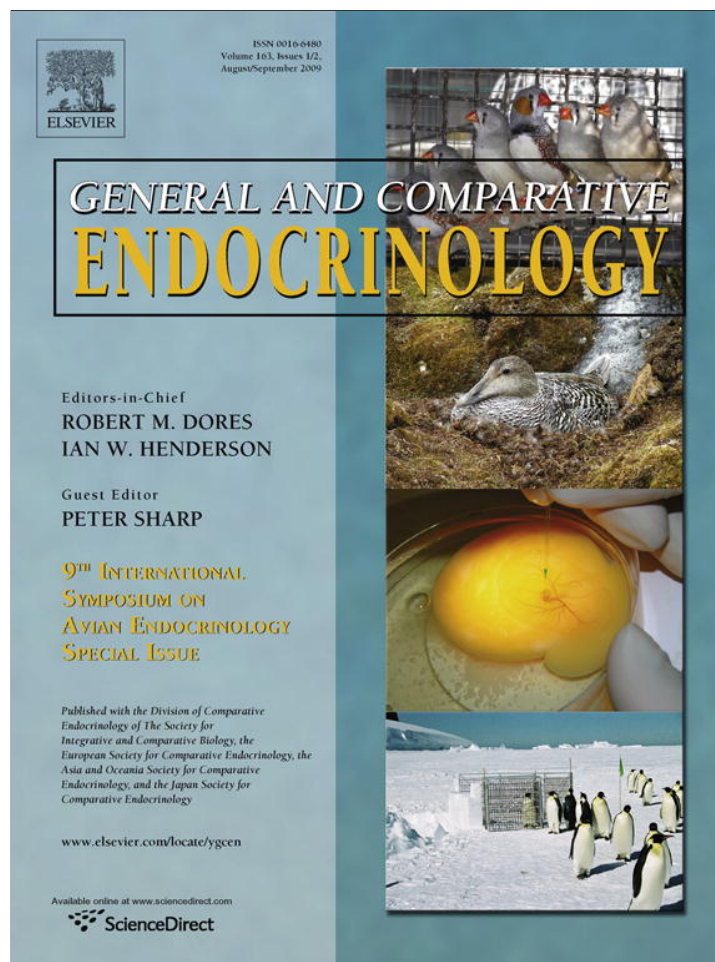


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Using life-histories to predict and interpret variability in yolk hormones

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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.

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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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Although it is well recognized that the adaptive value of a maternal effect is directly tied to variation in life-histories (Price, 1998; Heath et al., 2003; Love and Williams, 2008a), many studies employ life-history theory in a *post-hoc* manner to explain variation in yolk hormones once they have been measured, rather than using the underlying theory to predict patterns *a priori*. As such, researchers in general do not routinely ask *if* and *how* mothers of a given species would benefit from variation in a hormonally-mediated change in offspring phenotype. For example, although intra-clutch variation in yolk hormones is routinely considered to affect hatching asynchrony and sibling competition (reviewed in Groothuis et al., 2005a), few studies reporting intra-clutch variation have been able to predict that their species would exhibit and benefit from such a pattern *a priori*. As such, information on life-histories might help to explain why some species show little or no systematic intra-clutch variation in yolk hormones, despite significant variation patterns being observed in other species. Secondly, we know little about the underlying mechanisms that give rise to intra-clutch variation (Groothuis et al., 2005a; Groothuis and Schwabl, 2008) and an understanding of life-histories might also help to inform the field in this context. This is especially important since many studies currently assume that when a significant intra-clutch pattern is observed that it is evidence for adaptive intra-clutch deposition by the mother, even though it may be unlikely that females have this control (Groothuis et al., 2005a) and the fact that within-clutch patterns may arise by more simple, indirect mechanisms (Love et al., 2008; Groothuis and Schwabl, 2008). Finally, if life-history-driven studies on yolk hormones can help to put species that show little or no intra-clutch patterns into context with those species showing significant patterns, non-significant intra-clutch patterns can be better appreciated. This is most important, since without this appreciation new studies that do not reproduce the intra-clutch patterns documented in other species will likely be overlooked and under-represented in the yolk hormone literature, rather than being used to help us understand how variation (or lack of it) adds to the understanding of how this maternal effect evolved.

Here we present data on intra-clutch variation in yolk corticosterone in three avian species spanning a developmental continuum in an attempt to highlight the need for life-history based *a priori* hypotheses in yolk hormone studies. Glucocorticoids, such as corticosterone in birds, reptiles and amphibians, have the potential to be potent maternal effects since they mediate adaptive physiological and behavioral responses to maintain homeostatic energetic balance (Dallman et al., 1993; Remage-Healey and Romero, 2001; Kitaysky et al., 2001, 2003; Wingfield, 2005; Wada et al., 2007; Love and Williams, 2008b). Furthermore, embryos in a wide range of vertebrate taxa are sensitive to maternally-derived glucocorticoids and appear to express phylogenetically-conserved phenotypic adjustments when exposed to elevated maternal levels (i.e., reduced size at birth/hatching and reduced post-natal growth rates; see Love et al., 2008; Love and Williams, 2008a). We concentrate on intra-clutch variation since great effort has been made to understand the significance of how within-clutch patterns might affect offspring competition (reviewed in Groothuis et al., 2005a). We begin with the European starling (*Sturnus vulgaris*), a temperate passerine that lays comparatively large clutches (4–6 eggs), exhibits hatching asynchrony, has altricial young completely dependent on parental care during post-natal development and has significant sibling competition. We compare this passerine to the black guillemot (*Cepphus grylle*), a sea bird that lays only two eggs, with moderate hatching asynchrony, semi-precocial development and context-(resource-)dependent sibling competition. Finally, we compare these species to a precocial sea duck, the common eider (*Somateria mollissima*) that in general lays four eggs, has highly synchronous hatching and independent ducklings at

hatching. If maternally-derived yolk corticosterone acts as an adaptive maternal effect to modulate offspring competition via changes in quality at hatching (Love et al., 2005; Love and Williams, 2008a), we would predict a strong positive relationship between yolk corticosterone and laying order in starlings, a moderate relationship in guillemots and little or no relationship in eiders. While we fully appreciate that a controlled phylogenetic study is the ideal way in which to examine these questions, there are currently insufficient studies in a varied number of species to allow this (Love et al., 2008). As such, we feel that introducing this type of data within a life-history theory framework will help researchers to appreciate how variation in life-histories might impact variation in yolk steroids, information that can eventually be used to manipulate yolk steroid levels to proximately examine effects on offspring and ultimately the effects of variation on maternal fitness.

2. Methods

2.1. Study species, sites and egg collection

Starling research was undertaken at a wild colony consisting of 225 nest boxes at Davistead Dairy farm in Langley, BC, Canada (49°10'N, 122°50'W). Egg collection was conducted between April and May of 2004 under a Simon Fraser University Animal Care permit (657B-96), following guidelines of the Canadian Council on Animal Care (see Love et al., 2008). Common eider and black guillemot eggs were collected from long-term monitoring colonies located on Mitvik island, East bay, Southampton island, Nunavut (64°01'N, 81°47'W) in June and July (respectively) of 2006 under the following permits: Environment Canada (EC): NUN-MBS-02-06 and NUN-SCI-06-04; EC Animal Care Permit: 2006PNR008; Nunavut Impact Review Board Environmental Assessment (NIRB): 02YN064; Indian and Northern Affairs: N1999J0031; Nunavut Wildlife Research Permit: WL 00159. Nest boxes (starlings) and nests (eiders and guillemots) were checked daily to determine clutch initiation dates for individual females as well as the laying sequence of eggs. To examine intra-clutch variation in yolk corticosterone levels, freshly-laid eggs for a given clutch were collected daily (within 2–5 h of being laid for starlings, within 6–12 h for guillemots and eiders) by visiting nests during species-specific laying periods during the day. In starlings, removed eggs were replaced with wooden dummy eggs; eider and guillemot eggs were replaced with freshly-laid eggs from nearby conspecifics. We constrained analysis of yolk corticosterone by clutch size within each species examined with the clutch size chosen being the median for each species within each population (i.e., starlings: five eggs; guillemots: two eggs; eiders: four eggs), and eggs were collected within the peak of laying in each species' colony to limit variation in yolk corticosterone caused by variation in maternal quality (Love et al., 2008). Fresh eggs were marked, weighed and measured and immediately stored whole at –20 °C until further analysis, as suggested in Eising et al. (2001).

2.2. Yolk corticosterone determination

Yolks were bisected (to include all yolk layers) and the sub-sample weighed to the nearest 0.0001 g and steroids were extracted prior to assay by the methods outlined in Love et al. (2005, 2008). Briefly, following equilibration with distilled/deionized (dd) water, dilution with distilled-in-glass (DIG) methanol and centrifugation at 1500g for 7 min under refrigeration (2 ± 1.5 °C), supernatant was extracted on C18 columns (IS2200050C Isolute® SPE columns, Chromatographic Specialties, Inc., Brockville, Ont.) under vacuum filtration. Columns were primed with DIG methanol, followed by dd water, followed by the entire 10 ml sample volume, and then

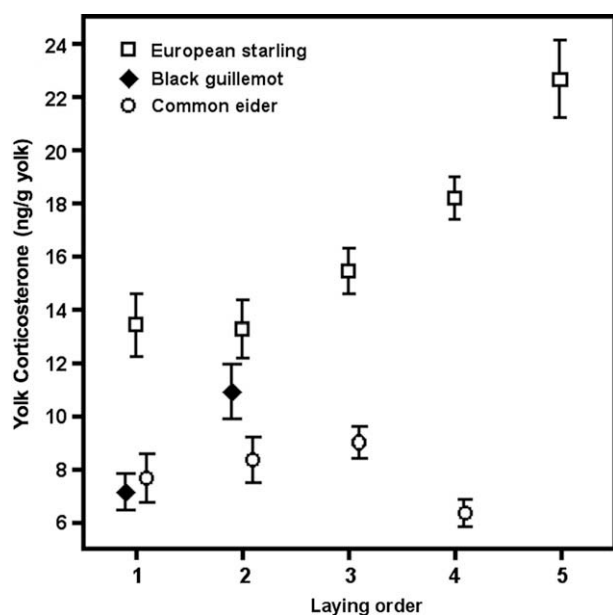


Fig. 1. Intra-clutch variation in yolk corticosterone in three avian species spanning a developmental continuum from altricial to precocial (Mean \pm SEM are shown).

washed with dd water. Corticosterone was eluted with 5 ml of 90% methanol into 7 ml borosilicate vials (03-337-26, Fisher). Each sample was evaporated to dryness under a stream of air and reconstituted in 1.2 ml of assay buffer (5% ethanol) prior to being quantified in triplicate on a single plate of the corticosterone EIA. To quantify extraction efficiency, yolks were combined for each species, mixed by hand using a mortar and pestil on dry ice, and 12 fractions were weighed from the combined yolk and thereafter treated as independent controls. After dilution into a total volume of 2 ml, six of the 12 samples were spiked with a 5 ng bolus of corticosterone in a 200 μ l volume drawn from commercial standards from a Corticosterone 125 I RIA kit (ICN, Orangeburg, NY) and the remaining six samples were spiked with 200 μ l of assay diluent from the same kit. The resulting samples settled overnight and were handled exactly the same way as the unknown yolk determinations so that the controls contained raw yolk, or raw yolk plus 5 ng of corticosterone. The concentration of total corticosterone (see Breuner and Orchinik, 2002; Love et al., 2004, 2005, 2008) in yolks was determined using a corticosterone EIA (0.13% cross-reactivity with Testosterone; 1.7% cross-reactivity with Progesterone, <0.03%: Pregnenolone/Cortisone/11-dehydrocorticosterone acetate; Assay Designs Inc., MI, USA) with a 4-parameter logistic fit. Dried samples were reconstituted in 5% ethanol in assay buffer and were run in triplicate across eight assay plates at a total volume of 100 μ l with 1:40 dilution and 1.5% steroid displacement buffer. As per kit instructions, plates were first incubated at 26 $^{\circ}$ C under shaking at 5000 rpm for 2 h and then at 26 $^{\circ}$ C without shaking for 1 h; the detection limit of the assay was calculated at 0.02 ng/well (0.5 ng/g) with average intra- and inter-plate variation of $7.5 \pm 1.2\%$ and $8.2 \pm 2.6\%$, respectively. Each plate contained three replicates of both the un-spiked control and spiked yolks for the correct calculation of both intra- and inter-assay variation, respectively. Average recovery of the 5 ng spike in the six replicates was $93.8 \pm 2.4\%$. Values are reported as corrected for the recovery efficiency.

3. Results

Variation in yolk corticosterone was normally distributed for all three species (Shapiro-Wilk Goodness of Fit Test, controlling for nest origin: starlings: $W = 97$, $p = 0.7$, $n = 55$ eggs from 11 nests;

guillemots: $W = 0.93$, $p = 0.39$, $n = 12$ eggs from six nests; eiders: $W = 0.97$, $p = 0.76$, $n = 24$ eggs from six nests). The mean level of corticosterone in yolks varied by species (starlings: 16.6 ± 0.83 ng/g yolk; guillemots: 9.00 ± 0.83 ng/g yolk; eiders: 7.88 ± 0.41 ng/g yolk). In the first-laid eggs of starlings and guillemots, we found no effects of laying date on yolk corticosterone levels (starlings: $F_{1,10} = 0.83$, $p = 0.37$; guillemots: $F_{1,5} = 1.41$, $p = 0.29$). However, we found a significant positive relationship between laying date and yolk corticosterone in first-laid eggs in eiders ($F_{1,5} = 11.05$, $p = 0.009$, $B = 2.07$) and as such, we controlled for this in analyses of intra-clutch variation for this species. We found a strong effect of laying order for starlings ($F_{4,34} = 4.63$, $p = 0.005$; Fig. 1) and guillemots ($F_{1,11} = 8.88$, $p = 0.014$; Fig. 1), but not for eiders ($F_{3,23} = 1.45$, $p = 0.13$, controlling for laying date in eiders; Fig. 1). In addition, there was significant inter-species variation in the relative difference in yolk corticosterone between first and last-laid eggs, with starlings showing large differences, guillemots showing moderate differences and no differences in eiders ($F_{2,22} = 5.13$, $p = 0.016$; Fig. 2). Finally, we also found a large degree of inter-individual variation in the intra-clutch patterns within each species (repeated-measures ANOVA: individual identity \times laying order: starlings: $F_{1,9} = 6.55$, $p = 0.03$; guillemots: $F_{1,4} = 8.12$, $p = 0.05$; eiders: $F_{1,4} = 7.69$, $p = 0.05$; Fig. 3) indicating that not all individuals showed the same intra-clutch patterns within species.

4. Discussion

We report significant variation in yolk corticosterone at three biologically and evolutionarily important levels: (1) intra-individual (intra-clutch), (2) inter-individual and (3) inter-specific. Exposure to elevated yolk glucocorticoids consistently reduces the 'quality' of offspring across taxa (see references in Love et al., 2008), including reductions in hatchling size, begging ability and growth in birds (Rubolini et al., 2005; Saino et al., 2005; Love et al., 2005; Love and Williams, 2008a). Based on the consistent maternal effects of this hormone, it has been proposed that intra-clutch patterns of yolk corticosterone may play an adaptive role in mediating competition within broods (Saino et al., 2005; Love et al., 2008). In support of this idea, increases in yolk corticosterone

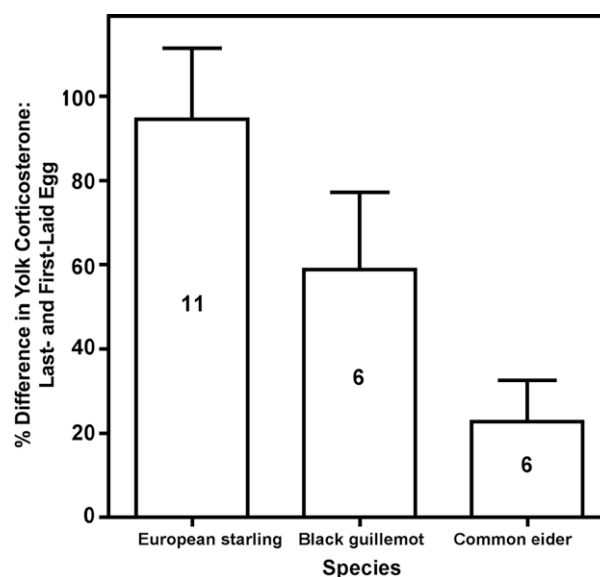


Fig. 2. Percent difference in yolk corticosterone between last- and first-laid eggs in three avian species spanning a developmental continuum from altricial to precocial (numbers in bars represent the number of clutches used; Mean \pm SEM are shown).

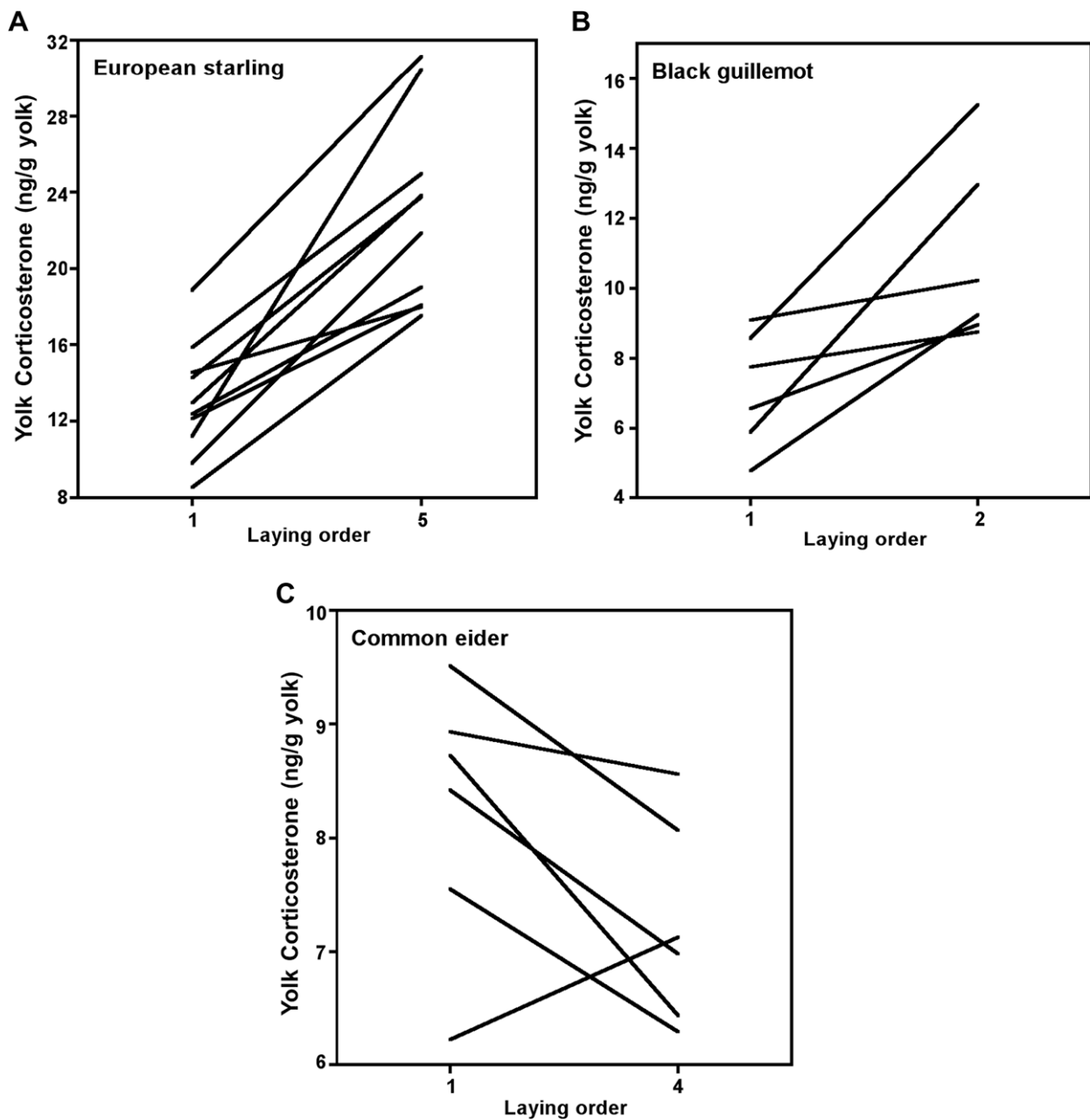


Fig. 3. Individual variation in intra-clutch patterns of yolk corticosterone (from first- to last-laid eggs in a clutch) in three avian species spanning a developmental continuum from altricial to precocial.

across the laying sequence have recently been linked to reductions in offspring demand in relation to laying order in starlings (Love and Williams, 2008a). Expanding these results to species with different life-histories should then allow us to predict *a priori* both the presence and direction of yolk corticosterone patterns within clutches for different species: we should expect to observe significant increases across the laying sequence in species where mothers would benefit from a reduction in the competitive ability of offspring across the clutch.

4.1. Life-histories and inter-specific variation in intra-clutch patterns

We found a strong increase in yolk corticosterone across the laying sequence in a representative temperate passerine, the European starling, which exhibits significant sibling competition and altricial, nest-bound, offspring in need of extensive post-natal care

(Cabe, 1993). In fact, we found that last-laid eggs contained almost twice as much corticosterone as first-laid eggs. A strongly increasing pattern of yolk corticosterone should benefit starling mothers by both spreading out sibling competition which optimizes energetic input into the brood (Wiebe and Bortolotti, 1994) and increasing the likelihood of adaptive brood reduction during low resource conditions (Love and Williams, 2008a).

In the black guillemot, which usually exhibits limited sibling competition and semi-precocial young (Butler and Buckley, 2002), we found a significant but less steep increase in yolk corticosterone from the first to second-laid egg. Guillemot mothers may benefit from depositing higher yolk corticosterone in second-laid eggs, a factor which may combine with hatching asynchrony to reduce sibling competition under normal feeding conditions in much the same way as for starling broods. Sibling aggression typically only occurs when food is limited and it is the chick hatching from

the first-laid egg that is typically the aggressor (Cook et al., 2000). Under these conditions, a yolk corticosterone-mediated reduction in the competitive ability of chicks hatching from second-laid eggs would further benefit mothers in a similar way as hypothesized for starlings by reducing competition and perhaps even leading to more efficient brood reduction if resources remain low.

In contrast to starlings and guillemots, hatching of young in the common eider is highly synchronous and within 1 h of reaching the ocean with their mother the precocial young are able to dive and feed independently (Goudie et al., 2000). There is little opportunity for maternally-mediated competition between ducklings, and mothers do not provide direct parental care (other than protection from aerial predators). As such, there is little adaptive reason for eider mothers to differentially invest in offspring across their brood and it is therefore not surprising to find no pattern of yolk corticosterone across the laying sequence in this species. Since offspring are largely independent of their mother at hatching, the goal of a precocial mother should be to synchronously hatch as many young as possible in a given clutch and lead them to safe foraging grounds. In fact, although mothers provide the opportunity of protection to young when predators are present, it is up to the individual offspring to seek protection from their mother during these times (Goudie et al., 2000). In this respect, it is individual duckling quality and not simply maternal behavior that increases duckling survival and as such a mother theoretically gains no benefit from differentially investing in certain offspring in the brood. The life-history traits of eiders (and potentially other precocial species) indicates that there would be no adaptive benefit to mothers in differentially modulating offspring quality within a given brood by varying yolk corticosterone levels differentially across the laying sequence. Once the field has more published data on yolk corticosterone across diverse avian taxa we will be able to examine the relative strength of these adaptive life-history-based hypotheses.

4.2. Inter-individual variation in intra-clutch patterns

Perhaps of equal interest to species differences in intra-clutch patterns is the fact that individual mothers differ in both the absolute amount of the hormone deposited into eggs and also in the patterns across the laying sequence. Inter-individual variation in maternally-derived yolk hormones has been proposed to act as a mechanism by which the quality of individual mothers or their breeding environment can be matched or mapped onto offspring phenotype (Groothuis et al., 2005a; Love et al., 2005, 2008). Interestingly, inter-female variation in yolk corticosterone has recently been proposed to act as an adaptive mechanism by which the rearing capacity of the mother is matched to offspring demand (Love et al., 2005; Love and Williams, 2008a). Yolk hormones therefore have the potential to differentially affect offspring both across individual mothers and across clutches as discussed earlier (Groothuis et al., 2005a,b). Incorporating life-histories into studies should help us to understand how different mothers and different species are differentially influenced by their pre-breeding or breeding environment, and hence we can better understand inter-individual differences in the overall amount of yolk hormones allocated to clutches. A final, and yet largely unappreciated, level of variation is inter-individual differences in the patterns of yolk hormones across clutches (Fig. 3). The result is that individual offspring of one mother can vary dramatically in their exposure to yolk hormones, while those of a second mother are exposed to very similar levels across the laying order. This variation is of great ecological and evolutionary interest since the presence or lack of this within-clutch “flexibility” is predicted to have fitness consequences and can be examined using a reaction-norm approach (see Williams, 2008). Taken together, this type of inter-female variation

underscores the need for researchers to concentrate on sources of variability not only among species, but also between and within individuals, to appreciate the potential role that a given hormone may play as a maternal effect.

4.3. Incorporating life-histories into future studies

In the present study we have shown that three species that differ greatly in their developmental mode, with corresponding inter-species differences in hatching asynchrony, sibling competition and the degree of parental care required, also differ significantly in the degree of intra-clutch variation in the yolk steroid corticosterone. Those species whose mothers would be predicted to benefit from hormone-induced variation in offspring quality across the laying sequence exhibited increasing levels of the hormone in eggs across the laying sequence (starlings, guillemots), whereas a species where all young are predicted to be of equal quality at hatching (eiders) show no pattern. The results underscore the value of incorporating variation in life-histories into studies of variation in yolk hormones as adaptive maternal effects. With more and more interest developing in non-androgenic yolk hormones (Love et al., 2005), researchers can soon employ some of the phylogenetically-controlled investigations that have recently been useful in elucidating the causes and consequences for inter-specific variation in yolk androgens (Gorman and Williams, 2005; Gil et al., 2007; Schwabl et al., 2007). These investigations have revealed that inter-species variation in life-history traits such as length of the prenatal period (Gorman and Williams, 2005; Schwabl et al., 2007) and the degree of breeding coloniality (Gil et al., 2007) can be explained by variation in yolk androgens. Indeed, in the present study we cannot yet begin to discuss the large species differences in absolute yolk corticosterone concentrations given that presently we have such little data; however, it is likely that life-history variation greatly contributes to species variation in absolute concentrations in much the same way as has been found for yolk androgens. Collectively, our results underscore the value of understanding how and why variation in yolk hormones occurs between and within individuals as well as between species since this information also provides significant insight into how hormones may play adaptive roles and mediate life-history trade-offs (Williams, 2008). Moreover, rather than some species being dismissed as ‘discrepancies’ compared to the norms in the literature, integrating life-history theory into studies on yolk hormones should help us understand why species would vary in this potential maternal effect before researchers begin investigations. Another important area of integration currently lacking appreciation is the potentially competing effect of different steroid hormones in both mothers and eggs. For example, it is beginning to be appreciated that androgens and glucocorticoids may interact in mothers (Husak and Moore, 2008) that may in turn influence both steroid deposition into eggs and subsequent phenotypic responses in offspring. Yolk hormones are undoubtedly powerful maternal effects in many species. Incorporating and understanding variation in life-histories will help researchers to predict in which species and under what circumstances yolk hormones will play evolutionary roles.

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