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# Migratory constraints on yolk precursors limit yolk androgen deposition and underlie a brood reduction strategy in rockhopper penguins

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Hormonally mediated maternal effects link maternal phenotype and environmental conditions to offspring phenotype. The production of lipid-rich maternal yolk precursors may provide a mechanism by which lipophilic steroid hormones can be transported to developing yolks, thus predicting a positive correlation between yolk precursors in mothers and androgen levels in eggs. Using rockhopper penguins (*Eudyptes chrysocome*), which produce a two-egg clutch characterized by extreme egg-size dimorphism, reversed hatching asynchrony and brood-reduction, we examined correlations between circulating concentrations of the primary yolk-precursor vitellogenin (VTG) and levels of yolk androgens. Previous work in *Eudyptes* penguins has shown that egg-size dimorphism is the product of migratory constraints on yolk precursor production. We predicted that if yolk precursors are constrained, androgen transport to developing yolks would be similarly constrained. We reveal positive linear relationships between maternal VTG and androgens in small A-eggs but not larger B-eggs, which is consistent with a migratory constraint operating on the A-egg. Results suggest that intra-clutch variation in total yolk androgen levels depends on the production and uptake of yolk precursors. The brood reduction strategy common to *Eudyptes* might thus be best described as the result of a migratory constraint.

Keywords: androstenedione; testosterone; physiological epiphenomenon hypothesis; vitellogenin;

other words, owing to a temporal separation between A- and B-egg development, migratory constraints on VTG production would affect androgen deposition to a greater extent in A- versus B-eggs.

## 2. MATERIAL AND METHODS

Sampling occurred at October–November 2008 at New Island, Falkland Islands [7]. Males return from sea in early October, with females days to weeks later. After arrival, females from 60 active nests were weighed and measured at three different times: after nest-establishment (n = 42), day of A-egg laying (n = 43) and B-egg laying (i.e. clutch completion, n = 39). Blood samples were collected from individuals serially: once (n = 15 individuals), twice (n = 26) and thrice (n = 19). We collected both eggs from each of the 60

colony, the demands of migration place constraints on VTG production. This migratory carryover effect leads to high variation in pre-laying VTG, which predicts egg-size (intra-clutch egg-size dimorphism; §]). Because androgen hormones are highly lipophilic, we hypothesized that constraints on VTG production would constrain androgen deposition to developing yolks, to a greater extent in small A-eggs (developed mostly at sea) than in larger B-eggs (developed mostly on land). Consistent with previous work in *Eudyptes* we found that VTG concentrations in newly arrived rockhopper penguins were directly related to egg-size dimorphism, thus indicating a potential migratory constraint, and that deposition of yolk androgens to

steroids. *Integr. Comp. Biol.* 48, 411-418. (doi:10.1093/icb/icn079)

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