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Are yolk androgens adjusted to environmental conditions? A test in two seabirds

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ARTICLE INFO

ABSTRAC

1. Introduction

Mothers possess considerable capacity to adjust their offsprings' phenotypes to prepare them to meet the challenges attention recently (Groothuis et al., 2005a). Androgens are steroid hormones that can have long term, beneficial effects on offspring behavior, growth and development (Schwabl, 1993; Eising et al., 2006). However, yolk androgens also could impose long term costs including reduced growth, survival and fecundity, and impairment of immune function (Sockman and Schwabl, 2000; Groothuis et al., 2005b; Rubolini et al., 2007). In addition, testosterone-enhanced traits often cited as beneficial, such as elevated growth rates and enhanced begging, are unlikely to be beneficial in all contexts (Kilner, 2001; Metcalfe and Monaghan, 2001; Uller and Olsson, 2003).

Given that suite of potential fitness costs and benefits, selection could operate on females to allocate androgens to offspring in a manner that maximizes fitness. If so, one prediction we can make is that the optimal strategy will vary with environmental conditions (Schwabl, 1996; Verboven et al., 2003). To date, most avian research on maternal androgens has focused on patterns of within-clutch allocation of yolk androgens in species that lay multi-egg clutches, and their consequences for sibling competition (Schwabl, 1993; Reed and Vleck, 2001; Müller et al., 2004). Due to the tight focus on sibling competition, we still know little about how females might allocate yolk androgens in direct response to environmental conditions (Groothuis et al., 2005a). Studies on species that lay single-egg clutches, in which sibling competition is not a factor, could help to fill the void.

The single-egg clutch is a characteristic life-history feature of offshore-feeding seabirds (Lack, 1968). Survival and growth of seabird chicks is tightly linked to food availability, which fluctuates dramatically over a range of temporal and spatial scales (Schneider and Duffy, 1985). Faced with such extreme environmental variation, and with brood reduction unavailable as a primary response to food shortages for all but a few species (Braun and Hunt, 1983), long-lived oceanic birds might be expected to make strong annual adjustments in maternal yolk androgen allocation. Specifically, we

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can hypothesize either (1) that early-laying (high quality) mothers will elevate yolk androgens in years of poor food availability, despite the associated risks, in order to enable their offspring to induce more feedings from parents through physiological and behavioral mechanisms. In many species, including several species of Alcidae (Harding et al., 2002; Litzow and Piatt, 2003; Gjerdrum, 2004), seabird chicks are able to induce changes in the rate at which their parents provision them (Hamer and Hill, 1994; Phillips and Croxall, 2003); or alternatively, (2) that early-laying mothers will reduce yolk androgen levels in years of poor food availability, when parents will not be able to keep up with the nutritional demands of fast-growing chicks (Benowitz-Fredricks and Kitaysky, 2005).

To test these hypotheses about androgen allocation, we measured concentrations of androstenedione [A4] and testosterone [T] in the yolks of the single-eggs laid by two alcids, Cassin's auklets and rhinoceros auklets , in each of 3 years. Our study site, Triangle Island, lies within the area influenced by the California Current, an extremely variable marine ecosystem in which feeding conditions and thus timing and success of seabird breeding vary dramatically among years (Ainley and Boekelheide, 1990; Bertram et al., 2001; Sydeman et al., 2006). That was true during our 3 year study, which bpayears was true d0e4.017 tud021bpa

natural selection (Williams et al., 2004; Williams, 2008). For example, several factors, including mate age (Michl et al., 2005) and quality (Gil et al., 1999, 2006; Tanvez et al., 2004), developmental stress (Gil et al., 2004), and frequency of intraspecific aggressive encounters (Wittingham and Schwabl, 2002) have been shown to influence circulating and yolk androgen concentrations, and may cumulatively contribute va

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