Are yolk androgens adjusted to environmental conditions? A test in two seabirds that lay single-egg clutches

BriAnne Addison [a,b,*], Z. Morgan Benowitz-Fredericks [c], J. Mark Hipfner [a], Alexander S. Kitaysky [c]

[a] Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada V5A 1S6
[b] University of Missouri—St. Louis, Biology Department, One University Boulevard, St. Louis, MO 63121, USA
[c] Institute of Arctic Biology, 311 Irving I, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

ARTICLE INFO

ABSTRACT

It is widely believed that female birds strategically allocate androgens to yolk in the manner that best equips offspring for feeding conditions during their development. Because most avian studies have focused on multi-egg clutch species, and interpreted results within the framework of sibling competition, we still know little about how yolk androgens might be allocated in direct response to environmental conditions. Most oceanic birds are long-lived and lay single-egg clutches, and their breeding success is tightly linked to highly variable marine production. That combination: a variable breeding environment, long lives, and single-egg clutches, makes oceanic birds good subjects to test hypotheses about yolk androgen allocation strategies. We measured concentrations of two yolk androgens, androstenedione (A4) and testosterone (T), in the single-egg clutches laid by early-laying Cassin's (*Ptychoramphus aleuticus*) and rhinoceros (*Cerorhinca monocerata*) auklets at Triangle Island, British Columbia, Canada, in 2002–2004. Environmental conditions including sea-surface temperatures and the timing and intensity of marine primary production varied over the 3 years, and in response, both the timing and success of seabird breeding varied. As in other avian species, concentrations of A4 and T varied markedly among individual eggs in both species (by factors of 3–8), yet contrary to expectation, little of the variation could be attributed to year effects. The high interindividual variation and the lack of interannual variation suggest a non-adaptive explanation for yolk androgen deposition relative to environmental conditions in these species.

© 2008 Elsevier Inc. All rights reserved.

1. Introduction

Mothers possess considerable capacity to adjust their off-springs' phenotypes to prepare them to meet the challenges posed by the environment in which they develop ("adaptive maternal effects"; Mousseau and Fox, 1998). The deposition by oviparous vertebrates of maternal androgens into egg yolks is one facet of maternal investment that has received considerable 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

* Corresponding author. Address: University of Missouri—St. Louis, Biology Department, One University Boulevard, St. Louis, MO 63121, USA. Fax: +1 314 516 6233.
E-mail address: brianne.addison@umsl.edu (B. Addison).

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 *Ptychoramphus aleuticus* and rhinoceros auklets *Cerorhinca monocerata*, 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 bridged the transition from a "cool and high productivity" oceanic period to a "warm and low productivity" oceanic period, and which affected the phenology and availability of prey for both of our study species (Mackas et al., 2007). We restricted our analyses to eggs laid early in the season, because early-laying females tend to be the older, more experienced members of seabird populations (deForest and Gaston, 1996; Pyle et al., 2001), those in better body condition (Gaston and Hipfner, 2006), and most likely to be employing the most effective strategies relative to environmental variation. To provide context, in each year we simultaneously monitored the timing and success of breeding of control groups of early layers, i.e. females of comparable ability to those whose eggs we removed.

2. Methods

2.1. Study site and field methods

The study was conducted at Triangle Island, British Columbia, Canada (50°52′N, 129°05′W) during the 2002–2004 breeding seasons. In each year, burrows of both species were checked every 2 days. Ten Cassin's auklet eggs and 10 rhinoceros auklet eggs were collected when first found, weighed (±0.1 g on an electronic balance), and then frozen immediately at −10 °C. All eggs were collected prior to the population-wide median laying date, and under permit from Simon Fraser University (Animal Care Permit) and the Canadian Wildlife Service (Migratory Bird Collection Permit). Breeding phenology and success were monitored on adjacent plots of the colony as outlined in Hipfner et al. (2004). The early-laying individuals on these plots served as control birds for the females from which eggs were collected as they are similar in laying date, and nest site features.

2.2. Hormone analysis

In the lab, the eggs were thawed and yolk and albumen separated. Homogenized yolks were aliquoted for hormone analysis, then re-frozen at −80 °C until assay at the University of Alaska Fairbanks. Yolk aliquots (average 1.3 g) were thawed and homogenized with 3 ml distilled water using a tissue grinder. A yolk pool was used

to validate that dilutions of yolk, and charcoal-stripped yolk spiked with hormone, were parallel to the standard curve. Approximately 0.02 g of yolk/water mix (9 mg yolk) was equilibrated with 2000 cpm of radiolabeled testosterone and androstenedione to assess the percent of hormone recovered from the extraction process, and correct final values for percent recovery.

Steroids were extracted using the following version of the protocol used by Schwabl (1993): Samples were extracted twice with 4 ml diethyl ether, dried under continuous nitrogen flow in a water bath at 40 °C, reconstituted in 1 ml 90% ethanol, and frozen for 24 h at −70 °C. The ethanol was decanted and dried using nitrogen. Androgens were then separated using column chromatography. Samples were reconstituted in 0.5 ml 10% ethyl-acetate in iso-octane, and added to short columns of diatomaceous earth, with a water trap and glycol phase. Androstenedione, testosterone and corticosterone were eluted in ethyl-acetate in iso-octane (following protocols described in Schwabl, 1993); however corticosterone levels were undetectable and so are not discussed further. We conducted separate radio-immunoassays for each species (Wingfield and Farner, 1975; Wingfield et al., 1991). Antibodies for testosterone and androstenedione were obtained from Wein Laboratories, Inc. (Concord, MA). For rhinoceros and Cassin's auklet, average testosterone recovery was 71% and 68%, respectively, average androstenedione recovery for both species was 66%, and post-extraction coefficient of variability among duplicates for both hormones in both assays was 2%.

2.3. Statistical analysis

Data met the requirements for parametric statistical analyses. For each species, concentrations of A4 and T were compared across years, using egg mass and lay date as covariates, and tested for parallelism of slopes with year*egg mass interaction terms in a multivariate ANCOVA using SAS (v. 6.12) proc glm. Univariate F-tests were generated for each androgen, as well as Wilks' lambda tests for each effect. For each species, mass of sampled eggs was compared using ANOVA with year as the predictor variable. Descriptive statistics were generated for breeding parameters of pre-median lay date nests, including hatching, fledging, and net reproductive success; as eggs were collected from pre-median lay date nests, these females are of comparable quality. We compared, hatching, fledging, and overall breeding success across years by contingency table analysis.

3. Results

Median laying dates varied by about 1 week across the 3 years of study, being earliest in 2002 (Cassin's auklet) or 2004 (rhinoceros auklet), and latest in 2003 in both species (Table 1). The proportion of control, early-laying pairs that raised chicks to fledging varied weakly among years in Cassin's auklets (Wald $\chi^2 = 4.67$, $P = 0.09$), but very strongly in rhinoceros auklets (Wald $\chi^2 = 11.07$, $P = 0.004$). Most of the variation in breeding success was due to hatching success, as fledging success was consistently high (Table 1). Fledging masses varied among years (Table 1) in Cassin's auklets (ANOVA, $F_{2,71} = 5.69$, $P = 0.005$), being lowest in 2003, but not in rhinoceros auklets (ANOVA, $F_{2,59} = 1.87$, $P = 0.16$). Collectively, the results presented in Table 1 indicate that environmental conditions for breeding for both species were better in 2002 and 2004 than in 2003.

Egg mass varied little among years (one-way ANOVA, year $R^2 < 0.01$ in both species). The overall variation in both [A4] and [T] was marked: in Cassin's auklet yolks, both [A4] (mean = 569.28 ng g^{-1} ± 90.15 95%CI; range = 141.5–1091.5 ng g^{-1}) and [T] (mean = 12.9 ng g^{-1} ± 2.22 95%CI; range = 3.6–28.6 ng g^{-1}) varied eightfold over 3 years. In rhinoceros auklet yolks, [A4] (mean = 837.03 ng g^{-1} ± 82.52 95%CI; range = 486.3–1386.9 ng g^{-1}) varied almost threefold,

Table 1
Timing of breeding for all females, and success of breeding for females that laid on or prior to the median laying date in 2002–2004

| Species	Year	Median lay date	No. eggs	% Hatched	% Fledged	% Success	Mean ± SD fledging mass (g)
Cassin's auklet	2002	31 Mar–4 Apr	43	72	97	70	162 ± 17
	2003	9–12 Apr	23	78	94	74	152 ± 15
	2004	2–6 Apr	36	89	100	89	169 ± 15
Rhinoceros auklet	2002	5–9 May	38	63	96	61	312 ± 26
	2003	7–11 May	24	46	91	42	294 ± 34
	2004	2–6 May	30	93	93	87	298 ± 40

All eggs analysed for androgens were collected on or before the median lay date in each year.

and [T] (mean = 22.82 ng g^{-1} ± 3.10 95%CI; range = 6.7–39.0 ng g^{-1}) almost sixfold. There were strong, positive correlations between [A4] and [T] in both Cassin's (r = 0.70, P < 0.001) and rhinoceros (r = 0.81, P < 0.001) auklet eggs (Fig. 1).

Contrary to expectation, little of the variation in [A4] and [T] could be explained by year, nor by egg mass, lay date or year*egg mass effects (Fig. 2; ANCOVA, all P > 0.4), except for year and year*egg mass interaction in Cassin's auklets, which were marginally non-significant (year: $F_{2,10}$ = 3.39, P = 0.07; year*egg mass: $F_{2,10}$ = 3.68, P = 0.06). Post-hoc univariate ANCOVAs of Cassin's auklet androgens showed no support for the year or year*egg mass interaction (both R^2 < 0.3, P > 0.4). Addressing our main hypothesis very directly, single factor ANOVAs showed that year effects were not important determinants of [A4] or [T] in either species (for Cassin's auklet, both R^2 < 0.09; for rhinoceros auklet, both R^2 < 0.14; all P > 0.14).
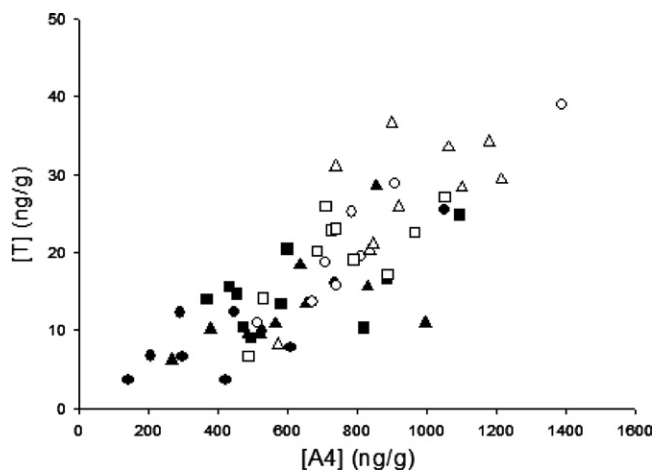
Fig. 1. Covariation between [A4] and [T] in the yolks of eggs laid by Cassin's (filled markers) and rhinoceros (open markers) auklets in each of 2002 (circles), 2003, (squares) and 2004 (triangles).
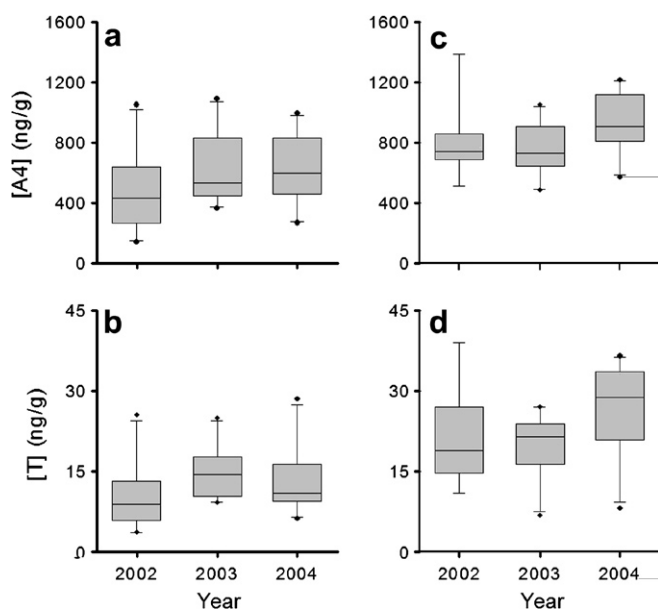
Fig. 2. Interannual variation in [A4] and [T] in the yolks of eggs laid by Cassin's (a and b) and rhinoceros auklets (c and d) in 2002–2004. There was no significant year effect on androgen concentrations in either species. Box-plots indicate the median, quartiles, and range of the data.

4. Discussion

Despite marked interannual variation in environmental conditions (Mackas et al., 2007), which affected the timing and success of seabird breeding (Hipfner et al., in press; Table 1), we found that the very marked, 3–8 fold interindividual variation in yolk androgen concentrations (A4 and T) in early-laid Cassin's and rhinoceros auklet eggs could not be attributed to year effects (Fig. 2). That result is not consistent with the hypothesis that females in these species strategically allocate yolk androgens to their single offspring in response to environmental variability. If we found no interannual variability in conjunction with very low interindividual variability, it would be difficult to ascertain whether auklet yolk androgen deposition was unaffected by interannual differences, or whether our subset of high-quality females were simply able to deposit some optimum level of androgens regardless of environmental conditions. However, because interindividual variability was so high, optimization by high-quality early breeders seems unlikely to explain the lack of interannual differences.

One possible explanation for the lack of interannual variation in yolk androgen concentrations is that the interannual variation in environmental conditions prior to laying was insufficient to trigger such a physiological response in females. However, we consider that most unlikely. As mentioned, Triangle Island lies within a highly variable marine ecosystem, and a variety of measures indicate that early-season conditions varied dramatically along the British Columbia coast in 2002–2004, with repercussions across trophic levels (Mackas et al., 2007). Our study years spanned the transition from "cold and productive" to "warm and less productive" oceanic periods, which featured dramatically different ocean phenologies (e.g. 3–4 week variation in the timing of the annual zooplankton biomass peak Mackas et al., 2007). In our study species, that was reflected in the observed variation in laying dates and especially hatching success, two sensitive measures (Ainley and Boekelheide, 1990; Bertram et al., 2001). Moreover, carbon and nitrogen isotope signatures of the same yolks assayed in our study indicate different foraging conditions during egg production across our study years for both species (Hipfner et al., in press; Hipfner, MacFarlane-Tranquilla and Addison, unpublished manuscript). It may be that environmental variation is of little consequence to yolk androgen allocation strategies in the absence of sibling competition.

Concurrent experimental studies on relaying propensity in the same two species at Triangle Island found that this breeding parameter, like yolk androgen concentration, was not modified in response to environmental conditions (90–100% relaying rates among early layers; Hipfner et al., in press). Combined with the observations on interannual variation in breeding success (Table 1; and 0–80% among experimental relayers), these data collectively suggest that Cassin's and rhinoceros auklets employ a fixed-investment strategy in producing their single-egg clutch, then adjust their investment as appropriate later in the reproductive effort (Table 1). In particular, we note that the marked interannual variation in hatching success likely reflects that widely variable proportions of pairs abandoned eggs. Whether the lack of responsiveness to pre-laying conditions is typical of all species that lay single-eggs, including other long-lived seabirds, remains to be determined.

If it is true that auklets and other oceanic seabirds employ such a fixed-investment strategy related to yolk androgens, then there should be little selection for offspring to respond to variations in androgen levels. Investigation into the effects of yolk androgens on offspring phenotype in auklets and other single-egg clutch species will be important tests of adaptive hypotheses for androgen allocation.

Why do yolk androgen concentrations vary so dramatically within a population breeding at the same time and place? Such issues lie at the heart of understanding phenotypic plasticity and

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 variability in the concentration of yolk androgens that a female deposits, independently of environmental conditions. There is increasing evidence that yolk androgen deposition levels are highly repeatable within females (Tobler et al., 2007; Eising et al., 2008), and this suggests that intrinsic factors may be more important than conditions measured here.

However, as noted previously (Williams et al., 2004), the high interindividual variability in yolk androgens is difficult to reconcile with the notion that the strategic maternal allocation of these hormones to egg yolks is important to offspring fitness, a notion for which there is considerable evidence in avian species that lay multi-egg clutches (Groothuis et al., 2005a). Yet not all studies have found beneficial effects of yolk androgens on offspring fitness (Navara et al., 2005), and effects on maternal fitness, which may be as important or even more so, have been little studied to date (Navara et al., 2006). Moreover, the question of whether females in oviparous vertebrates have the capacity to strategically allocate hormones to yolk, independently of their own hormonal state at the time, remains largely unresolved (Birkhead et al., 2000; Williams et al., 2004; but see Rhen et al., 2006). Eggs may in fact act as androgen sinks, enabling mothers to maintain optimal circulating levels (Navara et al., 2006). Clearly, a complete understanding of yolk androgen allocation strategies will require a better understanding of the ultimate drivers and physiological mechanisms involved in their transfer from female to offspring. At present, it remains difficult to determine whether yolk androgen allocation is an adaptation, an exaptation, or even a constraint (Ketterson and Nolan, 1999; Navara et al., 2006).

To summarize, results of our study of Cassin's and rhinoceros auklets, two species of long-lived oceanic birds that inhabit a highly variable environment and lay single-egg clutches, are not consistent with the hypothesis that females allocate yolk androgens in direct response to oceanographic environmental conditions for breeding. Instead, we found that in both species the more competent females in the population, i.e. early layers, made a relatively fixed investment in offspring at the egg stage, then adjusted effort later in the breeding episode. These results have potentially important implications to studies of optimal maternal investment and yolk allocation strategies.

Acknowledgments

References

Ainley, D.G., Boekelheide, R.J., 1990. Seabirds of the Farallon Islands. Stanford University Press, Stanford.

Benowitz-Fredricks, Z.M., Kitaysky, A.S., 2005. Benefits and costs of rapid growth in common murre chicks *Uria aalge*. J. Avian Biol. 36, 287–294.

Bertram, D.F., Mackas, D.L., McKinnell, S.M., 2001. The seasonal cycle revisited: interannual variation and ecosystem consequences. Prog. Oceanogr. 49, 283–307.

Birkhead, T., Schwabl, H., Burke, T., 2000. Testosterone and maternal effects—integrating mechanisms and function. Trends Ecol. Evol. 15, 86–87.

Braun, B., Hunt, G., 1983. Brood reduction in black-legged kittiwakes. Auk 100, 469–476.

deForest, L.N., Gaston, A.J., 1996. The effect of age on timing of breeding and reproductive success in the thick-billed murre. Ecology 77, 1501–1511.

Eising, C.M., Müller, W., Groothuis, T.G.G., 2006. Avian mothers create different phenotypes by hormone deposition in their eggs. Biol. Lett. 2, 20–22.

Eising, C.M., Pavlova, D., Groothuis, T.G.G., Eens, M., Pinxten, R., 2008. Maternal yolk androgens in European starlings: affected by social environment or individual traits of the mother? Behaviour 145, 51–72.

Gaston, A.J., Hipfner, J.M., 2006. Body mass changes in Brunnich's Guillemots *Uria lomvia* with age and breeding stage. J. Avian Biol. 37, 101–109.

Gil, D., Graves, J., Hazon, N., Wells, A., 1999. Male attractiveness and differential testosterone investment in zebra finch eggs. Science 286, 126–128.

Gil, D., Heim, C., Bulmer, E., Rocha, M., Puerta, M., Naguib, M., 2004. Negative effects of early developmental stress on yolk testosterone levels in a passerine bird. J. Exp. Biol. 207, 2215–2220.

Gil, D., Ninni, P., Lacroix, A., De Lope, F., Tirard, C., Marzal, A., Møller, A.P., 2006. Yolk androgens in the barn swallow (*Hirundo rustica*): a test of some adaptive hypotheses. J. Evol. Biol. 19, 123–131.

Gjerdrum, C., 2004. Parental provisioning and nestling departure decisions: a supplementary feeding experiment in Tufted Puffin *Fratercula cirrhata* on Triangle Island, British Columbia. Auk 121, 463–472.

Groothuis, T.G.G., Eising, C.M., Dijkstra, C., Müller, W., 2005b. Balancing between costs and benefits of maternal hormone deposition in avian eggs. Biol. Lett. 1, 78–81.

Groothuis, T.G.G., Müller, W., von Engelhardt, N., Carere, C., Eising, C.M., 2005a. Maternal hormones as a tool to adjust offspring phenotype in avian species. Neurosci. Biobehav. Rev. 29, 329–352.

Hamer, K.C., Hill, J.K., 1994. The regulation of food delivery to nestling Cory's Shearwaters *Calonectris diomedea*: the roles of parents and offspring. J. Avian Biol. 25, 198–204.

Harding, A.M., van Pelt, T.I., Piatt, J.F., Kitaysky, A.S., 2002. Reduction of provisioning effort in response to experimental manipulation of chick nutritional status in the Horned Puffin. Condor 104, 842–847.

Hipfner, J.M., Charleton, K., Davies, W.E., 2004. Rates and consequences of relaying in Cassin's Auklets and Rhinoceros Auklets breeding in a seasonal environment. J. Avian Biol. 35, 224–236.

Hipfner, J.M., MacFarlane-Tranquilla, L.A., Addison, B., in press. Do marine birds use envrionmental cues to optimize egg production? An experimental test based on relaying propensity. J. Avian Biol.

Ketterson, E.D., Nolan, V., 1999. Adaptation, exaptation, and constraint: a hormonal perspective. Am. Nat. 154, S4–S25.

Kilner, R.M., 2001. A growth cost of begging in captive canary chicks. Proc. Natl. Acad. Sci. USA 98, 11394–11398.

Lack, D., 1968. Ecological Adaptations for Breeding in Birds. Methuen, London, UK.

Litzow, M.A., Piatt, J.F., 2003. Variance in prey abundance influences time budgets of breeding seabirds: evidence from pigeon guillemots *Cepphus columba*. J. Avian Biol. 34, 53–64.

Mackas, D.L., Batten, S., Trudel, M., 2007. Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. Prog. Oceanog. 75, 223–252.

Metcalfe, N.B., Monaghan, P., 2001. Compensation for a bad start: grow now, pay later? TREE 16, 254–260.

Michl, G., Török, J., Peczely, P., Garamszegi, L.Z., Schwabl, H., 2005. Female collared flycatchers adjust yolk testosterone to male age, but not to attractiveness. Behav. Ecol. 16, 383–388.

Mousseau, T.A., Fox, C.W., 1998. The adaptive significance of maternal effects. TREE 13, 403–407.

Müller, W., Eising, C.M., Dijkstra, C., Groothuis, T.G.G., 2004. Within-clutch patterns of yolk testosterone vary with onset of incubation in black-headed gulls. Behav. Ecol. 15, 893–897.

Navara, K.J., Hill, G.E., Mendonça, M.T., 2005. Variable effects of yolk androgens on growth, survival, and immunity in eastern bluebird nestlings. Physiol. Biochem. Zool. 78, 570–578.

Navara, K.J., Siefferman, L.M., Hill, G.E., Mendonça, M.T., 2006. Yolk androgens vary inversely to maternal androgens in eastern bluebirds: an experimental study. Funct. Ecol. 20, 449–456.

Phillips, R.A., Croxall, J.P., 2003. Control of provisioning in grey-headed albatrosses (*Thalassarche chrysoma*): do adults respond to chick condition? Can. J. Zool. 81, 111–116.

Pyle, P., Sydeman, W.J., Hester, M., 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. J. Anim. Ecol. 70, 1088–1097.

Reed, W.L., Vleck, C.M., 2001. Functional significance of variation in egg yolk androgens in the American Coot. Oecologia 128, 164–171.

Rhen, T., Crews, D., Fivizzani, A., Alf, P., 2006. Reproductive trade-offs and yolk steroids in female leopard geckos, *Eublepharus macularius*. J. Evol. Biol. 19, 1819–1829.

Rubolini, D., Martinelli, R., von Engelhardt, N., Romano, M., Groothuis, T.G.G., Fasola, M., Saino, N., 2007. Consequences of prenatal androgen exposure for the repro-

ductive performance of female pheasants (*Phasianus colchicus*). Proc. R. Soc. B 274, 137–142.

Schneider, D.C., Duffy, D.C., 1985. Scale-dependent variability in seabird abundance. Mar. Ecol. Prog. Ser. 25, 211–218.

Schwabl, H., 1993. Yolk is a source of maternal testosterone for developing birds. Proc. Natl. Acad. Sci. USA 90, 11446–11450.

Schwabl, H., 1996. Environment modifies the testosterone levels of a female bird and its eggs. J. Exp. Biol. 276, 157–163.

Sockman, K.W., Schwabl, H., 2000. Yolk androgens reduce offspring survival. Proc. R. Soc. B 267, 1451–1456.

Sydeman, W.J., Bradley, R.W., Warzybok, P., Abraham, C.L., Jahncke, J., Hyrenbach, K.D., Kouskie, V., Hipfner, J.M., Ohman, M.D., 2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: unusual atmospheric blocking? Geophys. Res. Lett. 33, L22S09. doi:10.1029/2006GL02673.

Tanvez, A., Beguin, N., Chastel, O., Lacroix, A., Leboucher, G., 2004. Sexually attractive phrases increase yolk androgens deposition in Canaries (*Serinus canaries*). Gen. Comp. Endocrinol. 138, 113–120.

Tobler, M., Granbom, M., Sandell, M.I., 2007. Maternal androgens in the pied flycatcher: timing of breeding and within-female consistency. Oecologia 151, 731–740.

Uller, T., Olsson, M., 2003. Prenatal exposure to testosterone increases ectoparasite susceptibility in the common lizard (*Lacerta vivipara*). Proc. R. Soc. B 270, 1867–1870.

Verboven, N., Monaghan, P., Evans, D.M., Schwabl, H., Evans, N., Whitelaw, C., Nager, R.G., 2003. Maternal condition, yolk androgens and offspring performance: a supplemental feeding experiment in the lesser black-backed gull (*Larus fuscus*). Proc. R. Soc. B 270, 2223–2232.

Williams, T.D., 2008. Individual variation in endocrine systems: moving beyond the 'tyranny of the Golden Mean'. Phil. Trans. Roy. Soc. B 363, 1687–1698.

Williams, T.D., Kitaysky, A.S., Vezina, F., 2004. Individual variation in plasma estradiol-17B and androgen levels during egg formation in European starlings *Sturnus vulgaris*: implications for the regulation of yolk steroids. Gen. Comp. Endocrinol. 136, 346–352.

Wingfield, J.C., Farner, D.S., 1975. The determination of five steroids in avian plasma by radioimmunoassay and competitive protein binding. Steroids 26, 311–327.

Wingfield, J.C., Hegner, R.E., Lewis, D., 1991. Circulating levels of luteinizing hormone and steroid hormones in relation to social status in the cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali*. J. Zool. 225, 43–58.

Wittingham, L.A., Schwabl, H., 2002. Maternal testosterone in tree swallow eggs varies with female aggression. Anim. Behav. 63, 63–67.