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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Pre-breeding energetic management in a mixed-strategy breeder

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Abstract Integrative biologists have long appreciated that the effective acquisition and management of energy prior to breeding should strongly influence fitness-related reproductive decisions (timing of breeding and reproductive investment). However, because of the difficulty in capturing pre-breeding individuals, and the tendency towards abandonment of reproduction after capture, we know little about the underlying mechanisms of these life-history decisions. Over 10 years, we captured free-living, arctic-breeding common eiders (*Somateria mollissima*) up to 3 weeks before investment in reproduction. We examined and characterized physiological parameters predicted to influence energetic management by sampling baseline plasma glucocorticoids (i.e., corticosterone), very-low-density lipoprotein (VLDL), and vitellogenin (VTG) for their respective roles in mediating energetic balance, rate of condition gain (physiological fattening rate) and reproductive investment. Baseline corticosterone increased significantly from arrival to the initiation of reproductive investment (period of rapid follicular growth; RFG), and showed a positive relationship with body mass, indicating that this hormone may stimulate foraging behaviour to facilitate both fat deposition and investment in egg production. In support of this, we found that VLDL increased throughout the pre-breeding period, peaking as predicted during RFG. Female eiders exhibited unprecedentedly high levels of VTG well before their theoretical RFG period, a potential strategy for pre-emptively depositing available protein stores into follicles while females are simultaneously fattening. This study provides some of the first data examining the temporal dynamics and interaction of the energetic mechanisms thought to be at the heart of individual variation in reproductive decisions and success in many vertebrate species.

Keywords Energetic management · Corticosterone · Energetic metabolites · Breeding threshold · Mixed-strategy breeder

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Introduction

Reproduction is an energetically demanding life-history stage in which individuals must balance energetics between somatic needs and reproduction. After arriving at the breeding grounds following migration, individuals better able to optimally manage energetic allocation based on intrinsic (i.e., arrival condition) and extrinsic factors (e.g., resource availability) prior to reproduction are predicted to maximise fitness (Drent and Daan 1980; Stearns 1992; Rowe et al. 1994; McNamara and Houston 1996; Kisdi et al. 1998).

In highly seasonal environments, the timing of breeding is critical because of the trade-off between delaying reproduction to gain in body condition and reproductive investment against the declining survival probability of later produced offspring (Drent and Daan 1980; Rowe et al. 1994; Bêty et al. 2003). Although these relationships have been broadly tested empirically (Lepage et al. 2000; Bêty et al. 2003; Descamps et al. 2011; Sénéchal et al. 2011), the underlying mechanisms mediating the rapid and required change in body condition for reproduction, and the trade-off between self-maintenance and reproductive investment have not been well characterized (Williams 2005, 2012a).

A number of physiological traits have recently been identified for their potential preparative and mediatory role in reproductive investment decisions (Williams 2012a). Glucocorticoids (GCs) such as corticosterone (CORT) and cortisol are a group of hormones that mediate daily and annual energetic management (Romero 2002; Landys et al. 2006) and preparation for energetically demanding life-history stages (Love et al. 2014). Baseline GCs have been suggested as mediators of life-history decisions (e.g., Love et al. 2013, 2014), given that they are elevated during energetically demanding life-history stages (Dallman et al. 1993; Romero 2002; Landys et al. 2006; Crespi et al. 2013). Further, increases in baseline GCs are thought to stimulate foraging behaviour (Astheimer et al. 1992; Dallman et al. 1993; Angelier et al. 2008; Kitaysky et al. 2010; Lynn et al. 2010), which may influence an individual's ability to accumulate resources prior to reproductive investment (Holberton 1999; Kitaysky et al. 1999; Holberton et al. 2007). However, due to the logistical constraints of capturing free-living birds prior to breeding, the role GCs play in pre-breeding energetic management and endogenous resource accumulation are largely unknown.

Similarly, integrative ecologists have begun quantifying resource accrual (rate of condition gain) by measuring plasma levels of generic very-low-density lipoprotein (VLDL). Generic VLDL is a type of lipoprotein assembled in the liver from triglycerides, cholesterol, and apolipoproteins which transports triacylglycerides throughout the body following feeding in vertebrates (Gibbons et al. 2004), and is directly related to the rate of condition gain in many species (Seaman et al. 2005; Cerasale and Guglielmo 2006; Williams et al. 2007; Anteau and Afton 2008). In oviparous vertebrates, the period of rapid follicle growth (RFG) in which follicles increase in size quickly in preparation for ovulation (Drent and Daan 1980; Rowe et al. 1994; Bêty et al. 2003; Williams 2012a) results in a mechanistic shift from the production of generic VLDL to VLDLy (yolk-targeted VLDL). At this time, the production of vitellogenin (VTG), an egg yolk precursor of the lipoproteins and phosphoproteins that make up most of the protein content of yolk in nearly all oviparous species (Robinson 2008), also increases dramatically (Walzem et al. 1999; Challenger et al. 2001; Salvante and Williams 2002; Gorman et al. 2009). The secretion trends in VLDL and VTG have been well documented in income-strategy breeding species (European starlings, *Sturnus vulgaris*, Challenger et al. 2001; zebra finches, *Taeniopygia guttata*, Salvante and Williams 2002) in which follicles are fuelled entirely by resources from current foraging (Stephens et al. 2009). However, little is known about these dynamics in species using a mixed, capital-income breeding strategy in which individuals use largely endogenous, stored resources and some resources from current foraging to fuel follicle production (Stephens et al. 2009). Since the energetic demands and resource allocation strategies differ widely within the income-capital spectrum, there are likely also fundamental differences in the pre-breeding roles of GCs, VLDL and VTG in individuals reliant on a capital or partial-capital strategy.

We examined the temporal dynamics of plasma baseline GCs (corticosterone; CORT), VLDL and VTG during pre-breeding by sampling individual female arctic-breeding common eiders (*Somateria mollissima*) up to 3 weeks before a given individual's investment in reproduction. Females of this species are ideal for examining the physiological mechanisms which mediate pre-breeding resource allocation decisions because they arrive in varying condition after migration, and therefore must recover from migration while also rapidly accumulating enough body stores to fuel egg production (Descamps et al. 2011; Sénéchal et al. 2011), and simultaneously fatten to sustain a long incubation period without feeding (24 days; Korschgen 1977). Arctic-breeding eiders are further constrained by the short polar breeding season within which they must successfully time reproduction to maximise reproductive success (Love et al. 2010). Our goals were to (1) characterise the post-migration, pre-breeding energetic dynamics of plasma CORT, VLDL (i.e., generic VLDL and VLDLy; see "Materials and methods"), and VTG at the population scale, and (2) examine the relationships between body mass and these physiological traits to determine potential physiological thresholds associated with reproductive status. We predicted that baseline CORT would be significantly elevated both prior to recruiting follicles and RFG compared to arrival to match the energetic demands of depositing fat stores and follicle recruitment, with an associated increase in VLDL. Based on previous work in various avian species (Challenger et al. 2001; Salvante and Williams 2002; Gorman et al. 2009), we predicted a positive, rapid elevation in plasma VTG confined to the RFG period only. Finally, Sénéchal et al. (2011) found that a body mass threshold drives the initiation of follicle growth and the RFG period. Assuming that the secretion of the physiological traits we have chosen mediate the gain in body condition, we predicted strong non-linear relationships (with potential thresholds) between baseline CORT/VLDL/VTG and body mass, providing evidence that they represent relevant underlying mechanisms involved in RFG initiation and reproductive readiness.

Materials and methods

Study system and reproductive stage assignment

Data were collected from 2003 to 2013 (except 2005) from the largest known nesting colony of common eiders in the Canadian Arctic (up to 9,000 pairs annually) located on Mitivik Island (64°02′N, 81°47′W) a small (800 × 400 m), low-lying (<8 m elevation) island in the East Bay Migratory Bird Sanctuary, Nunavut, Canada. Females migrate from wintering grounds off the coasts of Greenland and Newfoundland, Canada in May, arrive in early June and lay between mid-June and early July (Mosbech et al. 2006).

Each year, eiders were captured using flight nets from mid-June to early-July overlapping with the eider's timing of arrival at the breeding grounds at Mitivik Island (Descamps et al. 2011). Following capture, a random sample of females ($n = 799$ across 10 years) were measured (tarsus in mm) and weighed (body mass in g), banded, and given a unique combination of temporary plastic nasal tags, attached with UV degradable monofilament, which fall off at the end of the season and do not impact survival (H.G. Gilchrist, unpublished). Subsequent breeding behaviour of individuals (e.g., laying date, clutch size, reproductive success) was monitored consistently across years from seven permanent observation blinds using spotting scopes, together with entering the colony 2–3 times each season to check nests.

Individuals were considered to be non-breeders if they were captured, but were neverfound to have laid an egg in the colony. Pre-breeding individuals were defined as being caught inflight nets without having yet initiated laying. Accurate breeding state of all individuals wasdetermined via consistent, twice-daily nest tracking on the island. When we were uncertain of anindividual's laying date, the nest was visited to determine clutch size and the duration ofincubation via egg candling. With the knowledge of a female's clutch size, incubation duration indays, and that female eiders lay one egg every 28 h (Watson et al. 1993), we were able toback-calculate the original laying date. Knowing the laying date, we were then able to ascertainthe reproductive stage of the female at capture. Pre-breeding birds were divided into twocategories based on follicle recruitment at the time of capture: RFG or pre-recruiting females.Individuals were identified as "pre-recruiting" if they were captured 8 days or longer before their laying date (Alisauskas and Ankney 1992; Watson et al. 1993). The length of the RFG period forthis species has been estimated theoretically (Alisauskas and Ankney 1992; Robertson 1995) tobe 6–9 days in length with a 28-h delay prior to laying for albumen and shell formation(Watson et al. 1993), giving a range of 7–10 days. We thus conservatively classified individualsas "RFG" if females were caught between 1 and 7 days prior to laying. Individuals were thereforeconsidered to be "laying" if they were caught 0–4 days into laying (based on an average clutchsize of 4 in this colony), and "incubating" if they were captured and sampled 5 days or morepost-laying based on back-calculations of laying date (as above). Although we categorize andpresent data for non-breeders, incubating, and laying females, we only include these groups offemales for reference to pre-breeding birds.

Blood sampling

In 2003 and 2004, a maximum of 300 µL of blood was collected within 10 min of capture to measure plasma VLDL and VTG from each female by puncturing the tarsal vein (2003: 26G needle and heparinized 75 µL capillary tubes; 2004: heparinized vacutainer with a 26G butterfly needle). From 2006 to 2013, blood samples were collected within 3 min of capture to obtain baseline CORT (Wingfield et al. 1982; Romero and Reed 2005; O. Love, unpublished data) and plasma VLDL using a 23G thin wall, 1-inch (c.25-mm) needle attached to a heparinized 1-mL syringe. Blood samples were kept at 4 °C and centrifuged at 10,000 rpm for 10 min within 6 h of collection. Plasma was separated from red blood cells and stored at −20 °C for further analysis.

Physiological assays

Baseline plasma CORT was analysed using a previously-validated enzyme-linked immunoassay (EIA; Assay Designs, Ann Arbor, MI, USA) run in triplicate at a 1:20 dilution with 1.5 % of kit-provided steroid displacement buffer (Love and Williams 2008). Each plate was run with a kit-provided standard curve by serially diluting a 200,000 pg mL^{-1} CORT standard, and a control of laying hen plasma (Sigma-Aldrich Canada, Oakville, ON, Canada). Assay plates were read on a spectrophotometer plate reader at 405 nM, and the mean inter- and intra-assay coefficients of variation across all plates were 8.54 and 5.87 %, respectively.

Samples were analysed for zinc (Zn) using a commercially-available kit (Zinc Kit; Wako Chemicals, VA, USA) as a measure of the plasma concentration of the yolk precursor vitellogenin (VTG) developed for chickens (Mitchell and Carlisle 1991), and validated in waterfowl (Gorman et al. 2009) and seabirds (Vanderkist et al.

2000; Crossin et al. 2010). Each plate was run with a kit-provided Zn standard (2 μg mL^{-1}) and a control sample of laying-hen plasma (Sigma-Aldrich, USA). Samples were read on a spectrophotometer plate reader, and the inter- and intra-assay coefficients of variation were 3.11 and 3.57 % for total Zn, and 12.49 and 9.17 % for depleted Zn, respectively.

Very low-density lipoprotein (VLDL) was quantified using a commercially-available and previously-validated kit which measures plasma triglycerides (TRIG; #TR0100-1KT; Sigma Aldrich, USA; Williams et al. 2007). Samples were run with spectrophotometer plate reader for the concentration of total and free glycerol which, when subtracted, provide the TRIG concentration (mmol L^{-1}). Each plate was run with a control of laying hen plasma (Sigma-Aldrich, USA) and a standard curve based on a serial dilution of the glycerol standard (2.54 mmol L^{-1}). Inter- and intra-assay coefficients of variation for total TRIG were 11.27 and 4.42 %, and for free glycerol 5.51 % and 6.29 %, respectively. The TRIG values from the assay indicated generic VLDL, which we corrected for body mass to obtain estimated fattening rate in pre-recruiting birds (Williams et al. 2007), and a proxy for the amount of VLDLy in RFG stage birds (Vanderkist et al. 2000; Crossin et al. 2010).

Statistics

To characterise the secretion dynamics of each physiological trait, we determined potential breakpoints in the relationship between physiological traits or body mass using segmented linear regression (Muggeo 2003) in pre-recruiting and RFG females. This analysis identifies sudden, significant positive or negative changes (i.e., breakpoints) in a series of data points, allowing us to detect if and when there were changes in the secretion patterns of CORT, VLDL, VTG or in body mass (dependent variables) across the pre-breeding period (with pre-laying interval as the independent variable). This procedure identifies and estimates breakpoints by iteratively fitting a model with a linear predictor. For each iteration, a standard linear model is fitted and the breakpoint value is updated until algorithm convergence occurs. This procedure was performed for each dependent variable separately. All segmented models were fitted using the Segmented R package (Muggeo 2003; R Core Team 2014).

To describe physiological trait dynamics, we first tested for the presence of several non-linear relationships between body mass and CORT, VLDL or VTG for all females to determine which best characterised the relationship between body mass and each physiological trait. Specifically, we compared Gompertz, logistic, Weibull, quadratic and linear (used as a null model) models with year included as a random factor. For each dependent variable (CORT, VLDL or VTG), we ranked the five models using Akaike information criterion (AIC; Burnham and Anderson 2002) to determine which model best described the relationship between each physiological trait and body mass. A linear model best described the relationship between body mass and CORT (the null model ranked at $\Delta AIC = 1.83$ compared to the logistic model). Logistic regressions best explained the relationship between body mass and VTG ($\Delta AIC = 1.02$ compared to the Gompertz model and $\Delta AIC = 5.31$ compared to the null model) and body mass and VLDL ($\Delta AICc = 6.27$ compared to the Gompertz model and $\Delta AIC = 20.1$ compared to the null model). For these non-linear relationships between VLDL or VTG and body mass, we used the lavielle function of the R package adehabitatLT (Calenge 2012) to identify segments (thresholds) on the fitted logistic relationships. This function performs a non-parametric segmentation using the penalised contrast method of Lavielle (1999) with the goal of determining the threshold values of body mass at which VTG and VLDL start changing in preparation for, or as a result of, reproduction. For both VLDL and VTG, we then obtained the body mass corresponding to the different identified sections. Previous research in this colony has shown that correcting body mass for body size (i.e., "body condition") accounts for only 1 % of the variation in body mass, and that body mass alone is a good proxy of body reserves, performing even better than body mass adjusted for wing (Descamps et al. 2010). As such, we used uncorrected body mass in all our analyses. All values are presented as mean ± SEM.

Results

Physiology and body mass dynamics across breeding stages

On average across the 9-year sampling period, females arrived on 174 ± 0.6 days and laid on 180 ± 0.8 days (both Julian dates). Although there was variation in arrival and laying dates across years, all mean arrival and laying dates were within 7–8 days of each other, respectively (Table 1).

Body mass increased slightly, but was consistently high throughout the pre-recruiting and RFG periods (Fig. 1a), and we detected no break points for body mass. Plasma VTG was low 20 days prior to laying, then increased steadily throughout the remaining pre-recruiting period, with the highest observed values between 14 and 7 days prior to laying (Fig. 1b), although no breakpoints were found for VTG. Baseline CORT was relatively low in the pre-recruiting period, with a sharp increase starting 8 days prior to

Table 1 Julian arrival and laying dates of female common eiders (*Somateria mollissima*) from East Bay, Nunavut from 2003 to 2013

Year	Julian arrival date					Julian laying date				
	n	Min	Max	Mean	SE	*n*	Min	Max	Mean	SE
2003	65	165	183	172.3	0.61	53	171	191	180.6	0.67
2004	91	165	189	178.5	0.78	51	176	199	186.2	0.74
2005[a]	276	163	178	167.8	0.3	161	164	194	178.0	0.5
2006	144	161	173	167.2	0.31	121	157	198	175.3	0.57
2007	135	169	174	172.3	0.14	94	164	192	183.0	0.53
2008	91	165	178	173.3	0.30	63	168	195	178.4	0.62
2009	103	169	189	178.8	0.56	55	175	196	183.7	0.68
2010	86	165	183	176.2	0.58	43	170	192	178.0	0.79
2011	39	168	180	173.1	0.59	35	168	193	181.0	0.94
2012	18	169	180	175.2	0.85	13	173	187	178.0	1.11
2013	27	167	84	174.5	0.89	19	170	189	179.9	1.24

[a] Physiological data were not available for this year

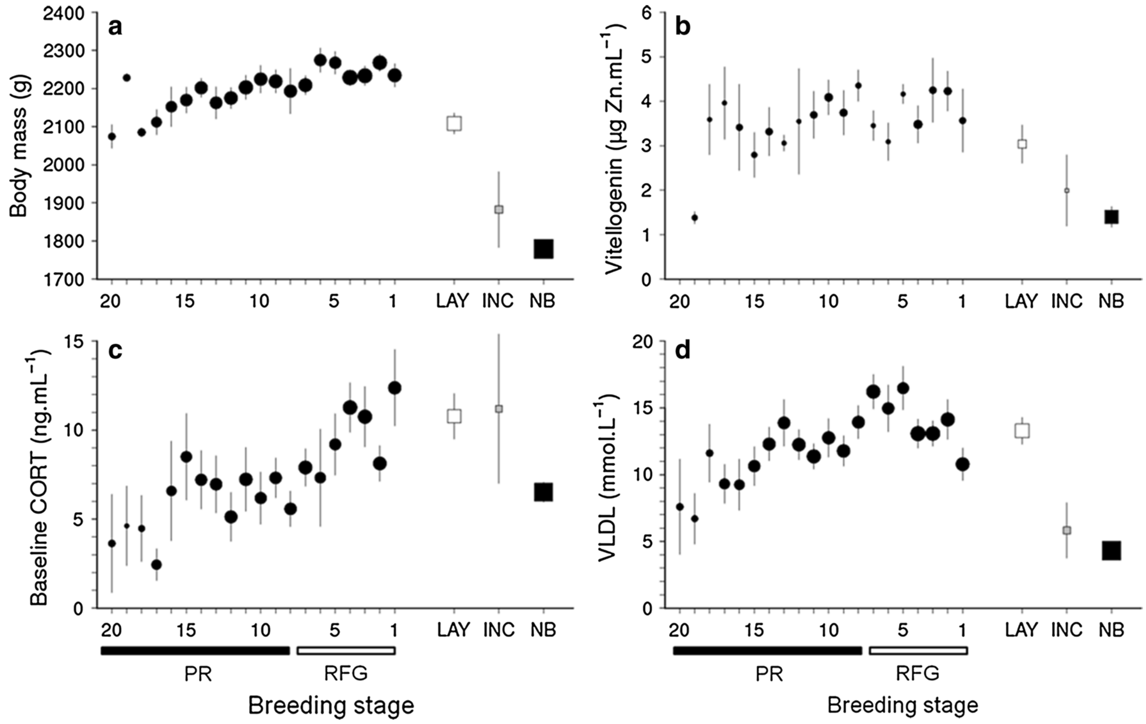

Fig. 1 Changes in body mass (**a**), vitellogenin-VTG (**b**), baseline CORT (**c**) and total VLDL (**d**) across breeding stages of female common eiders (*Somateria mollissima*). The *black rectangle* represents the duration of the pre-recruiting (*PR*) stage and the *open rectangle* denotes the rapid follicle growth (*RFG*) stage. Values are mean ± SEM. provided for each day prior to laying (*black dots*), during laying (*LAY*, *white squares*), incubation (*INC*, *gray squares*) and in non-breeding (*NB*, *black squares*) periods. Symbol sizes are proportional to log (*n*)

laying (breakpoint value: 8.0 ± 3.4 days), 1 day before the predicted RFG period (Fig. 1c). Plasma VLDL was low at the beginning of the pre-recruiting period, but henceforth increased rapidly, reaching the highest observed values 5.4 days prior to laying during the predicted RFG period (breakpoint value: 5.4 ± 1.0 days), before declining in concentration again until laying (Fig. 1d).

Physiological thresholds and reproductive stage change points

For VLDL the segmentation procedure indicated three different ranges: (1) low-range values (2.85 ± 0.39 mmol L^{-1}), (2) an increase phase, and (3) high-range values (13.11 ± 0.34 mmol L^{-1}; $n = 112$; Fig. 2a). In relation to body mass, the low-range values of VLDL occurred between 1,410 and 1,776 g, the increasing phase between 1,777 and 2,004 g, and the high-range values from 2,005 to 2,430 g (Fig. 2a). Similar to VLDL, VTG also showed three distinct ranges: (1) low-range values (1.05 ± 0.27 ug Zn mL^{-1}), (2) an increase phase, and (3) high-range values (3.61 ± 0.15 ug Zn mL^{-1}; $n = 67$; Fig. 2b). In relation to body mass, the low-range values of VTG occurred between 1,410 and 1,690 g, the increasing phase between 1,691 and 1,894 g, and the high-range values from 1,895 to 2,430 g (Fig. 2b). Since a linear model best described the relationship between CORT and body mass, we were unable to test for the presence of thresholds. However, a mixed model regression showed that body mass significantly predicted baseline CORT levels ($\beta = 0.006 \pm 0.001$, $F_{1,552} = 20.36$, $p < 0.0001$, conditional $R^2 = 0.08$; Fig. 2c).

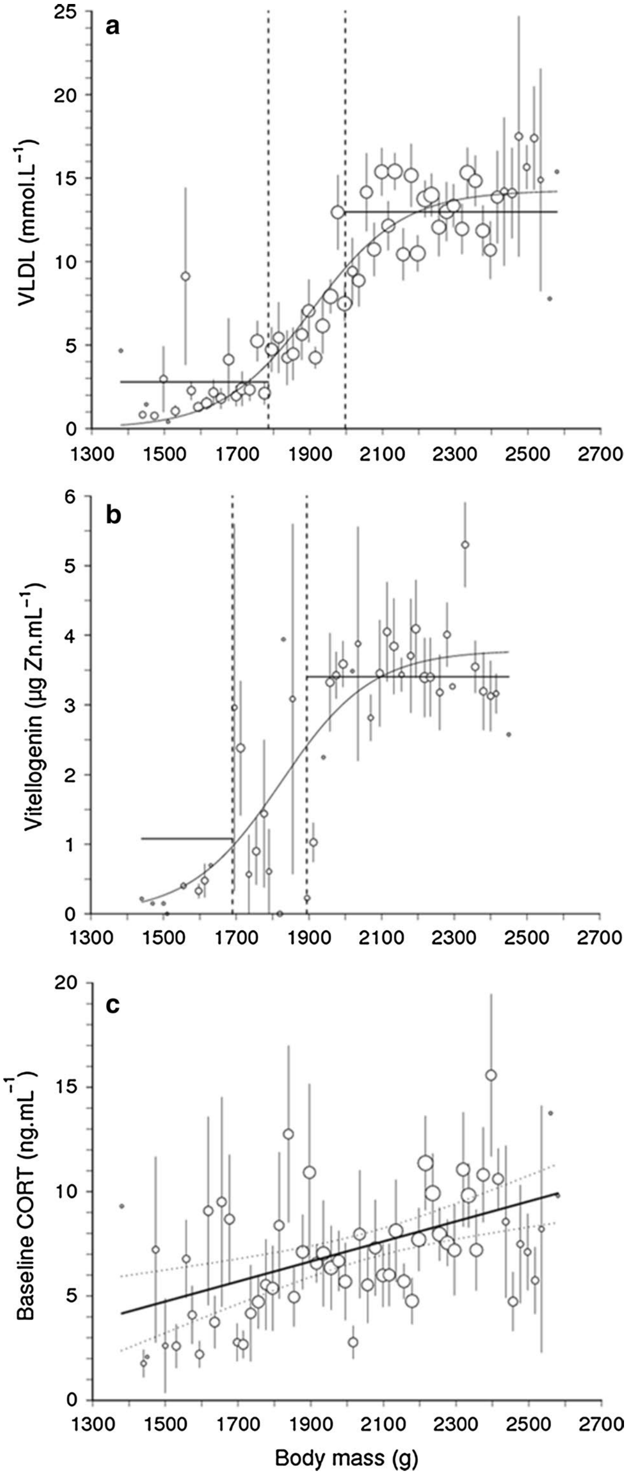

Fig. 2 Relationship between total VLDL (**a**), vitellogenin-VTG (**b**) and baseline CORT (**c**) with body mass at capture. Logistic regression are fitted (*solid black lines*) as well as sections (*dashed vertical lines*) with *horizontal black lines* indicating the mean for the identified sections. Values are mean ± SEM. Dot sizes are proportional to log(n)

Discussion

Given the difficulty in capturing individuals prior to reproductive investment, data on the pre-breeding mechanisms that mediate eventual reproductive decisions are extremely rare. As such, little is known about the pre-breeding dynamics of physiological traits governing the energetics of reproductive investment. We found that arctic-breeding female common eiders exhibited consistent and dramatic increases in baseline CORT prior to and throughout the period of follicle recruitment. As predicted, plasma VLDL (physiological fattening rate) subsequently increased throughout the pre-recruiting period and predictably declined in the middle of the RFG period. In contrast to previous studies in income breeding species, elevated VTG in the mixed capital-income strategy eiders was not confined solely to the RFG period, but instead began increasing more than 2 weeks in advance of laying and over a week prior to the predicted RFG period. Further, the secretion of VTG and VLDL across the pre-breeding period appeared to be uncoupled in relation to RFG. Specifically, elevations in VLDL were confined to the RFG period, whereas VTG was elevated throughout both the pre-recruiting and RFG periods. The secretions of VTG and VLDL were related to key changes in body mass that likely represent a threshold for shifting breeding stages. Finally, the secretion of baseline CORT was linearly related to body mass, indicating that it may be causally linked to increases in the rate of condition gain and follicle recruitment prior to laying. This study is one of the first to illuminate the potential mechanisms and responses underlying the decision to invest in reproduction, providing foundational information for future correlative and manipulative work examining how energetic physiology and environmental variation influence fitness in vertebrates.

Determining the RFG period in common eiders

Empirically determining an accurate RFG period and validating physiological markers of reproductive timing for common eiders is important, given this species' emerging use as a general model to examine the physiological, phenological and reproductive responses of seabirds to environmental variation across its circumpolar breeding range (Love et al. 2010; Mallory et al. 2010). Currently, the length of the RFG period for common eiders has only been estimated indirectly and theoretically, and without consensus (Alisauskas and Ankney 1992; Robertson 1995). Previous research in waterfowl (Gorman et al. 2009) and in income-breeding passerines (Challenger et al. 2001; Salvante and Williams 2002) have shown undetectable VTG concentrations and generally low levels of VLDL in pre-breeding, non-breeding and wintering birds, with a rapid increase and then decline of VTG and VLDLy within a clearly defined, easily identifiable RFG period (Challenger et al. 2001; Salvante and Williams 2002; Gorman et al. 2009; Palm 2012). We found that, on a population level, female eiders have unprecedented, consistent elevations of plasma VTG far earlier than predicted (18 days prior to laying rather than 6–9 days), and that only VLDL demonstrated a breakpoint (decrease) prior to laying. These data suggest that eiders may initiate VTG production up to 2 weeks prior to laying, although they may not initiate rapid follicular growth or uptake of VLDL to yolks until shortly prior to laying (continued discussion below). Captive studies with the ability to repeatedly sample individuals and monitor follicular growth on a daily basis will help to further determine the follicle growth patterns and the potential adaptive reasons for this earlier than expected elevation of VTG in common eiders.

Yolk-precursor secretion and thresholds

We found that both VTG and VLDL demonstrated threshold relationships with body mass, where females around 1,700–1,800 g were in an increasing phase, gaining in mass (increasing VLDL) and fuelling follicle development (increasing VTG) until reaching a mass plateau around 1,900–2,000 g. This is consistent with the body mass thresholds reported by Sénéchal et al. (2011) in which females that were 2,000 g or heavier were developing follicles and females under 1,800 g tended to be non-follicle recruiting. Females around 1,800 g may commit to breeding, initiate investment and begin secretion of VTG and VLDL through their continued foraging and gaining in body mass until they reach approximately 2,000 g. After achieving a body mass of 2,000 g, females then initiate follicle development with peak secretion of VTG and VLDL. It is important to note that the thresholds for VTG are about 100 g lighter than thresholds for VLDL, which supports our results demonstrating that elevations in VTG secretion occur earlier than elevations in VLDL secretion (Fig. 1). Although extrinsic energetic mechanisms acting as cues for initiating reproduction have been suggested and empirically tested broadly (i.e., food availability, energetic balance), our current understanding of the underlying (i.e., physiological) mechanisms influencing food intake, gain in condition, and initiation of reproductive state are poorly understood (Williams 2012b). As such, this is one of the first studies examining the underlying mechanisms influencing individual variation in the rate of condition gain and energetic management in pre-breeding birds. Continued investigations of energetic management and yolk-precursors interacting with body mass in other long-lived, capital-income strategy species may further our understanding of specific follicle recruitment strategies, and the associated trade-offs and constraints which may be dependent on life-history and reproductive strategy.

Pre-breeding energetics

Resource accrual and allocation during the pre-breeding period is critical in mixed capital-income breeding species such as common eiders to meet the multiple energetic requirements for reproductive investment (i.e., fattening and depositing protein stores for incubation and egg production; Bottitta et al. 2003; Sénéchal et al. 2011). As a mixed (i.e., capital-income) strategy breeder, after arriving at the breeding grounds female eiders must recover in condition from migration, then deposit substantial endogenous resources (i.e., body fat and protein) to fuel eventual long incubation bouts, and divert resources towards egg production. While we know that female eiders spend an increasing amount of time diving during the pre-breeding period (52 % more time foraging compared to annual average) declining after laying the first egg (Rigou and Guillemette 2010), we currently do not know the mechanisms mediating this increase in foraging rate. As we predicted, plasma CORT increased significantly throughout the pre-breeding period, peaking just prior to the predicted RFG period when female eiders are in peak energetic demand for reproductive investment (Sénéchal et al. 2011). Given that CORT levels have been linked to foraging behaviour (Astheimer et al. 1992; Dallman et al. 1993; Angelier et al. 2008; Kitaysky et al. 2010; Lynn et al. 2010; Crossin et al. 2012) and preparation for energetically demanding life-history stages (Love et al. 2014), we suggest that this dramatic increase in baseline CORT may be the mechanism stimulating foraging and facilitating resource accrual during this energetically demanding life-history stage. This idea is further confirmed via the positive relationship we detected between baseline CORT and body mass. Considering that this increase in baseline CORT occurs for much longer than 1 week after arrival on the breeding grounds, it is most likely that the elevation in CORT is related to reproduction rather than to post-migratory condition gains. Alternatively, elevations in baseline CORT may be a response from increased foraging rather than driving foraging behaviours. To determine whether baseline CORT is in fact causally driving pre-breeding fattening rates and reproductive investment, future studies will need to examine the relationship between baseline CORT, fattening rate and reproduction, using a combination of correlative and manipulative approaches (e.g., Hennin et al. 2012).

In addition to increases in baseline CORT throughout the pre-breeding period, there was a relative increase in VLDL up until 5.4 days prior to laying at which time the mean concentration decreased. This decline in plasma VLDL may be driven by the transition between females achieving the minimum amount of endogenous fat stores they require for reproduction and the initiation of allocating fewer exogenous resources (and potentially some endogenous resources) to rapid follicular growth in preparation for ovulation. This result is again in stark contrast to the secretion patterns previously found in other avian species (Challenger et al. 2001; Salvante and Williams 2002; Gorman et al. 2009), where VTG and VLDL secretion are tightly coupled. Since pre-breeding females are within a life-history stage in which the accumulation and management of fat stores is critical to successfully complete reproduction, females may deposit their less critical and possibly less required protein stores (VTG) to follicles much earlier than other species. Early protein deposition may initiate early follicle recruitment while females are still acquiring endogenous fat stores for themselves, thereby potentially uncoupling the secretion of VTG and VLDLy. Once females have accumulated enough endogenous fat for reproduction, they may forage at a low rate to ensure their endogenous stores remain as full as possible, requiring only minimal rates of fat deposition to maintain body stores and therefore decreased plasma VLDL. As such, early protein deposition to follicles may be an adaptive strategy in mixed-strategy breeders for optimising reproductive investment and success within stochastic polar environments.

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