General and Comparative Endocrinology 216 (2015) 39–45

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Sources of diel variation in energetic physiology in an Arctic-breeding, diving seaduck

Rolanda J. Steenweg[a,b,*,1], Holly L. Hennin[b,1], Joël Bêty[c], H. Grant Gilchrist[d], Tony D. Williams[e], Glenn T. Crossin[a], Oliver P. Love[b]

[a] Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada
[b] Department of Biological Sciences, University of Windsor, Windsor, Ontario N9B 3P4, Canada
[c] Département de Biologie and Centre d'Études Nordiques, Université du Québec à Rimouski, Rimouski, Québec G5L 3A1, Canada
[d] Environment Canada, National Wildlife Research Centre, Carleton University, Ottawa, Ontario K1A 0H3, Canada
[e] Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

ARTICLE INFO

Article history:
Received 17 September 2014
Revised 14 April 2015
Accepted 19 April 2015
Available online 23 April 2015

Keywords:
Corticosterone
Triglyceride
Energetic physiology
Diel rhythm
Arctic
Sea duck

ABSTRACT

Diel variation in baseline glucocorticoid (GC) secretion influences energetics and foraging behaviors. In temperate breeding, diurnal vertebrates, studies have shown that daily patterns of baseline GC secretion are influenced by environmental photoperiod, with baseline GCs peaking prior to sunrise to stimulate waking and foraging behaviors. Measures of physiological energy acquisition are also expected to peak in response to foraging activity, but their relationship to GC levels have not been well studied. In contrast to temperate breeding species, virtually nothing is known about diel GC and energetic metabolite secretion in Arctic breeding species, which experience almost constant photoperiods in spring and summer. Using a ten-year dataset, we examined the daily, 24-h pattern of baseline corticosterone (CORT) and triglyceride (TRIG) secretion in approximately 800 female pre-breeding Arctic-nesting common eiders (*Somateria mollissima*). We related these traits to environmental photoperiod and to tidal cycle. In contrast to temperate breeding species, we found that neither time of day nor tidal trend predicted diel variation in CORT or TRIG secretion in Arctic-breeding eiders. Given the narrow window of opportunity for breeding in polar regions, we suggest that eiders must decouple their daily foraging activity from light and tidal cycles if they are to accrue sufficient energy for successful breeding. As CORT is known to influence foraging behavior, the absence of a distinct diel pattern of CORT secretion may therefore be an adaptation to optimize reproductive investment and likelihood for success in some polar-breeding species.

1. Introduction

Many species exhibit diel patterns of foraging activity, which can be influenced by exogenous factors like prey abundance and environmental variation (Steiger et al., 2013) as well as endogenous factors like physiological condition (Breuner et al., 1999). Variation in exogenous factors, like daily photoperiod or the availability of food resources, require species to prioritize energy to various activities, resulting in the evolution of trade-offs between events like foraging efficiency, courtship, and predator avoidance (Quillfeldt et al., 2007; Steiger et al., 2013). For example, some petrel species (*Procellariiformes*) forage at sea during the day, but only return to breeding areas to feed their chicks at night so as to avoid predation (Quillfeldt et al., 2007). Theoretically, the time available in the day for foraging could have a strong impact on energy acquisition and thus breeding investment. For migratory animals, pre-breeding energetic condition is known to be causally linked to breeding investment and thus success (Descamps et al., 2011). Environmental cues such as variation in light levels are known drivers of circadian rhythms (Brandstätter, 2003), but whether daily variation in environmental cues influences the physiological mechanisms that regulate activity levels and energetic condition are not well understood (Breuner et al., 1999).

Changes in physiological traits, such as the regulation of metabolic and energetic hormones, are directly influenced by temporal changes in energetic demands (Carere et al., 2003; Quillfeldt et al., 2007). For example, modulation of baseline glucocorticoid (GC) hormone levels function to satisfy the changing energetic needs on a daily, seasonal, and life-history stage timeframe (Crespi

---

* Corresponding author at: Department of Biology, Dalhousie University, 1355 Oxford St, Halifax, Nova Scotia B3H 4R2, Canada.

E-mail address: rsteenweg@dal.ca (R.J. Steenweg).

[1] These authors contributed equally to this work.

http://dx.doi.org/10.1016/j.ygcen.2015.04.012

et al., 2013; Landys et al., 2006; Romero, 2002). Changes in baseline GCs have been shown to directly influence daily foraging behavior during reproduction (Angelier et al., 2007; Crossin et al., 2012a), influence variation in reproductive investment decisions (Crossin et al., 2012b; Love et al., 2014), affect the acquisition of lipid stores and resources in association with migration (Holberton, 1999; Holberton et al., 2007), and cue the timing of reproduction (Hennin et al., 2015). It is also well established that baseline GCs show a diel rhythm in temperate-breeding vertebrates (including in humans). Levels peak prior to sunrise in anticipation of active periods (Breuner et al., 1999; Malisch et al., 2008; Mohawk et al., 2007; Nyberg, 2012; Romero and Remage-Healey, 2000), which helps to stimulate waking (Breuner et al., 1999; Carere et al., 2003) and foraging (Romero and Remage-Healey, 2000). Following morning peaks, plasma GCs usually decline and remain low throughout the remainder of the day (Breuner et al., 1999).

In response to an increase in foraging rate, circulating triglyceride (TRIG) levels, an energetic metabolite, increase (Cersale and Guglielmo, 2006; Jenni and Schwilch, 2001; Jenni-Eiermann and Jenni, 1994; Williams et al., 2007; Zajac et al., 2006). Increases in TRIG at the onset of energetically demanding life-history stages is correlated with increased rates of resource intake and fat deposition (Anteau and Afton, 2008; Hennin et al., 2015; Williams et al., 2007). Given that increases in baseline GCs stimulate foraging behavior, there may follow a detectible, delayed peak in TRIG secretion (see Remage-Healey and Romero, 2000) indicating increased foraging.

Most of what is known about the proximate, environmental drivers of GC and TRIG secretion is derived from studies of temperate or tropical species; much less is known about this in polar regions. Two potentially important environmental factors for marine polar species are (1) the number of daylight hours an individual is exposed to, and (2) tidal cycles which influence the availability of marine food resources. Previous work with Antarctic-breeding Adélie penguins (*Pygoscelis adeliae*), where light levels are continuous during the breeding season, suggests a lack of diel rhythmicity in baseline corticosterone secretion (CORT; Vleck and Van Hook, 2002). With near-continuous exposure to daylight, diel patterns of foraging behavior by polar species may be less constrained relative to temperate species exposed to shorter days, which could result in a disconnect between foraging activity and CORT secretion across the day. With respect to tidal cycles, previous research has shown that wintering common eiders (*Somateria mollissima*) forage at higher rates during the low tide, when diving conditions are presumably safer and less energetically strenuous (Heath et al., 2010). Since tides can limit foraging behavior and thus resource intake, we may predict a relationship between tidal cycles, baseline CORT, and TRIG secretion.

In this paper, we examine the relationship between the time of day, tidal trend, and baseline CORT and TRIG levels in Arctic-nesting, pre-breeding, female common eiders. Common eiders are capital-income breeders, which requires that females achieve a minimum pre-breeding body mass in order to fuel follicle development and clutch completion, and to sustain a month-long incubation fast (Sénéchal et al., 2011). We focus exclusively on pre-breeding hens, as successful breeding ultimately depends on how efficiently individual females manage foraging activity upon arrival at their Arctic breeding grounds and to ensure the interpretation of physiological traits is consistent across individuals (Hennin et al., 2015). At this stage of the breeding season, eiders are exposed to almost continuous daylight during the late spring arrival period, although subtle variation in light levels may influence underwater visibility of prey items while diving to the ocean floor to forage. Drawing from a 10-year data set with blood samples from approximately 800 pre-breeding females, we predict that eiders would not exhibit a diel pattern of CORT secretion since foraging activity is presumably not limited by a lack of daylight. We therefore predict that a correlated peak in TRIG secretion would be absent when related to time of day. However, unlike light levels, tidal cycles are predictably variable, and so the foraging activity of females might be constrained by resource availability resulting from tidal variation. This could result in higher foraging rates during low tides as a means for limiting the energetic cost of diving activity. If common eiders synchronize their foraging activity to the tides, then we predict that patterns in CORT and TRIG secretion will be correlated with tidal cycles, with CORT peaking just prior to low tide.

2. Materials and methods

2.1. Study site and sampling methods

Our study took place in June and July at Mitivik Island (64°02′N, 81°47′W), East Bay Migratory Bird Sanctuary, Nunavut, Canada from 2003 to 2013. Mitivik Island is considered a sub-Arctic field site and as such, light levels vary only slightly when the sun dips below the horizon, with a lack of complete night time darkness. Consequently eiders experience 24 h periods of light with relatively little variation in brightness. Eiders breeding at Mitivik Island winter largely off the coast of Western Greenland, or along the coast of Labrador and Newfoundland, Canada (Mosbech et al., 2006). Duration of migration to the breeding grounds varies across individuals, with birds initiating migration from the wintering grounds between late-April and early-May with most females arriving in early June with 2–4 stopovers en route (Mosbech et al., 2006). We captured pre-breeding female eiders using flight nets from June 10 to July 3 in the study years, coinciding with the timing of arrival at the breeding grounds (Love et al., 2010). Upon capture each eider was blood sampled, weighed, measured, banded and marked with a unique set of shaped and colored nasal tags. This allowed us to follow individuals and determine lay dates, incubation behaviors and reproductive success (Hennin et al., 2015).

During a 10-year period running from 2003 to 2004 and 2006 to 2013, we collected 828 blood samples from pre-breeding female eiders. Blood samples were collected as part of a larger on-going project at East Bay focussing specifically on female eiders. Therefore, only females were included in this study. From 2006 to 2013 blood was collected from tarsal veins using 23G thin-wall needles attached to a 1 mL syringe, and stored in heparinized eppendorf tubes and kept cool (5–10 °C) until centrifugation. All samples were collected within 3 min of capture to obtain baseline physiological values of CORT (Romero and Reed, 2005). In 2003 and 2004, blood samples were taken within 10 min of capture using either a 26G needle to puncture the tarsal vein and heparinized 75 μL capillary tubes (2003) or a heparinized vacutainer with a 26G butterfly needle (2004). Thus samples from 2003 to 2004 were only used for TRIG analyses ($n = 134$). All blood samples were centrifuged at 10,000 rpm for 10 min, the plasma was separated from the red blood cells, and both stored separately at −80 °C until analysis.

2.2. Physiological assays

We measured baseline CORT using a commercially-available enzyme immune-assay (EIA; Assay Designs, Ann Arbor, MI, USA), previously validated in common eiders breeding at East Bay (Hennin et al., 2015). All samples were run in triplicate at a 1:20 dilution with 1.5% steroid displacement buffer by volume, and samples were randomized (i.e., samples were not run in the order in which they were collected). Each plate included a control of serially diluted laying hen plasma (Sigma–Aldrich Canada, Oakville, Ontario, Canada) and a kit-provided standard curve (200,000 pg/mL). Plates were read at 405 nm using a Biotek Powerwave HT microplate reader, and the inter- and intra-assay coefficient of variation was 8.54% and 5.87%, respectively.

We quantified plasma triglycerides (TRIG) using a commercially available assay kit previously validated in East bay common eiders (Sigma Aldrich, USA, #TR0100-1KT; Hennin et al., 2015). Samples were run in duplicate with a control of laying hen plasma (Sigma–Aldrich Canada, Oakville, Ontario, Canada) and serially diluted glycerol standard (2.54 mmol/L; Sigma Aldrich, USA). Samples were run either at a 1:2 or 1:10 dilution (Williams et al., 1999), then added to 96-well microplates with Reagent A to measure free glycerol, followed by Reagent B to measure total glycerol. After the addition of each reagent, the plates were shaken for 10 min at 37 °C. Samples were read using a Biotek Powerwave HT microplate reader for the concentration of total and free glycerol. The free glycerol value was subtracted from the total glycerol value to obtain the final TRIG concentration (mmol/L). Plasma TRIG levels were corrected for body mass to estimate physiological fattening rate (Williams et al., 1999). Inter- and intra-assay coefficients of variation were 11.27% and 4.42% for total TRIG, respectively, and 5.51% and 6.29% for free glycerol, respectively.

2.3. Statistical analyses

We categorized time of day into six, four-hour categories based on patterns of eider activity in the colony and previous research on diel variation in the physiological traits of interest (Romero and Remage-Healey, 2000; Breuner et al., 1999): “night” 0000–0359 h, “early morning” 0400–0759 h, “late morning” 0800–1159 h, “early afternoon” 1200–1559 h, “late afternoon” 1600–1959 h and “evening” 2000–2359 h. Based on the time of day and the tidal cycle at capture, individuals were also placed into one of four tidal categories: “low tide”, “rising tide”, “high tide” and “falling tide”. We obtained tidal data for Coral Harbour, Southampton Island, Nunavut (60 km from Mitivik Island) from WWW Tide/Current Predictor, and added 50 min to tidal times to account for differences between high tide in Coral Harbour and Mitivik Island. High tides were on average 12 h, 24 min apart and low tides 6 h, 12 min from high tides. To categorize tidal trend we determined the times for high and low tides, and split them into four 3 h, 6 min segments. As such, high tide was considered 1 h, 33 min before and after peak tide heights, falling tides were the 3 h, 6 min between high and low tides, low tide was considered 1 h, 33 min before and after the lowest tide height and rising tides were the 3 h, 6 min between low and high tides.

To test for the effect of time of day and tidal trends on variation in (a) baseline CORT and (b) TRIG we ran generalized linear mixed models with random effects using restricted maximum likelihood (REML). We controlled for variables known to influence CORT and TRIG secretion in all models by including body mass at arrival, capture date (i.e. arrival at colony), breeding status (see below), and year (random effect) as independent variables. Previous research at this colony has shown that correcting body mass for size only enhanced the predictability of condition by 1% compared to using body mass alone (Descamps et al., 2010). Therefore, we use uncorrected body mass as our metric of body condition.

Previous studies have shown that there are temporal changes in both CORT and TRIG secretion during the period of rapid follicle growth (RFG) in which females recruit their follicles in preparation for ovulation (Hennin et al., 2015). Since the interpretation of the role of these physiological traits differs between the pre-recruiting and RFG stages (Hennin et al., 2015), we focused only on pre-recruiting females. If pre-recruiting females did not breed that year they were categorized as “non-breeding”. We included “breeding status” in our analyses as an independent variable to control for any potential differences in CORT or TRIG that may occur between our pre-recruiting and non-breeding groups. In instances where females were caught multiple times across or within years, we only included the first capture (occurring in <30 birds). Although sample sizes from 2011 to 2013 were smaller due to two separate manipulations occurring in the colony (Hennin and Love, unpubl. data), only control individuals were included in our analyses. All data met the assumptions for a parametric test. Baseline CORT was log transformed to meet the assumptions for normality and all analyses were run in JMP (version 10, SAS Institute Inc., Cary, NC).

3. Results

Across all years 724 birds were sampled for CORT and 828 were sampled for TRIG (Table 1), although sample sizes were variable across years. Neither time of day (Figs. 1A and 2A), nor tidal trend (Fig. 3A) explained variation in secretion of baseline CORT, although body mass and breeding status were related to variation in baseline CORT (Tables 2 and 3). Variation in plasma TRIG was not explained by time of day (Figs. 1A and 2B), nor tidal trend (Fig. 3B) however, it was explained by capture date (Tables 2 and 3). Although the time of day did not show a significant relationship with TRIG, there is a potential trend suggested by the parameter estimates in which females had slightly higher TRIG during the “evening” (i.e., 2000–2359 h) relative to the other time categories.

4. Discussion

4.1. Time of day and light levels

In contrast to temperate species that exhibit marked diel patterns of baseline CORT (Breuner et al., 1999; Romero and Remage-Healey, 2000; Mohawk et al., 2007), Arctic-nesting common eiders exhibited relatively consistent levels of baseline plasma CORT across a 24-h cycle. Our findings are consistent with previous research conducted in Antarctic-breeding Adélie penguins that showed a lack of diel patterns in baseline CORT secretion under similarly near-constant light conditions during summer breeding (Vleck and Van Hook, 2002). This lack of variation may result from suppression of melatonin secretion (Yamada et al., 1988), which requires periods of darkness and inactivity in order to establish circadian rhythmicity in endocrine activity (Brandstätter, 2003; Steiger et al., 2013). For example, when light levels are held constant, the resultant suppression of melatonin disrupts the gene expression responsible for the secretion of adrenocorticotropic hormone (ACTH) from the pituitary gland (Park et al., 2013), which in turn regulates CORT secretion from the adrenal glands. We might therefore predict a diel pattern of hypothalamic–pituitary–adrenal axis activation and GC secretion (Christiansen et al., 2012) to be driven by light–dark cycles (Breuner et al., 1999; Romero, 2002), but these are largely absent in polar springs and summers.

Our inability to detect a temporal pattern of baseline CORT secretion may be the underlying reason for the lack of a correlated relationship with TRIG levels. Although our data suggest that TRIG secretion may be slightly elevated during the “evening” hours (2000–2359 h) relative to other times of day (see model parameter estimates in Table 3), the overall effect in our model was weak (Table 2). Generally, elevated levels of plasma TRIG in pre-breeding eiders are indicative of high fattening rates (Hennin et al., 2015; Williams et al., 2007). Given the lack of a diel CORT pattern it is not surprising that we could not detect a diel pattern of TRIG secretion. There are two possible, related reasons for this

Table 1
Summary of sample sizes of non-breeding and pre-recruiting female common eiders assayed for baseline corticosterone (CORT) and triglycerides (TRIG) split by breeding status from 2003 to 2013 at Mitivik Island, Nunavut. In 2003 and 2004 CORT samples were not collected, and no physiological samples were collected in 2005.

Year	Non-breeding		Pre-recruiting	
	CORT	TRIG	CORT	TRIG
2003	n/a	19	n/a	23
2004	n/a	64	n/a	28
2005	n/a	n/a	n/a	n/a
2006	70	59	52	50
2007	78	70	55	52
2008	91	92	17	17
2009	122	120	17	16
2010	116	118	9	9
2011	34	33	17	12
2012	12	10	1	1
2013	26	28	7	7
Total	549	613	175	215

lack of relationship. First, because pre-breeding female eiders are at a life history stage where gaining fat stores quickly is essential for successful reproduction (Sénéchal et al., 2011; Hennin et al., 2015), individuals must forage efficiently and intensely throughout the 24-h day to ensure optimal pre-breeding condition (*sensu* Descamps et al., 2011). Secondly, to achieve this goal, females likely have individually-optimized foraging strategies, wherein different females may target their effort to specific times of day, although repeated measures would be required to test this. Future studies that attempt to link individual baseline CORT secretion with foraging behavior should pay special attention to the potentially correlated effects of TRIG secretion and the effects on fattening rates.

To help put our pre-breeding into a broader context, it is useful to review what is known about the biology of common eiders and other Arctic-breeding bird species across the whole year. Common eiders nesting on Mitivik Island spend their winters either off the coast of Western Greenland or in Canada along the coasts of Newfoundland and Labrador (Mosbech et al., 2006). Depending on the latitude of nesting and of overwintering locations, different birds will experience different and highly variable daily light levels throughout the year, ranging from periods of near complete darkness in the winter to periods of constant light in the summer. As such, it is possible that female eiders may exhibit a diel pattern of baseline CORT/TRIG secretion only at certain times of year when night-day periods are more equal. However, previous research in Arctic-breeding semipalmated sandpipers (*Calidris pusilla*) demonstrated that individuals do not exhibit a predictable pattern of activity during the pre-breeding period, but then switch to predictable schedules during incubation that are synchronized to their mates' activity (Steiger et al., 2013). In this example, environmental photoperiod is perhaps a less important driver of foraging activity in a species characterized by bi-parental care. Unlike sandpipers, female eiders are solely responsible for incubation and the rearing of chicks, and so the flexibility to forage continually during the pre-breeding period, irrespective of time of day, may increase the likelihood of successful breeding, via optimal reproductive investment strategies and timing of laying. But at other times of year, we do not know whether eiders maintain a pattern of CORT/TRIG secretion and/or activity levels that are driven principally by environmental conditions. Given the highly variable

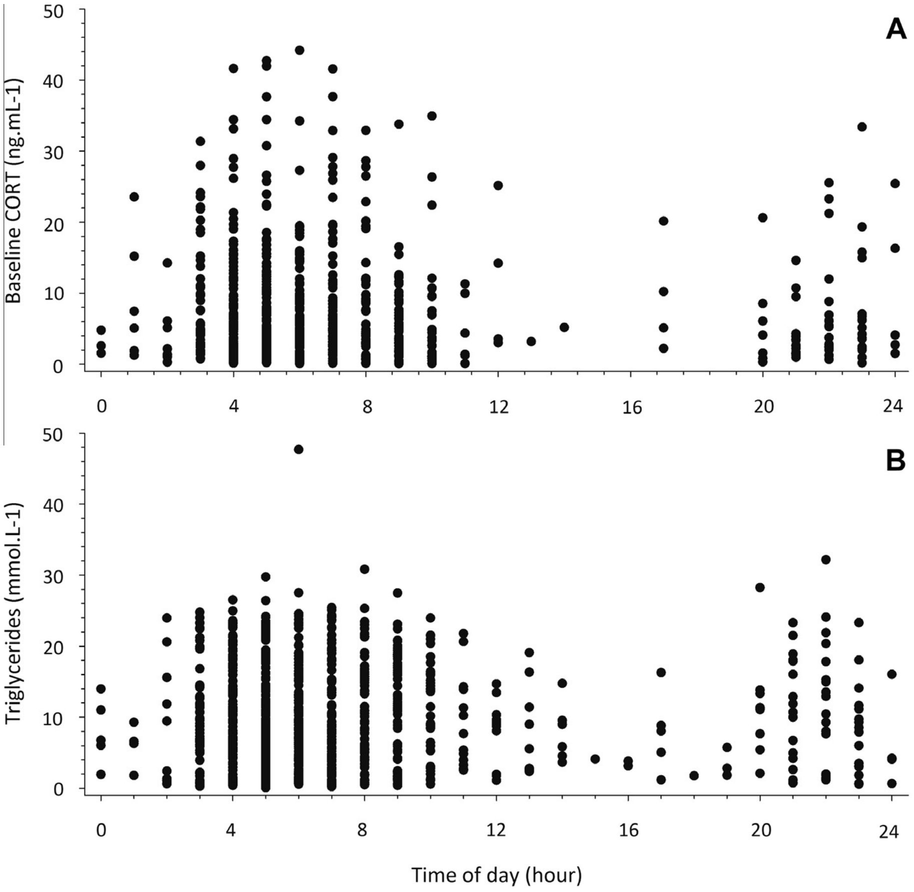

Fig. 1. Daily variation in baseline corticosterone (A) and triglyceride (B) secretion by time of day. Times correspond to the time of day categories as follows: "night" 0000–0359 h, "early morning" 0400–0759 h, "late morning" 0800–1159 h, "early afternoon" 1200–1559 h, "late afternoon" 1600–1959 h and "evening" 2000–2359 h.

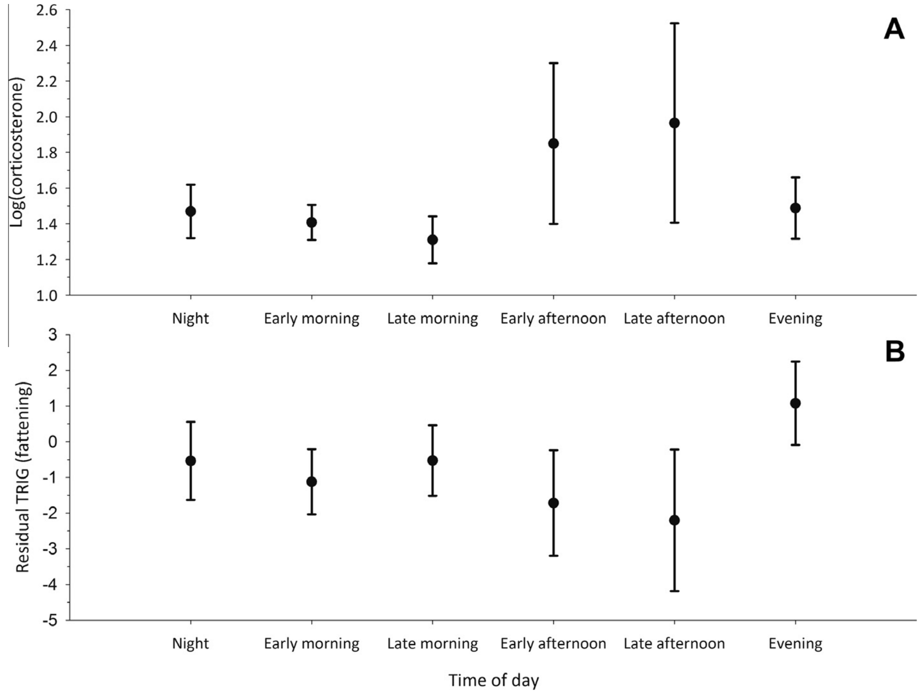

Fig. 2. Daily variation in log transformed corticosterone (A) and residual TRIG (fattening rate) (B) secretion categorized by time of day. Data are presented as model-corrected least square means and standard errors. Sample sizes for each time category in (A) are $n = 74$, $n = 450$, $n = 137$, $n = 6$, $n = 4$ and $n = 55$, respectively. Sample sizes in (B) are $n = 74$, $n = 480$, $n = 178$, $n = 25$, $n = 11$, and $n = 58$, respectively.

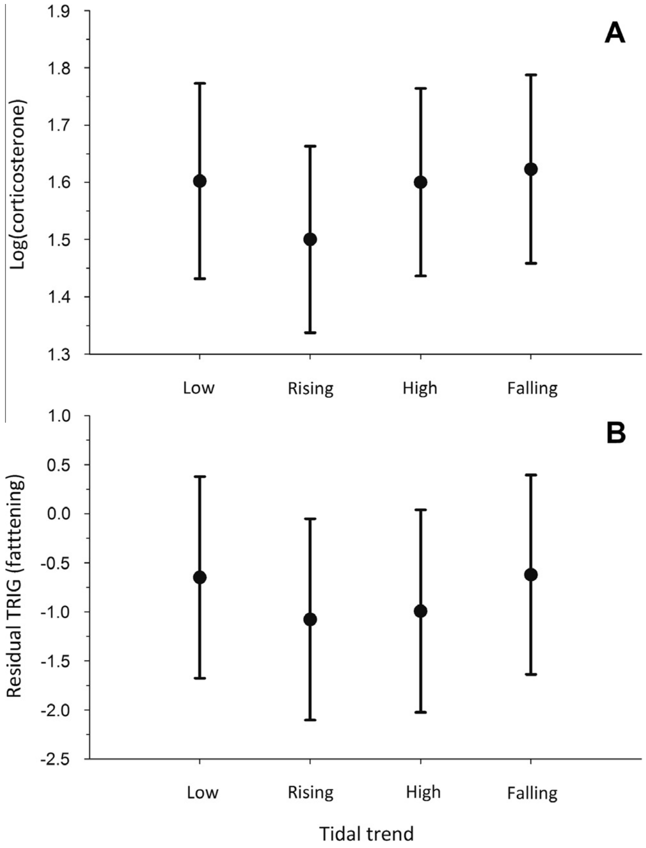

Fig. 3. Daily variation in log transformed corticosterone (A) and residual TRIG (fattening rate) (B) secretion by tidal trend. Data are presented as model-corrected least square means and standard errors. Sample sizes for each time category in (A) are $n = 270$, $n = 152$, $n = 164$ and $n = 140$, respectively. Sample sizes in (B) $n = 300$, $n = 164$, $n = 195$ and $n = 167$, respectively.

environmental conditions that they can experience in winter as well as summer, however, it is possible that no clear links exist, as is the case for Antarctic-breeding Adélie penguins (Vleck and Van Hook, 2002) and Arctic-breeding lapland longspur (*Calcarius lapponicus*; Steiger et al., 2013). Although wintering eiders typically forage diurnally, they are in fact capable of adjusting their behavior to forage at twilight and even in complete darkness in order to avoid predation by white-tailed eagles (*Haliaeetus albicilla*, Merkel and Mosbech, 2008). Studies in other Arctic species like reindeer (*Rangifer tarandus platyrhunchus*) have shown that more northern populations are more likely to forage throughout the entire day relative to more southerly populations (van Oort et al., 2007). Although principally an Arctic breeder, common eiders can in fact breed in temperate areas as far south as Massachusetts (Goudie et al., 2000). To our knowledge, it has not been determined whether temperate-breeding eiders, exposed to an obvious day/night *zeitgeber*, exhibit diel patterns of baseline CORT or TRIG secretion. If this were the case, it would suggest that populations are locally adapted to light levels. Comparative studies

Table 2
Variation in baseline corticosterone (CORT) and triglycerides (TRIG) in relation to time of day, tidal trend, capture date, body mass and breeding status (non-breeding vs pre-recruiting) in female common eiders. Significant relationships are bolded.

Analysis	Variable	*F*	df	*p*
Baseline CORT	Time of day	0.71	5, 695.5	0.62
	Tidal trend	0.39	3, 704.5	0.75
	Capture date	1.98	1, 303.2	0.16
	Body mass	51.15	1, 704.7	**<0.0001**
	Breeding status	7.77	1, 703.4	**0.006**
TRIG	Time of day	1.71	5, 811.8	0.13
	Tide trend	0.31	3, 808.0	0.82
	Capture date	3.94	1, 805.2	**0.05**
	Mass	0.00	1, 810.5	0.95
	Breeding status	2.94	1, 811.6	0.09

Table 3
Summary of parameter estimates of fixed effects on secretion of baseline corticosterone and triglycerides. Significant relationships are bolded.

Variable	Corticosterone				Triglycerides			
	Estimate	±95% CI	*t*	*p*	Estimate	±95% CI	*t*	*p*
Intercept	−3.45	−0.02	−1.97	**0.05**	−16.21	0.1756	−1.94	**0.05**
Time of day (early morning)	−0.17	0.0848	−1.33	0.193	−0.28	0.6608	−0.59	0.55
Time of day (late morning)	−0.27	0.024	−1.83	0.07	0.31	1.388	0.56	0.57
Time of day (early afternoon)	0.27	1.0148	0.7	0.48	−0.88	1.178	−0.83	0.41
Time of day (late afternoon)	0.38	1.3012	0.82	0.41	−1.37	1.57	−0.91	0.36
Time of day (evening)	−0.09	0.2628	−0.53	0.6	1.92	3.4096	2.53	**0.01**
Tide trend (high)	0.02	0.1768	0.25	0.8	−0.16	0.5848	−0.42	0.68
Tide trend (falling)	0.04	0.1576	0.65	0.52	0.21	0.8372	0.67	0.51
Tide trend (low)	0.02	0.1768	0.27	0.79	0.19	0.9348	0.49	0.62
Capture date	0.01	0.0296	1.41	0.16	0.09	0.1684	1.98	**0.05**
Body mass	0	0	7.15	**<0.0001**	0	0	−0.07	0.95
Breeding status (non-breeder)	0.14	0.238	2.79	**0.006**	−0.43	0.06	−1.71	0.09

across a range of populations, spanning a range of latitudes and times of year, would be required to test this hypothesis.

4.2. Tidal trends and resource availability

In winter, common eiders are known to forage in high-current polynyas but generally at the start and end of the tidal cycle, which presumably reduces the energetic demands of high diving activity (Heath et al., 2010). However, in our pre-breeding birds, we found no relationship between baseline CORT or TRIG secretion with tidal patterns in spring. Again, this lack of a relationship may indicate a requirement for females to forage continually throughout the day, regardless of either time of day or tidal trend. Our analyses only explore population-level trends rather than individually-optimized strategies, however, so studies of individual variation and repeated measures would be required to test for optimization. Furthermore, the tidal dynamics between open-water polynyas in winter and the near shore areas and ice floe edges at Mitivik Island in spring are strikingly different. Eiders foraging in open-water polynyas experience extreme variation in current strength, so individuals tend to synchronize their diving and foraging activity to coincide with the start and end of the tidal cycle, when currents are at their slackest, to maximize foraging success while minimizing energetic loss and the risk of being swept under the ice (Heath et al., 2010). In contrast, eiders arriving at Mitivik Island in springtime forage in shallow, protected and productive near-shore areas (Sénéchal et al., 2011), where tidal variation is relatively small (max heights of 3 m in spring and summer). These comparatively benign spring tides may not be variable enough to warrant foraging at only the low tide. Coupled with the shallow, productive waters around the island, eiders may experience only a negligible energetic cost of foraging, irrespective of tidal trends, which may explain the lack of correlation between baseline CORT and TRIG secretion. Future studies would benefit from the direct measurement of foraging behavior and tidal trends/strength, and linking this to variation in baseline CORT and TRIG.

Acknowledgments

We extend thanks to the East Bay Island field crews from 2003 to 2013 for data collection, I. Butler and R. Kelly for data organization, R.W. Steenweg for graphing assistance, and Bettina Almasi and one anonymous reviewer for their helpful comments. Research was logistically supported by Environment Canada, and through funding from Natural Sciences and Engineering Research Council of Canada, Polar Continental Shelf Program, the Canada Research Chairs Program, the Northern Scientific Training Program, Dalhousie University and the University of Windsor.

References

Angelier, F., Shaffer, S.A., Weimerskirch, H., Trouvé, C., Chastel, O., 2007. Corticosterone and foraging behavior in a pelagic seabird. Physiol. Biochem. Zool. 80, 283–292. http://dx.doi.org/10.1086/512585.

Anteau, M.J., Afton, A.D., 2008. Using plasma-lipid metabolites to index changes in lipid reserves of free-living lesser scaup (*Aythya affinis*). Auk 125, 354–357.

Brandstätter, R., 2003. Encoding time of day and time of year by the avian circadian system. J. Neuroendocrinol. 15, 398–404.

Breuner, C.W., Wingfield, J.C., Romero, L.M., 1999. Diel rhythms of basal and stress-induced corticosterone in a wild, seasonal vertebrate, Gambel's white-crowned sparrow. J. Exp. Zool. 284, 334–342.

Carere, C., Groothuis, T.G.G., Mostl, E., Daan, S., Koolhaas, J.M., 2003. Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. Horm. Behav. 43, 540–548.

Cersale, D.J., Guglielmo, C.G., 2006. Dietary effects on prediction of body mass changes in birds by plasma metabolites. Auk 123, 836–846.

Christiansen, S., Bouzinova, E.V., Palme, R., Wiborg, O., 2012. Circadian activity of the hypothalamic–pituitary–adrenal axis is differentially affected in the rat chronic mild stress model of depression. Stress 15, 647–657. http://dx.doi.org/10.3109/10253890.2011.654370.

Crespi, E.J., Williams, T.D., Jessop, T.S., Delehanty, B., 2013. Life history and the ecology of stress: how do glucocorticoid hormones influence life-history variation in animals? Funct. Ecol. 27, 93–106. http://dx.doi.org/10.1111/1365-2435.12009.

Crossin, G.T., Phillips, R.A., Trathan, P.N., Fox, D.S., Dawson, A., Wynne-Edwards, K.E., Williams, T.D., 2012a. Migratory carryover effects and endocrinological correlates of reproductive decisions and reproductive success in female albatrosses. Gen. Comp. Endocrinol. 176, 151–157. http://dx.doi.org/10.1016/j.ygcen.2012.01.006.

Crossin, G.T., Trathan, P.N., Phillips, R.A., Gorman, K.B., Dawson, A., Sakamoto, K.Q., Williams, T.D., 2012b. Corticosterone predicts foraging behavior and parental care in macaroni penguins. Am. Nat. 180, E31–E41. http://dx.doi.org/10.1086/666001.

Descamps, S., Bêty, J., Love, O.P., Gilchrist, H.G., 2011. Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. Funct. Ecol. 25, 671–681. http://dx.doi.org/10.1111/j.1365-2435.2010.01824.x.

Descamps, S., Yoccoz, N.G., Gaillard, J.-M., Gilchrist, H.G., Erikstad, K.E., Hanssen, S.A., Cazelles, B., Forbes, M.R., Bêty, J., 2010. Detecting population heterogeneity in effects of North Atlantic Oscillations on seabird body condition: get into the rhythm. Oikos 119, 1526–1536. http://dx.doi.org/10.1111/j.1600-0706.2010.18508.x.

Goudie, I.R., Robertson, G.J., Reed, A., 2000. Common Eider (Somateria mollissima) [WWW Document]. Birds North Am. Online. URL <http://bna.birds.cornell.edu/bna/species/546>.

Heath, J.P., Gilchrist, H.G., Ydenberg, R.C., 2010. Interactions between rate processes with different timescales explain counterintuitive foraging patterns of arctic wintering eiders. Proc. Biol. Sci. 277, 3179–3186. http://dx.doi.org/10.1098/rspb.2010.0812.

Hennin, H.L., Legagneux, P., Bêty, J., Williams, T.D., Grant Gilchrist, H., Baker, T.M., Love, O.P., 2015. Pre-breeding energetic management in a mixed-strategy breeder. Oecologia. http://dx.doi.org/10.1007/s00442-014-3145-x.

Holberton, R.L., 1999. Changes in patterns of corticosterone secretion concurrent with migratory fattening in a Neotropical migratory bird. Gen. Comp. Endocrinol. 116, 49–58. http://dx.doi.org/10.1006/gcen.1999.7336.

Holberton, R.L., Wilson, C.M., Hunter, M.J., Cash, W.B., Sims, C.G., 2007. The role of corticosterone in supporting migratory lipogenesis in the dark-eyed junco, *Junco hyemalis*: a model for central and peripheral regulation. Physiol. Biochem. Zool. 80, 125–137. http://dx.doi.org/10.1086/508816.

Jenni, L., Schwilch, R., 2001. Plasma metabolite levels indicate change in body mass in reed warblers *Acrocephalus scirpaceus*. Avian Sci. 1, 55–65.

Jenni-Eiermann, S., Jenni, L., 1994. Plasma metabolite levels predict individual body-mass changes in a small long-distance migrant, the garden warbler. Auk 111, 888–899.

Landys, M.M., Ramenofsky, M., Wingfield, J.C., 2006. Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. Gen. Comp. Endocrinol. 148, 132–149. http://dx.doi.org/10.1016/j.ygcen.2006.02.013.

Love, O.P., Gilchrist, H.G., Descamps, S., Semeniuk, C.A.D., Bêty, J., 2010. Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. Oecologia 164, 277–286. http://dx.doi.org/10.1007/s00442-010-1678-1.

Love, O.P., Madliger, C.L., Bourgeon, S., Semeniuk, C.A., Williams, T.D., 2014. Evidence for baseline glucocorticoids as mediators of reproductive investment in a wild bird. Gen. Comp. Endocrinol. 199, 65–69. http://dx.doi.org/10.1016/j.ygcen.2014.01.001.

Malisch, J.L., Breuner, C.W., Gomes, F.R., Chappell, M.A., Garland, T., 2008. Circadian pattern of total and free corticosterone concentrations, corticosteroid-binding globulin, and physical activity in mice selectively bred for high voluntary wheel-running behavior. Gen. Comp. Endocrinol. 156, 210–217. http://dx.doi.org/10.1016/j.ygcen.2008.01.020.

Merkel, F.R., Mosbech, A., 2008. Diurnal and nocturnal feeding strategies in common eiders. Waterbirds 31, 580–586.

Mohawk, J.A., Pargament, J.M., Lee, T.M., 2007. Circadian dependence of corticosterone release to light exposure in the rat. Physiol. Behav. 92, 800–806. http://dx.doi.org/10.1016/j.physbeh.2007.06.009.

Mosbech, A., Gilchrist, G., Merkel, F., Sonne, C., Flagstad, A., Nyegaard, H., 2006. Year-round movements of Northern Common Eiders Somateria mollissima borealis breeding in Arctic Canada and West Greenland followed by satellite telemetry. ARDEA 94, 651–665.

Nyberg, C.H., 2012. Diurnal cortisol rhythms in Tsimane' Amazonian foragers: new insights into ecological HPA axis research. Psychoneuroendocrinology 37, 178–190. http://dx.doi.org/10.1016/j.psyneuen.2011.06.002.

Park, S.Y., Walker, J.J., Johnson, N.W., Zhao, Z., Lightman, S.L., Spiga, F., 2013. Constant light disrupts the circadian rhythm of steroidogenic proteins in the rat adrenal gland. Mol. Cell. Endocrinol. 371, 114–123. http://dx.doi.org/10.1016/j.mce.2012.11.010.

Quillfeldt, P., Poisbleau, M., Chastel, O., Masello, J.F., 2007. Corticosterone in thin-billed prion Pachyptila belcheri chicks: diel rhythm, timing of fledging and nutritional stress. Naturwissenschaften 94, 919–925. http://dx.doi.org/10.1007/s00114-007-0275-6.

Remage-Healey, L., Romero, L.M., 2000. Daily and seasonal variation in response to stress in captive starlings (*Sturnus vulgaris*): glucose. Gen. Comp. Endocrinol. 119, 60–68.

Romero, L.M., 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. Gen. Comp. Endocrinol. 128, 1–24.

Romero, L.M., Reed, J.M., 2005. Collecting baseline corticosterone samples in the field: is under 3 min good enough? Comp. Biochem. Physiol. Part A 140, 73–79. http://dx.doi.org/10.1016/j.cbpb.2004.11.004.

Romero, L.M., Remage-Healey, L., 2000. Daily and seasonal variation in response to stress in captive starlings (*Sturnus vulgaris*): corticosterone. Gen. Comp. Endocrinol. 119, 52–59. http://dx.doi.org/10.1006/gcen.2000.7491.

Sénéchal, E., Bêty, J., Gilchrist, H.G., Hobson, K.A., Jamieson, S.E., 2011. Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. Oecologia 165, 593–604. http://dx.doi.org/10.1007/s00442-010-1853-4.

Steiger, S.S., Valcu, M., Spoelstra, K., Helm, B., Wikelski, M., Kempenaers, B., 2013. When the sun never sets: diverse activity rhythms under continuous daylight in free-living arctic-breeding birds. Proc. Biol. Sci. 280, 20131016. http://dx.doi.org/10.1098/rspb.2013.1016.

Van Oort, B.E.H., Tyler, N.J.C., Gerkema, M.P., Folkow, L., Stokkan, K.-A., 2007. Where clocks are redundant: weak circadian mechanisms in reindeer living under polar photic conditions. Naturwissenschaften 94, 183–194. http://dx.doi.org/10.1007/s00114-006-0174-2.

Vleck, C.M., Van Hook, J.A., 2002. Absence of daily rhythms of prolactin and corticosterone in Adelie penguins under continuous daylight. Condor 104, 667–671.

Williams, T.D., Guglielmo, C.G., Egeler, O., Martyniuk, C.J., 1999. Plasma lipid metabolites provide information on mass change over several days in captive western sandpipers. Auk 116, 994–1000.

Williams, T.D., Warnock, N., Takekawa, J.Y., Bishop, M.A., 2007. Flyway-scale variation in plasma triglyceride levels as an index of refuelling rate in spring-migrating western sandpipers (*Calidris mauri*). Auk 124, 886–897.

Yamada, H., Oshiman, I., Sato, K., Ebihara, S., 1988. Loss of the circadian rhythms of locomotor activity, food intake, and plasma melatonin concentration induced by constant bright light in the pigeon (*Columba livia*). J. Comp. Physiol. A 163, 459–463.

Zajac, R.M., Cerasale, D.J., Guglielmo, C.G., 2006. The rapid response of plasma metabolites to changes in feeding rate in a small passerine Wilson's warbler *Wilsonia pusilla*. J. Avian Biol. 37, 405–408.