



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



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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.

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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

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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 Ramage-Healey, 2000), which helps to stimulate waking (Breuner et al., 1999; Carere et al., 2003) and foraging (Romero and Ramage-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 Ramage-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

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