Baseline Corticosterone in Wintering Marine Birds: Methodological Considerations and Ecological Patterns

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ABSTRACT

Previous studies have related levels of plasma corticosterone (CORT) of seabirds to variation in foraging conditions during the breeding period, but it is unclear whether similar relationships between foraging conditions and baseline CORT exist during other life stages. We validated methods for identifying baseline CORT of lethally sampled birds and assessed variation in baseline CORT relative to winter habitat conditions. We collected free-living white-winged scoters (*Melanitta fusca*) at four wintering sites during December and February. We found increasing CORT values beyond 3 min after time since flush (the duration between initial flush and death), presumably reflecting acute stress responses. Our results demonstrate that it is possible to obtain baseline CORT from lethally sampled birds if the time from initial flush until death is measured. Our study sites varied appreciably in exposure to wind and waves, predation danger, diving depths, and the fraction of preferred foods in scoter diets. Despite these habitat differences, baseline CORT did not vary across sites or winter periods. We interpret this lack of variation as evidence that birds select wintering areas where they can successfully manage site-specific costs and maintain physiological homeostasis.

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Introduction

Plasma corticosterone (CORT) increasingly has been used as a tool to infer local habitat conditions for many vertebrate species and to contrast relative condition of individuals and populations (Kitaysky et al. 1999; Homan et al. 2003; Walker et al. 2005; Wikelski and Cooke 2006; Bonier et al. 2009). Secretion of plasma CORT quickly increases in response to temporary stressors, such as a predatory attack, severe storms, or capture by researchers (Breuner et al. 2008). However, behavioral and physiological effects of an acute stress response are markedly different from those associated with variation in baseline CORT. Baseline levels of CORT are those that are sufficient for animals to carry out normal physiological functions and maintain energetic balance (Romero 2004). Baseline levels may increase in response to prolonged environmental challenges, such as decreased food availability, increased predation danger, or increased frequency of inclement weather (Kitaysky et al. 1999; Clinchy et al. 2004). Increased baseline CORT is correlated with increased foraging, movement, and mobilization of energy reserves and is thus presumed to be an adaptation for overcoming environmental stressors (Sapolsky et al. 2000; Landys et al. 2006; Angelier et al. 2007). However, chronically elevated concentrations of plasma CORT can negatively affect fitness (Romero 2004).

There are many studies describing variation in baseline CORT in free-living birds. This research shows that baseline CORT may vary with environmental conditions or endogenously over time. Some diurnal species exhibit pronounced daily rhythms in CORT levels in captivity and in the wild, with peak levels occurring in the morning hours, often at or just prior to the onset of activity (Westerhof et al. 1994; Breuner et al. 1999; Romero and Remage-Healey 2000; Tarlow et al. 2003). Because CORT helps regulate acquisition, mobilization, and deposition of energy, a peak in CORT levels near dawn may help prepare birds for energetic demands immediately before feeding (Breuner et al. 1999). Elevated baseline CORT also can drive accumulation of energetic stores in preparation for long-distance migration (Holberton et al. 1999; Reneerkens et al. 2002). Research on some wintering passerines shows consistently lower CORT concentrations across a wide geographical area during winter compared to levels during spring migration and breeding, suggesting that seasonal fluctuations may be endogenously regulated rather than in response to local habitat conditions (Romero et al. 1997). In seabirds, baseline CORT can increase as food availability declines (Kitaysky et al. 1999; Buck et al. 2007). These findings have prompted researchers to suggest that baseline CORT could be used as a proxy for food availability (Buck et al. 2007; Kitaysky et al. 2007). How-

ever, most studies relating plasma CORT in seabirds to foraging conditions have focused on the breeding period (Romero 2002), and it is unclear whether similar relationships between foraging conditions and baseline CORT exist during other life stages.

Measuring blood plasma levels of baseline CORT in the field is challenging because capture and bleeding are stressors that can result in acute stress responses (Romero and Romero 2002). The relationship between time since capture and acute CORT response has been well documented, and it is clear that CORT levels rise within minutes of exposure to stressors; thus, accurate assessment of baseline CORT requires that time between capture and bleeding be below the point at which acute CORT responses are detected (Wingfield et al. 1982; Romero and Romero 2002; Romero and Reed 2005).

In some species (e.g., open-water seabirds) or during particular stages of the annual cycle, lethal sampling may be the only viable means to collect blood samples. Such sampling eliminates stress associated with capture and handling, but approaching or pursuing birds also may result in acute stress. However, the few studies that have published CORT data from lethally collected birds have not assessed changes in CORT levels as a function of the time between initial disturbance and death (Lisano et al. 1977; Whatley et al. 1977; Wingfield et al. 1982; Marra et al. 1995).

White-winged scoters (*Melanitta fusca*) are sea ducks that spend most of the year in marine habitats. Although the British Columbia (BC) coastline entails a significant portion of their wintering range on the Pacific coast of North America, there are few wintering areas in BC where white-winged scoters occur in high concentrations (J.-P. L. Savard, unpublished data). This may be due in part to their preference for soft-bottom habitats with abundant bivalve foods, which are relatively uncommon in BC. However, even among such sites, there is considerable variation in habitat conditions that may affect baseline CORT levels of white-winged scoters. Widespread population declines in white-winged scoters and other sea duck species have prompted efforts to identify functional roles of different habitats used throughout the annual cycle by analyzing body condition, prey availability, foraging effort, diet composition, and plasma metabolite analyses (e.g., Žydelis et al. 2006; Anderson and Lovvorn 2008, 2011; Anderson et al. 2008; Lewis et al. 2008; Palm et al. 2012). Baseline CORT could complement these measures by providing additional insight into the relative values of different sea duck wintering habitats.

We measured plasma CORT levels in free-living white-winged scoters that were lethally collected at four wintering areas along coastal BC (fig. 1). These sites varied markedly in terms of exposure, predation danger, diving depths, and the fraction of preferred foods in scoter diets (see below). Live capture of scoters at two of these sites was not feasible because they fed mainly in deep water >5 km from shore. Thus, lethal collections entailed the only viable means of obtaining blood samples and also allowed for analyses of body composition, diet, and digestive morphology (Palm 2012; Palm et al. 2012). Our specific objectives were to delineate appropriate methods of identifying baseline CORT from lethally collected birds and
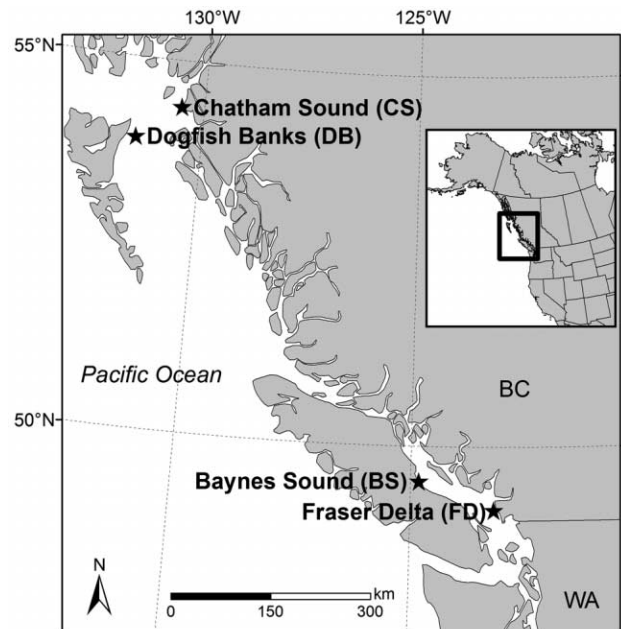

Figure 1. Map of four study sites along coastal British Columbia where studies of plasma CORT in wintering white-winged scoters were conducted during 2009–2011.

to assess variation in baseline CORT relative to winter habitat conditions. We predicted that in sites with less favorable foraging conditions white-winged scoters would have elevated levels of baseline CORT that would reflect the challenge of dealing with these poor conditions (Wasser et al. 1997; Suorsa et al. 2003) or help trigger behavioral and physiological adaptations to successfully cope with them (Wingfield and Ramenofsky 1997; Reneerkens et al 2002).

Methods

Sample Collection

We collected a total of 119 adult male white-winged scoters using a shotgun from a small boat at four wintering areas along coastal BC (fig. 1), under the authority of permits from Environment Canada (BC-09-0182) and Simon Fraser University Animal Care (992B-06). There were a total of eight collection events across the four sites: Dogfish Banks (December 2009 [$N = 20$] and February 2010 [$N = 18$]), Chatham Sound (December 2009 [$N = 13$] and February 2010 [$N = 10$]), Fraser River Delta (December 2010 [$N = 13$] and February 2011 [$N = 15$]), and Baynes Sound (December 2010 [$N = 15$] and February 2011 [$N = 15$]). By conducting all collections before the end of February, we assumed that any differences in baseline CORT among wintering areas would be a result of variation in local habitat conditions rather than physiological changes associated with spring migration, which does not occur until April or later (W. S. Boyd, unpublished data).

To eliminate potential variation in baseline CORT related to age class or sex (Bonier et al. 2007; Wada et al. 2008), we

collected only after-hatch-year (i.e., mature/adult) males as verified by plumage (Brown and Fredrickson 1997). We recorded the time since flush for each bird, which we defined as the period between initial flush and death. Because of the difficulty of determining when a bird first began to respond to our presence on our approach, times since flush were estimated and rounded to the nearest whole minute. We generally approached small flocks at speeds of 15–25 knots and shot flying birds from a moving boat. We made all efforts to ensure that all birds were killed cleanly and quickly. Within 5 min of retrieval, we sampled heart blood using a sterile 18-gauge needle and transferred up to 5 mL of blood to a heparinized vial for CORT analyses. We centrifuged whole blood within 8 h of collection to separate plasma and cells and stored all tissues at −20°C. To facilitate examination of relationships between CORT and metrics of individual condition, Long Point Waterfowl's Avian Energetics Lab (Port Rowan, Ontario) conducted analyses of body composition (total protein, lipid, water, and ash) from ingesta-free dry carcass mass, including plumage, following methods of Afton and Ankney (1991).

CORT Assay

We determined concentration of total CORT in nonextracted plasma using a corticosterone enzyme-linked immunoabsorbent assay (EIA-Assay Designs, catalog no. 901-097) with a four-parameter logistic fit based on Love and Williams (2008). We ran all samples in triplicate across six assay plates at a total volume of 100 μL with 1 : 40 dilution and 1.5% steroid displacement buffer. As per kit instructions, we first incubated plates at 26°C under shaking at 500 rpm for 2 h and then at 26°C without shaking for 1 h; we calculated the detection limit of the assay at 0.018 ng/well (0.72 ng/mL), with intra- and interassay coefficients of variation of 6.89% and 10.15%, respectively.

Study Sites

Each study site (fig. 1) represented a different combination of three habitat conditions, which we assessed for their influence on baseline CORT: exposure to wind and waves, water depth, and predation danger (table 1). Along the Pacific Coast, many white-winged scoters winter in somewhat protected nearshore areas. Dogfish Banks (53°55′N, 131°30′W) is a notable exception because it is an offshore site that is particularly susceptible to

turbulent seas during winter storms due to frequent high winds from the southeast (LGL Limited 2009). Combined with a mobile substrate of sand or a sand-gravel mixture, these conditions result in a frequently changing benthic foraging habitat. At Dogfish Banks, there is virtually no presence of bald eagles (*Haliaeetus leucocephalus*), which are the most likely predator of white-winged scoters (Anderson et al. 2012). Relative to other study sites, Dogfish Banks birds feed on a more diverse suite of prey (Palm et al. 2012). Water depths at the study site range from 4 to 20 m, and the maximal tidal range is approximately 5 m (Amos et al. 1995).

Situated among many large islands and the mainland coast, Chatham Sound (54°27′N, 130°25′W) is more protected from high winds and large swells than Dogfish Banks. Birds at Chatham Sound feed in deep water (5–30 m), searching for prey in sandy and muddy substrate situated between rock outcrops (E. Palm, personal observation). Bivalves are the main prey taken by white-winged scoters at this site, but during some periods, birds at Chatham Sound consume a wider variety of foods, including echinoderms and crustaceans (Palm et al. 2012).

Baynes Sound (49°39′N, 124°53′W) contains extensive intertidal flats and high densities of wild and cultured bivalves, providing nearshore habitat for about 6,500 white-winged and surf scoters during winter (W. S. Boyd, unpublished data). Because it provides an abundant and temporally stable source of bivalve prey and white-winged scoters wintering in the area show relatively low foraging effort, Baynes Sound is thought to be high-quality foraging habitat (Lewis et al. 2007, 2008). Unlike on Dogfish Banks, white-winged scoters wintering on Baynes Sound and Chatham Sound often forage in close proximity to high densities of bald eagles.

Thousands of white-winged scoters use the shallow intertidal mudflats on the Fraser River Delta (49°06′N, 123°16′W) annually for molting, wintering, and staging (J. R. Evenson, unpublished data). The Fraser River Delta offers very few potential perches for bald eagles. Similar to scoter diets in Baynes Sound, diets on the Fraser River Delta consist almost entirely of bivalve prey (Palm et al. 2012).

Data Analysis

Quantification of Time Line to Acute Stress. Before running the models corresponding to each of our a priori hypotheses describing possible sources of variation in baseline CORT, we

Table 1: Variation in habitat conditions and diet composition among four wintering sites for white-winged scoters in British Columbia

Study site	Exposure	Water depth	Proportion of bivalves in diet	Predation danger
Chatham Sound	Low	High	High to very high	High
Dogfish Banks	High	High	Medium to high	Low
Baynes Sound	Low	Low	Very high	High
Fraser River Delta	Low	Low	Very high	Low

quantified the time between initial flush of targeted birds and acute stress response, represented by an increase in plasma CORT concentration. We excluded a single data point from all analyses, with a CORT concentration of 151.3 ng/mL and an associated time since flush of 1 min, because it far exceeded baseline values found in a separate study of wintering sea ducks, which ranged from approximately 15 to 50 ng/mL (Nilsson et al. 2008). An initial plot of CORT versus time since flush showed average CORT to be relatively stable until approximately 3–4 min, after which it increased (fig. 2). We ran a series of multiple linear regressions in R (R Development Core Team 2011) to determine the appropriate cutoff time that would separate baseline values from values of potentially acutely stressed birds (Nickerson et al. 1989).

Using 1 min as the first potential cutoff time, we separated CORT data into two groups based on associated time since flush: (1) 0–1 min and (2) >1 min. For each of the two groups in the linear model, we allowed both the intercept and the slope to vary. We then repeated the process using every time since flush from 2 to 6 min as the potential cutoff time between the two groups. We expected to see a relatively flat line for baseline values, followed by a linear increase in CORT over time, which would represent acute stress. To choose the cutoff time that provided the best fits of both baseline CORT and the acute stress response, we calculated Akaike's Information Criterion adjusted for small sample size (AIC_c) for each of the models and chose the model with the lowest value (Burnham and Anderson 2002). We log transformed CORT data to meet assumptions of normality in our linear models, but we report untransformed data.

Geographic Variation in Baseline CORT. Based on the analyses described above, we excluded birds for which time since flush exceeded the determined cutoff and thus may have exhibited acute CORT response. Eliminating these birds ensured that values included in subsequent analyses represented baseline levels. We compared baseline CORT data across study sites and collection periods using least squares analyses in an information-theoretic context. We pooled data from the eight separate collection events in specific ways to test relative support for different biologically plausible, a priori hypotheses describing possible sources of variation in baseline CORT. Exposure, water depth, diet composition, predation danger, and collection period were all factors potentially influencing baseline CORT, and these factors varied across study sites (table 1). To account for the potential effect of collection period (December vs. February), we included models that pooled data based on period in addition to another factor. For example, if the hypothesis was that baseline CORT varied by water depth and period, the explanatory variable would have four levels: (1) midwinter deep-water sites, (2) midwinter shallow-water sites, (3) late-winter deep-water sites, and (4) late-winter shallow-water sites. In addition, we included a null model, representing the hypothesis that CORT did not vary geographically or by collection period. To account for assumed daily fluctuation in CORT levels, time of day was a covariate in all models except the null.
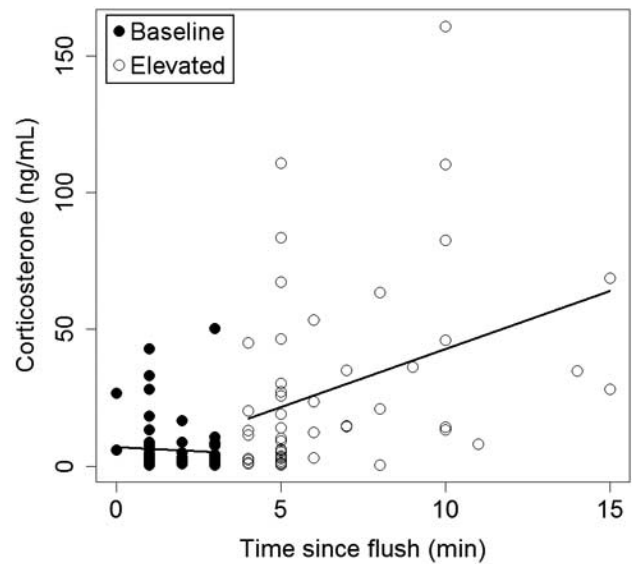

Figure 2. Plasma CORT concentrations as a function of time since flush (i.e., the period between initial flush and death). Separate regression lines for baseline levels (0–3 min) and elevated levels (>3 min) were derived from the best-supported model evaluating appropriate cutoff time.

We also included a model with time of day as the only explanatory variable. Below, we describe and justify our predictions for effects of three habitat factors, diet composition, and time of day on baseline CORT.

Exposure. At more exposed sites, baseline CORT in seabirds may vary in response to a greater frequency in storms, which can limit access to food resources (Smith et al. 1994). For the exposure hypotheses, we pooled Dogfish Banks data separately from data from other sites (table 2).

Water Depth. Increased baseline CORT may trigger increased explorative behavior for locating food (Reneerkens 2002). At greater depths, where locating benthic prey may require more time and effort, such a behavioral response could be beneficial for white-winged scoters. Alternatively, an increase in explorative behavior at some sites may induce increased baseline CORT. To group CORT data by water depth, we pooled data from Dogfish Banks and Chatham Sound separately from the remaining two sites (table 2).

Predation Danger. Increased predation danger has been associated with increased baseline CORT in a number of bird species (Scheuerlein et al. 2001; Cockrem and Silverin 2002; Hawlena and Schmitz 2010). For the predation danger hypotheses, we pooled Fraser River Delta and Dogfish Banks data separately from Baynes Sound and Chatham Sound (table 2).

Diet Composition. Diet composition can be used as another indicator of the availability of food resources in that area, which

Table 2: Candidate models describing variation in baseline levels of plasma CORT in male white-winged scoters across four wintering areas in British Columbia

Explanatory variable	Site and period grouping	K	ΔAIC_c	w	r^2
Time-of-day covariate only	CS = DB = BS = FD	3	.00	.31	.04
Null	CS = DB = BS = FD	2	.82	.21	...
Diet composition	CSM = DB; CSL = BS = FD	4	.87	.20	.06
Predation danger	CS = BS; DB = FD	4	1.21	.17	.06
Water depth	CS = DB; BS = FD	4	1.80	.13	.05
Period	CSM = DBM = BSM = FDM; CSL = DBL = BSL = FDL	4	2.01	.12	.05
Exposure	DB; CS = BS = FD	4	2.22	.10	.05
Exposure, period	CSM = BSM = FDM; CSL = BSL = FDL; DBM; DBL	6	4.84	.03	.07
Water depth, period	CSM = DBM; CSL = DBL; BSM = FDM; BSL = FDL	6	5.44	.02	.07
Predation danger, period	CSM = BSM; CSL = BSL; DBM = FDM; DBL = FDL	6	5.64	.02	.06

Note. BS = Baynes Sound; CS = Chatham Sound; DB = Dogfish Banks; FD = Fraser River Delta; M = midwinter; L = late winter. Results account for inclusion of a covariate for time of day for all models except the null.

can influence baseline CORT levels (Reneerkens et al. 2002). We grouped CORT data from both December and February at Dogfish Banks with February CORT data from Chatham Sound in our examination of the diet composition hypotheses (table 2).

Post Hoc Analysis

Based on past studies that found relationships between baseline CORT and measures of body condition (Kitaysky et al. 1999; Müller et al. 2007), we ran a post hoc analysis to test the hypotheses that baseline CORT varied by body mass, lipid mass, or protein mass. Structural body size, which we estimated separately using measurements of culmen, wing cord, tarsus, and the first principal component of all three, explained <16% of variation in body mass and was not correlated with total lipid mass (all $r^2 < 0.06$) or total protein mass (all $r^2 < 0.03$). Therefore, we did not correct measures of individual condition for body size. We included time of day as a covariate in all models except the null.

Model Selection

We used information-theoretic methods to direct model selection and used R (R Development Core Team 2011) for all statistical analyses. To infer the relative support of each model included in the candidate set, we calculated AIC_c, ΔAIC_c values, and Akaike weights (w; Burnham and Anderson 2002). Both ΔAIC_c and w values measure the relative amount of support for each model compared to other models in the candidate set.

Results

Quantification of Time Line to Acute Stress

The model using 3 min as the cutoff time ($r^2 = 0.31$) to separate baseline values from values representing acute stress provided the best fit of the observed data. Therefore, we excluded all CORT values with associated time since flush (t) of >3 min in subsequent analyses. The regression equations (parameter

estimates [SE]) for this model reflected our expectation that baseline CORT values would form a relatively flat line below a certain time since flush (3 min), after which CORT would increase linearly, corresponding to acute stress (fig. 2):

$$\text{baseline CORT} = 6.97\,(5.55) - 0.61\,(3.01)t,$$

$$\text{collected after 3 min} = 0.39\,(9.65) + 4.24\,(3.20)t.$$

Geographic Variation in Baseline CORT

Across all sites, average ($\pm$ SE) baseline CORT was 6.64 ± 1.19 ng/mL. Five models describing variation in baseline CORT had ΔAIC_c scores ≤ 2, with the most parsimonious model being that with the time-of-day covariate only. We observed a negative relationship between baseline CORT and time of day, which is consistent with past research on daily rhythms of CORT in diurnal birds. After accounting for the effect of time of day, the null model was the next most supported model (w = 0.21), indicating similar CORT levels across sites and periods. Overall, >92% of the variation in CORT was not explained by any of the models in our candidate set (table 2). There was no evidence indicating that exposure, water depth, predation danger, or diet composition influenced baseline CORT. In addition, baseline CORT did not differ between December and February. In our post hoc analyses examining relationships between individual condition and baseline CORT, all three measures of condition outperformed the null model, while both protein mass and body mass models outperformed the model with the time-of-day covariate only (table 3). The protein mass model was most parsimonious, explaining 18% of the variation in baseline CORT. The correlation between protein mass and baseline CORT suggested that elevated CORT was associated with lower protein mass.

Discussion

Our results demonstrate that it is possible to measure baseline CORT levels from lethally collected birds if the time from initial

Table 3: Post hoc candidate models describing variation in baseline levels of plasma CORT in male white-winged scoters across four wintering areas in British Columbia

Explanatory variable	K	ΔAIC_c	w	r^2
Protein mass	4	.00	.89	.18
Body mass	4	5.02	.07	.11
Time-of-day covariate only	3	7.86	.02	.04
Lipid mass	4	8.33	.01	.07
Null	2	8.68	.01	...

Note. Results account for inclusion of a covariate for time of day for all models except the null.

flush until death is measured. We found increasing CORT values above a time since flush of 3 min, presumably reflecting acute stress responses. That result is consistent with past studies indicating that blood samples taken within 3 min of capture represented baseline CORT (Wingfield et al. 1982; Romero et al. 1997; Silverin and Wingfield 1998; Romero and Romero 2002; Romero and Reed 2005). Our methods, which determined the appropriate cutoff time between baseline and stressed concentrations of CORT in shot birds, can be applied in subsequent studies requiring lethal sampling of birds.

Despite differences in habitat conditions, baseline CORT of white-winged scoters did not differ across sites. These results suggest three possibilities: (1) overall foraging conditions were not markedly different among our study sites, (2) fluctuations in baseline CORT levels were largely endogenously regulated and dependent on season, or (3) baseline CORT was not affected by the habitat factors we considered. If baseline CORT levels in wintering white-winged scoters were driven primarily by unfavorable foraging conditions, values should have been greatest at Dogfish Banks because of its frequent storms, strong currents, mobile substrate (LGL Limited 2009), and relatively low dietary fraction of bivalves (Palm et al. 2012).

Combining baseline CORT with data on body condition may provide more insight into differences in habitat conditions than either metric on its own (Kitaysky et al. 1999). White-winged scoters employed different energy management strategies across sites on the basis of habitat conditions. Wintering birds at Dogfish Banks maintained relatively high lipid mass, which likely functioned as a buffer against frequently changing foraging conditions (Palm 2012). During both December and February, average lipid mass at Dogfish Banks was more than twice as high as at Baynes Sound, which has an abundant, predictable source of prey and more favorable weather (Lewis et al. 2008). Consistent with baseline CORT, levels of plasma metabolites varied little across sites, suggesting that, irrespective of body composition, birds at all sites maintained physiological homeostasis (Palm 2012). Our results suggest that individual condition of birds may have influenced baseline CORT; however, irrespective of their energy management strategy, birds were largely successful in maintaining homeostasis and avoiding physiological stress across sites.

Site selection based on physiological phenotype also may have contributed to the relatively low variation in baseline CORT across sites. In waterfowl, there is evidence that adult male birds often compose high proportions of populations that winter in northern sites or sites with relatively harsh weather (Jorde et al. 1982; D. Esler, unpublished data). The larger body size of male white-winged scoters relative to that of females confers lower mass-specific energy demands, making males better equipped to handle cold or windy environments (Goudie and Ankney 1986). Larger birds also may be more resistant to fluctuations in energy status as a result of variable foraging conditions (Richman and Lovvorn 2009). Further, older, more experienced birds may be more likely to find food resources in an unpredictable foraging environment. Relative to other sites, we saw a higher ratio of adult males to other cohorts at Dogfish Banks. Similar baseline CORT levels across our study sites may indicate that white-winged scoters select wintering areas where they can successfully maintain physiological homeostasis and that site selection may depend on individual specific suitability. Also, unlike breeding birds, wintering birds have more opportunity to abandon a site if conditions deteriorate (Kirk et al. 2008), allowing them to select sites amenable to the maintenance of physiological homeostasis.

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