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Assessing physiological and behavioural energetics as biomarkers of environmental change in seabirds

By

Graham H. Sorenson

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Assessing physiological and behavioural energetics as biomarkers of environmental change in seabirds

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DECLARATION OF CO-AUTHORSHIP/ PREVIOUS PUBLICATION

I. Co-Authorship Declaration

I hereby declare that this thesis incorporates material that is result of joint research. I am the sole author of chapters 1 and 4, and primary author of chapter 2 and 3. Both chapters 2 and 3 are co-authored with my supervisor, Dr. Oliver Love and my collaborator, Dr. Christine Madliger. Chapter 2 is also co-authored with Dr. Cody Dey. Chapter 3 is also co-authored with Thomas Lazarus, Travis White, Dr. Grant Gilchrist, Michael Janssen, and Dr. Kyle Elliott. In all cases, the primary ideas, study designs, and data analysis and interpretation were performed by the author. Dr. Love has provided guidance and feedback in all aspects of the project.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-authors to include the above materials in my thesis.

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II. Declaration of Previous Publication

This thesis includes one original paper that has been submitted for publication in a peer reviewed journal, as follows:

Thesis Chapter	Publication title/full citation	Publication status*
Chapter 2	Effectiveness of baseline corticosterone as a monitoring tool for fitness: a meta-analysis in seabirds	In review (*Oecologia*)

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ABSTRACT

Environmental change is occurring at an unprecedented rate, making traditional demographic monitoring techniques less practical and giving rise to more proactive monitoring methods. Although many ‘biomarkers’ such as physiology and behaviour are used in field research, testing their effectiveness as indicators of environmental change across multiple biological scales is key to using these tools confidently. In Chapter 2, I use a phylogenetically-controlled meta-analysis across seabird species to demonstrate the strength of the relationship between baseline corticosterone and common fitness-related traits. I found food availability and reproductive success to have strong negative relationships with corticosterone. In Chapter 3, I use an integrative approach (physiology, foraging behaviour, energetic expenditure) across multiple biological scales within a natural environmental ‘experiment’ to determine the relative sensitivity of key traits to sea ice changes in an Arctic seabird, the thick-billed murre (*Uria lomvia*). I found corticosterone and non-esterified fatty acids were higher and foraging strategy consisted of more frequent, short foraging trips during the low ice year. However, average daily foraging distance, estimated daily energetic expenditure, triglycerides, and beta-hydroxybutyrate remained constant across years. In the face of environmental change the birds appear to be working harder, but maintaining energy intake and energetic expenditure. Overall, my thesis serves as a model for biomarker validation and answers questions about physiological and behavioural environmental responses and fitness outcomes across seabirds.

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LIST OF ABBREVIATIONS/SYMBOLS

CORT – corticosterone

TRIG – triglyceride

BOH – beta-hydroxybutyrate

NEFA – non-esterified fatty acid

GPS – Global Positioning System

eDEE – estimated daily energetic expenditure

CHAPTER 1

General Introduction

Monitoring a changing world

Rapid, human-induced environmental change is causing shifts in temperature and weather patterns across the planet, with extremes seen at the poles (Mauritsen 2016; Navarro et al. 2016). These rapid environmental changes are already affecting biodiversity in a number of diverse ways (e.g., decreased productivity, regime shifts, genetic variation, population declines; Bellard et al. 2012, Mantyka-Pringle et al. 2012, Pauls et al. 2013) and range shifts are expected to continue at individual to large environmental scales (Parmesan 2006; Bellard et al. 2012). To date a fairly large degree of the detailed mechanistic focus on the impacts of climatic change on wildlife has been focused on terrestrial habitats (Walther et al. 2002; Parmesan 2006; Duarte 2014), given that oceanic ecosystems may be harder to study given the vast size of the overall marine environment making the determination of unifying mechanisms more difficult (Duarte 2014; Hussey et al. 2015). Nonetheless, it is well-appreciated that oceans are changing dramatically as they absorb much of the heat and carbon dioxide from anthropogenic factors (Hoegh-Guldberg and Bruno 2010). Indeed, these temperature and acidity shifts are driving dramatic changes in weather patterns, ocean currents and ice dynamics, all of which can influence marine species distribution and abundance. Nowhere are these changes in sea temperature and ice extent changing more intensely than in the Arctic (Hansen et al. 2006; Bindoff et al. 2007). Many Arctic species rely on sea ice for reproduction, foraging, and movement as sea ice and ice edges represent hot spots for primary productivity in the Arctic, and thus support much of the trophic system (Darnis et al. 2012; Post et al. 2013). Declines in ice extent have resulted in decreased distribution of low trophic species (clams Doney et al. 2012; Arctic Cod Gaston et al. 2005) and changes in condition and abundance of top-level predators (polar bears, Iversen et al. 2013; seals and walruses, Doney et al. 2012). Unfortunately, predictions of sea ice extent indicate the possibility of no summer sea ice within the next 30 years (Wang and Overland 2012) which is expected to have major multi-dimensional impacts on polar wildlife across the globe (Post et al. 2013).

Recognizing the impacts of these large scale environmental changes on wildlife health has traditionally relied on long-term demographic studies that track population changes in relation to environmental variation (Paleczny et al. 2015). While long-term monitoring of populations or species can provide strong historical data on how trends may be correlated with environmental change, by design they do not provide the underlying mechanisms necessary for the results to be predictive to further increases in variation or change (Satterthwaite et al. 2012). Also, because environmental change is now happening more rapidly than scientists can monitor population demography, the study-longevity required to collect enough data to show statistically significant trends often makes these approaches too slow to detect changes before species management is possible (Ewers and Didham 2006). An increase in the use of integrative, individual based techniques such as physiological and behavioural traits promises the possibility for rapid, predictive methods for examining the success of individuals and therefore populations in relation to environmental variation (Cooke et al. 2004; Wikelski and Cooke 2006; Hussey et al. 2015). While measuring physiology and behaviour in wildlife is not a new field, determining whether these traits respond to environmental variation and in turn are predictive of fitness metrics still remains poorly studied, especially in at-risk species (Madliger et al. 2016). As such, the use of these potential biomarkers of environmental change requires validation both within and across species, as well as across environmental gradients to confirm their effectiveness at relating environmental change to potential population changes (Madliger and Love 2015).

The Use of Biomarkers to Assess Environmental Change

Individual metrics that represent fitness of an individual, or success within a population, are broadly considered biomarkers by conservationists and ecological biologists (Cooke and O'Connor 2010; Madliger and Love 2015). For biomarkers to be most informative, they ideally need to also translate the link between environmental variation and individual performance or success so that biomarker information at the level of the individual can be scaled up to appreciate how environmental change ultimately impacts population demography (Madliger and Love 2014). From a practical standpoint, the proposed power of biomarkers is therefore that they can capture complex environmental impacts on populations with relatively few, ideally simple, measurements or metrics, ultimately saving time and money for managers and researchers. Ecologists have long used absolute measures or changes in body mass or measures of body condition as biomarkers to monitor responses to environmental variation (Toïgo et al. 2006). More complex biomarkers have had a long history within the field of toxicological research for monitoring the direct human impact of contaminants on individuals, populations and ecosystems (e.g. Braune et al. 2014). In more recent decades isotopic tracers have been used extensively to track and monitor trophic structure and changes in trophic assemblages across taxa (Hussey et al. 2014). Integrative ecologists are now employing multiple physiological, genetic and behavioural metrics in an attempt to monitor larger-scale environmental quality (e.g., Seaman et al. 2006, Piatt and Harding 2007, Slabbekoorn and Ripmeester 2008, Aylagas et al. 2014), although there is a still a general lack of appreciation or ability to ultimately link these measures to individual performance or fitness (Madliger and Love 2015; Madliger et al. 2016).

Energetic Physiology as a Biomarker

Physiological metrics in general are thought to be especially useful biomarkers of environmental variation and change because physiology links the individual to its environment (Cooke et al. 2013; Madliger and Love 2015). Since a source of energy should be a key limiting resource for any population (Hairston et al. 1960), and we expect rapid environmental change to be altering not only the quantity but the quality of resources available to organisms (Fernandes et al. 2013; Morrison et al. 2014), many ecological physiologists have recently turned to measures of energetics in an attempt to capture an individual's response to changes in resource bases (Seaman et al. 2006; Benowitz-Fredericks et al. 2008). The hope then is that information on energetic management at the individual level can be linked to fitness outcomes and therefore more immediate predictions about population health and demographic responses before they occur (Angelier et al. 2010). Energetic physiology encompasses a suite of individual metrics regulating or enabling energetic stores in individuals including daily energetic expenditure (Elliott et al. 2013a; Elliott et al. 2013c), energetic metabolites (Guglielmo et al. 2002), stress hormones as measures of energetic stress (Angelier et al. 2009) and thyroid hormones as measures of resource limitation (Wasser et al. 2010; Ayres et al.

2012). In my thesis I am focusing on four physiological metrics that are all commonly used in the literature to measure the current state of an individual.

Baseline Glucocorticoids: Glucocorticoids (often referred to as 'stress hormones' for their transitory role in responding to acute environmental stressors; Romero and Wikelski 2001) such as corticosterone (birds, reptiles, amphibians) and cortisol (humans, fish) are an increasingly popular group of hormones being employed to examine responses to environmental variation (Cooke et al. 2014; Madliger et al. 2016). Although glucocorticoids serve an important role in the stress response, baseline levels serve a highly important role in regulating daily energetic balance or homeostasis, both via regulating plasma glucose levels (Dallman et al. 1993) and via providing the cues to flexibly modify important behaviours like activity and foraging (Astheimer et al. 1992; Breuner et al. 1998; Crossin et al. 2012). Importantly, baseline glucocorticoid levels respond to environmental variation such as food availability (Lanctot et al. 2003; Kitaysky et al. 2007; Barrett et al. 2015) and to changes in energetic demands across life-history stages (Michael Romero 2002; Williams et al. 2008). Overall therefore they act to maintain the individual in allostasis - the process of achieving homeostasis through change (McEwen and Wingfield 2003). Since baseline glucocorticoids work to maintain allostasis, changes in energetic demand that are not met with increases in energetic intake result in increases in glucocorticoid levels to facilitate changes in foraging behaviour and physiology such as increased glucose mobilization (McEwen and Wingfield 2003; Busch and Hayward 2009). As such, elevated GC levels indicate or should be interpreted as high energy use or lack of sufficient calorie resources.

Plasma Triglycerides: Energetic metabolites have been employed recently either as a measure of the energetic condition of an individual (i.e. increasing fat stores or burning internal resources; Stutchbury et al. 2011) or more globally as a metric of habitat (i.e., resource) quality (Williams et al. 2007). Since they are the storage form of fatty acids, plasma triglyceride levels have been used as strong indicators of fat deposition in a number of species of birds (Guglielmo et al. 2005; Anteau and Afton 2008; Dietz et al. 2009). Higher plasma levels generally indicate an individual in a positive energetic state, or one that is gaining in condition (Cerasale and Guglielmo 2006). In many studies of migratory avian species, triglyceride (TRIG) levels have been used as an indicator of stopover site (location for birds to refuel) quality (Jenni and Jenni-Eiermann 1998; Guglielmo et al. 2002). Plasma TRIG levels are assayed with a colourimetric kit that works by converting triglycerides to glycerol and measuring total and free glycerol. The assay only requires 8 uL of plasma and TRIG levels are not impacted by short periods of capture and handling stress.

Plasma Beta-hydroxybutyrate: Beta-hydroxybutyrate (BOH) forms from the biochemical conversion acetyl CoA in the liver following energetic expenditure. Measures of plasma BOH generally indicate the opposite of plasma TRIG (Anteau and Afton 2008), where high levels correspond with fasting and body mass (i.e., lipid) loss, and lower energetic condition (Cherel et al. 1988; Guglielmo et al. 2002; Seaman et al. 2006). During these periods of fasting or mass loss, BOH is synthesized from free fatty acids as a primary fuel for some tissues (Williams et al. 1999) and is thus a marker for lipid catabolism (Lamarre et al. 2016). Measurements of BOH are assayed with a colourimetric kit, require small amounts of plasma (11 uL) and are unaffected by sampling time.

Non-esterified Fatty Acids: Detailed fatty acid signatures from lipid stores have been used to infer diet of marine mammals and seabirds (Iverson et al. 2004; Iverson et al. 2007). Due to the diversity of fatty acids (FAs), analysis of fatty tissues can reveal broad differences in diet, or reveal specific diet choices by comparing signatures to the FA signature of prey (Iverson et al. 2007). While these detailed analyses from fat tissues reveal diet choices, non-specific measures of free fatty acids in the blood can indicate energy balance (Williams and Buck 2010). Free fatty acids, or non-esterified fatty acids (NEFA), are formed as a result of the hydrolysis of triacylglycerol and adipose tissues during periods of higher energetic demand than intake (Jenni and Jenni-Eiermann 1996; Price 2010; Williams and Buck 2010). As such, plasma NEFA levels in both birds and mammals rise as the individual increases exercise (Basu et al. 1960; Mcwilliams et al. 2004; Jeanniard du Dot et al. 2009). Measurements of plasma NEFA levels require small volumes (5 uL) of blood and indicate energy balance, making them practical indicators of energetic state. Taken together, because both BOH and NEFA levels rise in response to fasting (negative energy balance) and in response to exercise (Beaulieu et al. 2010; Williams and Buck 2010), they can be used to assess the level of energetic demand individuals are experiencing beyond their energetic intake.

Foraging and Movement Behaviour as a Biomarker

Behaviour is a traditional field of study, but relating behaviour to environmental variation (Harding et al. 2007) or fitness metrics (Stillman 2003) increases its relevance as a viable biomarker of environmental change. Traditionally, tracking wildlife movement has been undertaken with telemetry technologies (Cooke et al. 2004). However, recent and dramatic advances in technologies has increased our ability to not only track both terrestrial and aquatic organisms, but also to link these behaviours with environmental variation and fitness (Franke et al. 2004; Paredes et al. 2014; Hussey et al. 2015). Over the past decade, the number of studies tracking the spatial movement of vertebrates has particularly increased, with units ranging from small sub-gram geolocation devices for tracking small mammals and songbirds (DeLuca et al. 2015), to larger satellite units for tracking larger species over greater distances and time periods (Weimerskirch et al. 2014). Recently, the use of miniaturized Global Positioning System (GPS) units in particular has increased since this technology has allowed the accurate assessment of fine-scale behaviours in fairly small species over large spatial scales (Wakefield et al. 2009). A range of GPS tracking devices are currently available and range from very inexpensive models that must be recovered to obtain the data, to more expensive units which can remotely download data via telemetry, and even to solar-powered units which can collect data year-round (Meyburg et al. 2004). Tracking fine scale behaviours beyond direct observation is possible by setting small intervals between GPS points, allowing behaviours to be recorded at nesting sites and across the large foraging areas or migratory routes (Wakefield et al. 2009). For example, behaviours related to energetic use such as distance travelled, flight time, and foraging trip length and patterns can be measured. In my thesis we use two types of GPS devices that provide highly accurate data, small size, and withstand the extreme pressures associated with deep diving.

Seabirds as At-Risk Models

Although large-scale environmental change is difficult to monitor, especially in large, complex systems such as oceans (Hoegh-Guldberg and Bruno 2010), studying key ‘model’ species that can essentially monitor the environment and therefore indicate patterns and problems across that broad environment can help scientists more effectively monitor large areas. Despite these complexities of documenting and interpreting all of the effects of large-scale environmental change, studying marine top predators (e.g., whales, pinnipeds, sharks, tuna) can provide important information about overall marine health and changes in lower trophic levels (Frederiksen et al. 2007; Benowitz-Fredericks et al. 2008; Hussey et al. 2014). Seabirds provide an opportunity to assess environmental changes over the wide area that individuals forage and travel over during breeding and migration, and seabird population trends have been related to environmental factors in many studies (e.g., Jenouvrier et al. 2005; van de Pol et al. 2010; Gaston et al. 2012; Descamps et al. 2013; Robertson et al. 2014; Paleczny et al. 2015). Many seabird populations are also in global decline at higher rates than any other avian group (BirdLife International 2012; Croxall et al. 2012), and yet we know fairly little about the mechanisms underlying these changes. Nonetheless, since there is significant variation in seabird life history with different species responding to and indicating different changes in marine systems (Parsons et al. 2008), there may be important context-specific indicators of environmental conditions that are being overlooked. In addition, seabirds also represent a very practical group of species for monitoring. Most seabird species breed colonially, meaning they can be accessed readily during the breeding season. Individuals also forage widely from their colony, meaning that physiology and condition measures as well as tracking unit deployments at the colony represent the environment experienced over a wide area. Seabirds are also long-lived species and robust enough to handle repeated sampling, tracking unit deployment, and occasional colony disturbance. Because of the large sampling scale, sensitivity to the environment, global decline, and practicality of study, seabirds are used commonly as indicators of changes in the marine environment (Frederiksen et al. 2007; Parsons et al. 2008).

Individual performance or fitness is commonly measured or estimated in seabird research. There are limits to measuring actual fitness in wild study species, so a number of metrics are used as proxies within seabird literature. Research is often carried out within a particular study year, so reproductive success within a year is often considered ‘fitness’, and this is based on measures such as hatching success, clutch size, chick weight, or fledging success. Ideally, the later in the breeding season reproductive success is measured, the more accurately it will reflect the outcome of the breeding attempt, and it will be a stronger estimate of fitness. However, data collection constraints mean many measures of fitness are used will be discussed as fitness in this thesis.

Study Species

Thick-billed murres (*Uria lomvia*) are a sturdy, medium-sized diving seabird found throughout the circumpolar region (Figure 1.1). Adults of both sexes are monomorphic in coloration, sport entirely black and white patterning (Figure 1.2), weigh between 800-1000 grams during the breeding season (Gaston and Hipfner 2000) and live approximately 20 years (maximum 29 years, Gaston and Hipfner 2000). The sexes are also similar in all relevant morphological dimensions although male bill depth is larger (Gaston and Hipfner 2000). Thick-billed murres are a colonial-nesting species that breed on ledges on cliffs along the ocean and pairs are socially monogamous and invest in a single egg and offspring per year. Birds begin breeding at 5 years, and return to the same location on a given ledge with the same partner year after year (Gaston and Hipfner 2000). The timing of breeding varies throughout their range, but in the Eastern Canadian

Arctic (e.g., the Digges Island colony that is the focus of this research – see below) egg-laying begins between June 28 and July 3 on average (Gaston and Hipfner 2000). The single egg is then incubated for 32 +/- 1.4 days (Gaston et al. 1985). Thick-billed murre parents equally alternate incubation and chick-rearing duties with long foraging bouts. Just prior to fledgling, male parents take over the majority of the duties and remain with the chick through fledging and the first month on the open ocean.

Thick-billed murres represent an extreme of the Family *Alcidae* as they are one of the deepest diving seabirds still able to fly, resulting in extremely high wing-loading in flight (Elliott et al. 2013b). These traits make the energetic demands of travelling to and from foraging grounds from the breeding colony very energetically costly. Thick-billed murres are known as "ice-dependent" in that they primarily forage on fish species found commonly along sea ice edges in their North American range (Arctic cod, sandlance, capelin) as well as some crustaceans, benthic fishes, and some deep-water fishes (Springer et al. 1986; Gaston and Hipfner 1998; Gaston and Hipfner 2000). Populations across the globe have generally been declining (Gaston et al. 2000; Gaston et al. 2012; Descamps et al. 2013; Merkel et al. 2014) and studies in the Canadian Arctic suggest ice extent and the timing of ice break-up as well as the spatial distribution and availability of food resources are primary drivers of these declines (Gaston et al. 2005, 2009a,b).

Study Site

My thesis focuses on field work at a breeding colony located within Digges Sound, Quebec where long-term demographic data has been collected since 1980 (Gaston et al. 2000). Digges Island (62° 33' 11.1 N, 77° 43' 56.1 W) is located just north of Quebec in Nunavut in the Hudson Strait while Cape Wolstenholme (62° 32' 51.9 N, 77° 32' 19.9

W) is located on the northern border of Quebec in Nunavik (Figure 1.3). The colonies at Digges Island (300,000 birds) and Cape Wolstenholme (700,000 birds) face each other across the 7 kilometer wide Digges Sound (Figure 1.4). Birds are captured at one site on Cape Wolstenholme and four separate sites on Digges Island spread across the 2 kilometer long section of cliff with nesting birds on it. Due to the constraints of working on a cliff environment, these sites have been selected based on their access to sufficient numbers of breeding pairs and safe descent to the colony (Figure 1.5). Working with thick-billed murres in these environments requires careful rappelling descent to "working ledges", relatively flat areas from which to capture, handle and process birds (Figure 1.6). Individual murres are selected based on proximity to the ledge, ability to recapture, and status as breeding adult and are captured using noose-poles. Within 3 minutes of capture, individual murres are blood sampled (up to 1mL) from the brachial vein, then banded with a numbered aluminum band, weighed, morphological measurements are taken, and a GPS device is attached to their back (Figure 1.7). As described in Chapter 3, GPS units collect positions every 5 minutes to a resolution of 0.75m and data is collected remotely via ultra-high frequency link or by recapture of the bird upon the birds return to the colony. Units represent on average 1.5% of their body weight (i.e., under the 3% requirement outlined for birds; Phillips et al. 2003) and units are retrieved upon return if possible, at which time a second blood sample and body mass measurement is taken (to determine the change in these metrics across the foraging trip). If GPS units cannot be retrieved, they fall off within 10-15 days of deployment.

Thesis Goals

My thesis aims to test the effectiveness of individual metrics (i.e., biomarkers) as representatives of environmental change and fitness using both systematically reviewed literature data and multi-year field data. In my first data chapter, I focus on a widely-used and assumed individual-based metric of internal/external environmental variation, baseline corticosterone, which is commonly assumed (but rarely tested) to be a relevant biomarker of variation in both fitness and environmental change (Kitaysky et al. 2007; Satterthwaite et al. 2012). To quantitatively assess the strength of corticosterone-fitness relationships in seabirds, I present a phylogenetically controlled effect size meta-analysis relating corticosterone to environmental- and fitness-related traits across seabird species. My second data chapter focuses on and provides insights into the physiological and behavioural responses of one seabird species (thick-billed murre) to varying environmental conditions. In this data chapter, I use data from a two-year natural "climate experiment", where the two years differed dramatically in ice conditions, to determine how individual physiological and behavioural metrics respond to environmental change and relate to each other. By combining these two approaches, I hope to demonstrate which potential biomarkers show strong correlations with environmental variation and fitness, thereby providing insight into the use of these biomarkers for future work in predicting how species and populations with respond to further environmental change.

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Figures

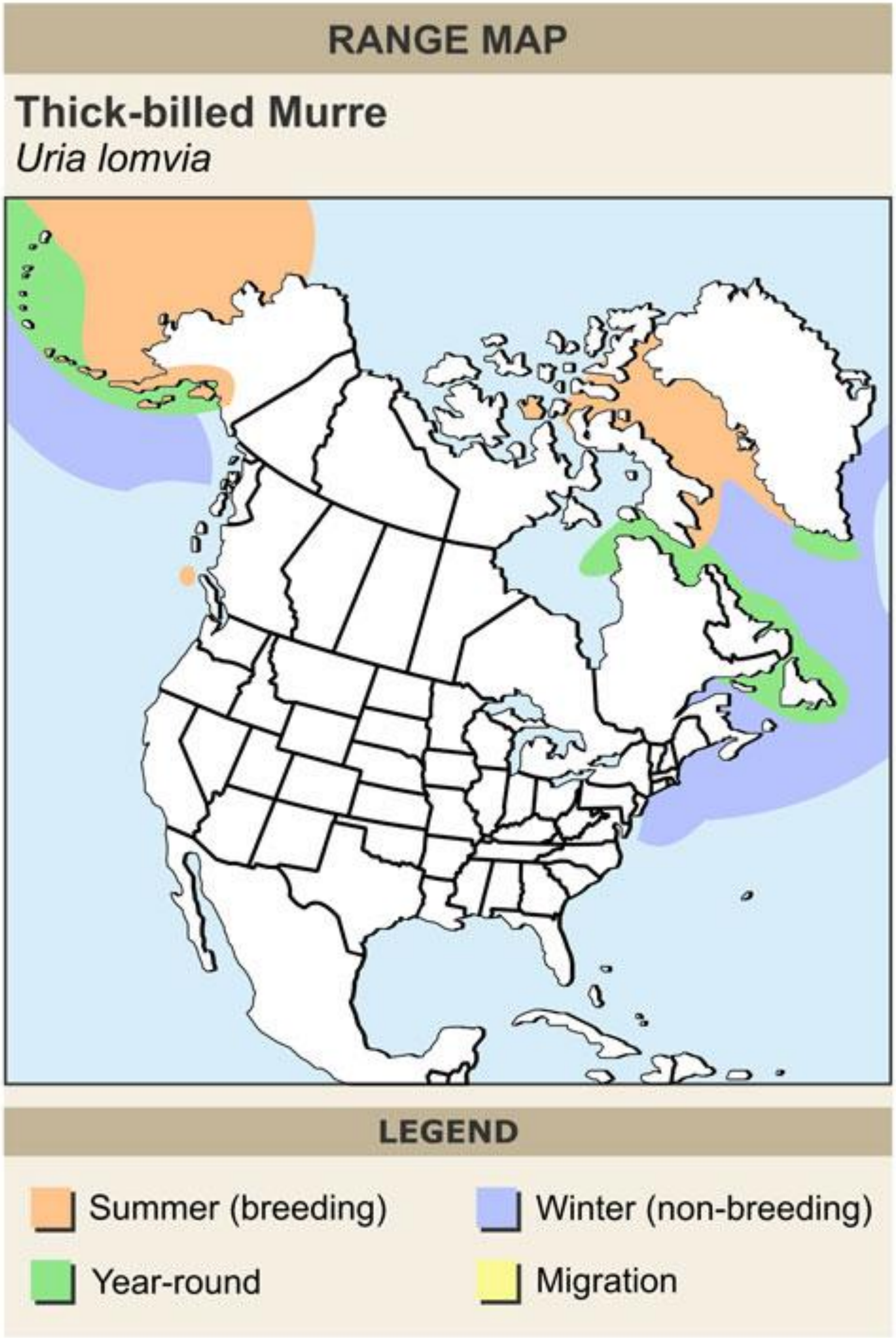

Figure 1.1 - Range map of thick-billed murre (*Uria lomvia*) from Whatbird.com.

Figure 1.2 - Thick-billed murre (*Uria lomvia*) adults, one with chick and one with egg at Digges Island, Nunavut. Photo by G. Sorenson.

Figure 1.3 - Location of Digges Island, and main locations in Digges Sound. Images from Google Maps and Google Earth.

Figure 1.4 - View of Cape Wolstenholme and east end of Digges Island from top of Digges Island cliffs. Photo by G. Sorenson.

Figure 1.5 - Location of a thick-billed murre (*Uria lomvia*) capture site within the Digges Island colony; researchers and rope leading to access point (top photo), researchers among murre colony (bottom photo). Photos by G. Sorenson.

Figure 1.6 - Accessing thick-billed murres (*Uria lomvia*) from a cliff ledge at Digges Island. Clockwise from top left: Rappelling to capture site, working on cliff ledge, view of “working ledge” in relation to cliff, view of murres from ledge. Photos by G. Sorenson.

Figure 1.7 - Handling of thick-billed murres (*Uria lomvia*) on a cliff ledge at Digges Island. Clockwise from top left: Blood sampling, leg banding, tarsus measurement, weighing, bill measurement, Ecotone Ltd. GPS device deployment. Photos by W. Black, G. Sorenson, and T. Lazarus.

CHAPTER 2

Effectiveness of baseline corticosterone as a monitoring tool for fitness: a meta-analysis in seabirds

Chapter Summary

Many ecosystems have experienced anthropogenically-induced changes in biodiversity, yet predicting these patterns has been difficult. Recently, individual behavioural and physiological measures have been proposed as more rapid links between environmental variation and fitness compared to demographics. Glucocorticoid hormones have received much attention given that they mediate energetic demands, metabolism, and foraging behaviour. However, it is currently unclear whether glucocorticoids can reliably predict environmental and fitness-related traits and whether they may be useful in specific groups of taxa. In particular, seabirds are a well-studied avian group often employed as biomonitoring tools for environmental change given their wide distribution and reliance on large oceanic patterns. Despite the increase in studies attempting to link variation in baseline corticosterone (the primary glucocorticoid in birds) to variation in fitness-related traits in seabirds, there has been no comprehensive review of the relationship in this taxa. We present a phylogenetically-controlled systematic review and meta-analysis of correlative and experimental studies examining baseline corticosterone as a predictor of fitness-related traits relevant to predicting seabird population health. Our results suggest that, while variation in baseline corticosterone may be a useful predictor of larger-scale environmental traits such as overall food availability and fitness-related traits such as reproductive success, this hormone may not be sensitive enough to detect variation in

body condition, foraging effort, and breeding effort. Overall, our results support recent work suggesting that the use of baseline glucocorticoids as conservation biomarkers is complex and highly context-dependent, and we suggest caution in their use and interpretation as simplified, direct biomarkers of fitness.

Introduction

Ocean ecosystems have experienced extensive changes in biodiversity and species abundance as a result of anthropogenic impacts (Hoegh-Guldberg and Bruno 2010). Unfortunately, isolating the precise mechanisms underlying these changes has not always been straightforward (Halpern et al. 2008). Increasingly, wide-ranging marine vertebrates are being employed as useful and biologically-relevant bio-monitoring species of both fine- and large-scale variation in oceanic conditions (Hussey et al. 2015). Seabirds (penguins – Sphenisciformes, tubenoses - Procellariiformes, gannets and cormorants - Pelecaniformes, and gulls and auks - Charadriiformes; Fig. 2.1) represent an increasingly well-studied and diverse sub-group of predators, and are often considered prime biomonitoring tools given their wide distribution and reliance on oceanographic patterns across large spatial areas (Piatt and Sydeman 2007). Specifically, because oceanic environments are changing rapidly, yet are so large and complex to study, seabirds have the potential to act as very practical and sensitive biomarkers to changes in oceanic patterns, food supply and location, and temperature regime shifts for a number of reasons (Frederiksen et al. 2007; Parsons et al. 2008). First, seabirds range over very large areas of temperate, tropical and polar oceans during different stages of their life-history (e.g., breeding, migration and wintering; Weimerskirch et al. 2014). Second, because many seabird species are central place foragers, a result of colonial breeding (Orians and Pearson 1979), researchers also often have the capacity to monitor individuals and populations to determine causal links between large-scale oceanographic change and individual fitness and/or population health (Satterthwaite et al. 2012; Descamps et al. 2013). Third, seabirds are experiencing significant population declines with 28% of species listed as globally threatened and 10% near threatened (BirdLife International, Croxall et al. 2012). Finally, many of these declines are thought to be both directly and indirectly related to anthropogenically-induced changes (e.g., Bodey et al. 2014). As such, it is important to ensure biomonitoring tools reflect the impacts of environmental variation on factors important to population demographics.

Traditionally, examining how environmental variation impacts the health of colonially breeding species has been accomplished via the long-term monitoring of population demography (Gaston et al. 2012; Descamps et al. 2013). Indeed, demographic studies have been important for inferring broad-scale linkages between oceanic changes and seabird colony trends (Paleczny et al. 2015). However, given that trends often show long temporal lags between environmental variation and population responses (Ewers and Didham 2006), they can be less effective for predictive, proactive or rapid-response management endeavours (Satterthwaite et al. 2012). In response to this information gap, integrative ecology has seen a surge in the use of field analytical techniques aimed at connecting finer-scale, individual-level mechanisms (e.g., behaviour, stable isotopes, immune system metrics, energetic physiology) as biomarkers of larger-scale environmental change with the hope of ultimately predicting population responses before they occur (Ozgul et al. 2010; Moody et al. 2012; Cooke et al. 2013; Ramos et al. 2014;

Hussey et al. 2015). By focusing on specific traits that can reveal how environmental variation is impacting individuals, it is hypothesized that researchers can extrapolate these mechanisms to the population level and proactively determine how and why a given population may be changing (Madliger and Love 2016). For example, Harding et al. (2007) studied behaviour in relation to food availability in Common Murres (*Uria algae*) and demonstrated that time budgets could indicate large-scale food availability within certain spatial ranges. The authors suggest that by establishing the link between prey species and murre foraging, seabird behaviour can ultimately be used as a tool for estimating aspects of ocean productivity. In addition, physiological traits have recently been employed to examine a diversity of responses to the environment across taxa (Cooke and O'Connor 2010; Chown and Gaston 2015), and conservation physiologists have increasingly focused their efforts on traits associated with energetic management (Madliger and Love 2015).

Glucocorticoids (often referred to as 'stress hormones' for their role in the acute stress response; Benowitz-Fredericks et al. 2008), such as corticosterone (CORT) in birds, play an important regulatory role at baseline levels. Importantly, they provide a central function in allostasis by mediating variation in energetic demand, glucose management and foraging/feeding behaviour (Astheimer et al. 1992; Ricklefs and WIlkelski 2002; Landys et al. 2006; Angelier et al. 2008). Given that baseline glucocorticoids (GCs) should be sensitive to changes in the environment that impact allostatic management (McEwen and Wingfield 2010; Madliger and Love 2014; Madliger and Love 2015), it is not surprising that they are a recently popular trait measured in seabirds (Appendix 1), and across avian species and other taxa (Bonier et al.

2009; Busch and Hayward 2009). For example, Kitaysky and colleagues (Kitaysky et al. 1999; Kitaysky et al. 2007; Kitaysky et al. 2010; Satterthwaite et al. 2012) have demonstrated that metrics of CORT from Common Murres have the capacity to reflect current and past food abundance, as well as predict both a decrease in reproductive performance and the disappearance of individuals from a declining colony. Links between CORT and individual condition (Angelier et al. 2010) and reproductive success (Kitaysky et al. 2010) have also been reported in some seabird species, and while there is a general, but often complicated, assumption that variation in baseline GC levels should correlate with fitness (Bonier et al. 2009), empirical and meta-analytic studies have begun to indicate the often complex and context-dependent nature of the use of baseline GCs as direct links between environmental change and fitness (Lanctot et al. 2003; Hayward et al. 2011; Strasser and Heath 2013; Dantzer et al. 2014; Riechert et al. 2014; Madliger and Love 2016). As such, further work is needed to determine whether direct and predictive relationships exist between baseline GCs, fitness-related traits and environmental variation (Madliger and Love 2014; Thierry et al. 2014; Madliger and Love 2015). Crucially, while the frequent use of baseline CORT across seabird studies has resulted in a large body of research, we currently lack a quantitative assessment of how well these results predict key fitness-related traits that ultimately result in population-level changes.

The goal of the current paper was to evaluate whether variation in baseline plasma CORT can predict variation in metrics of fitness and the environment across seabird species. Such a study is both timely and useful for conservation and seabird biologists alike given that a large body of published research relating CORT levels to various metrics of fitness and environmental variation in seabirds exists with no general summary or consensus. We compiled all papers linking seabird baseline CORT to regularly measured traits related to seabird fitness: body condition, effort at foraging or nesting, and reproductive success, or to a key metric of environmental quality: food availability. Given that all of these traits are assumed to relate to individual success (Ponchon et al. 2014) and are used in seabird literature to represent "success", we consider these metrics 'fitness-related traits'. Thus, to quantitatively assess the viability of using baseline CORT as a physiological biomarker, we used a phylogenetically-controlled meta-analysis to analyze general trends between CORT and fitness-related traits using effect sizes. Given that it has commonly been assumed that elevated GCs have a negative association with fitness (although see Bonier et al. 2009) and low environmental quality (Kitaysky et al. 2010; Satterthwaite et al. 2012), we predicted a negative association between elevated baseline CORT and most fitness-related measures (e.g., body condition, food availability, reproductive success). However, given that baseline GCs are responsible for managing daily energetics (Angelier et al. 2007a), we also predicted a positive relationship with measures of individual effort in foraging and nesting.

Methods

We performed a systematic review and meta-analysis in which we collected data on the relationship between CORT and fitness-related traits from the literature and tested whether this relationship was influenced by the type of trait examined, study methodology, and the phase of breeding. We used Bayesian meta-regression techniques similar to Horvathova et al. (2011) and Prokop et al. (2012). We chose five fitness-related traits for the analysis based on their prevalence in the literature and the ease of obtaining similar data for both seabird and conservation managers: body condition, foraging effort, nesting effort, food availability, and reproductive success (Table 2.1). We began with a Google Scholar and Web of Science search for the terms “corticosterone” and “seabird” (including papers available by June of 2015) across both correlative and manipulative studies that focused on links between baseline CORT and our chosen fitness-related traits (Fig. 2.2). We used only these general search terms to avoid missing papers that did not subscribe to the same terminology for the fitness-related traits that we chose. Manipulative studies included those, for example, where researchers either manipulated CORT levels directly (via implants or other supplementation), or manipulated the foraging ability or condition of individuals (via feather clipping or weight handicaps) and then examined impacts on CORT (e.g., Angelier et al. 2007, Leclaire et al. 2011). Our searches were limited to studies of adult seabirds (Orders Sphenisciformes (penguins), Procellariiformes (tubenoses), Pelecaniformes (gannets, cormorants, etc.), and the Charadriiformes (gulls and auks) during the breeding period (incubation, chick-rearing, or across both stages). Only studies of breeding adults were included due to prevalence in the literature (few studies of chick CORT and fitness) and due to the challenges of monitoring most seabirds outside of breeding. Of the 2,129 papers returned from the initial search, the majority (2,050) were rejected because they did not meet the basic criteria of pertaining to seabirds, CORT and fitness (Fig. 2.2). We retained 79 relevant papers for more thorough analysis by including all seabird papers studying CORT and traits that could be related to fitness. We then removed an additional 48 unusable studies from this group for one of more of the following reasons: i) contained no direct examination of a relationship between CORT and a fitness-related trait; ii) had unusable statistics or no statistics presented (i.e., only presented figures and/or estimates of p-value); iii) examined stress-induced as opposed to baseline CORT levels; or iv) did not measure adults. Our final dataset contained 31 published papers (Appendix 2) and one unpublished dataset (K. Elliott, G. Anderson & T. Gaston, unpublished data from collaborators) representing 16 species with between one and 13 studies published on each species (Appendix 3).

We examined all relevant papers and recorded each statistic, p-value, and sample size presented for a reported relationship between CORT and a given fitness-related trait. Correlation coefficients (r) were used when available as they already represent effect sizes. In the absence of correlation coefficients, we used F-values, t-statistics, and Chi-square values. Several studies presented none of this information, and as such p-values were then used. We classified each effect size by: i) type of study (correlational or experimental); ii) reproductive stage (incubation, chick-rearing or across both stages); and iii) fitness-related trait (adult condition, effort foraging, effort nesting, food availability or reproductive success, Table 2.1). These broad categories were used to determine whether certain fitness-related traits more strongly correlated with baseline CORT than others.

All analyses were performed in the R environment (3.1.2) using RStudio (0.99.879) as the working interface. Using the R package *compute.es*, we first calculated effect sizes as correlation coefficients (r) with a 95% confidence interval for every relationship found (Cooper et al. 2009). However, because *r* values are bounded at -1 and 1, and therefore do not meet the assumptions of parametric analyses, we transformed the values to Fisher's Z and calculated the appropriate sampling variance and standard error of variance according to standard methods (Boncoraglio and Saino 2007). The Fisher's Z values and corresponding sampling variance were used for further analysis.

Although all species in the current analysis are seabirds, and thus represent an already narrowed phylogenetic group, controlling for phylogenetic effects remains important (Adams 2008) as phylogenetic relationships could explain some variance in the relationship between CORT and fitness. To account for phylogenetic relationships in our analysis, we created a phylogenetic tree including all species in our dataset. First, we sampled 1000 trees based on our species list from birdtree.org, using the Hackett tree backbone (Hackett et al. 2008; Jetz et al. 2012). Then, we calculated the maximum clade credibility tree using TreeAnnotater from the BEAST software, using the default settings (burnin = 0, node heights = median, output = maximum clade credibility tree) (Drummond et al. 2012).

The meta-analysis was conducted using the R package *MCMCglmm* version 2.22 (Hadfield 2010). We first created univariate models without intercepts with fitness-related trait, study method, and breeding stage independently as the fixed effect in each model, with phylogenetic and non-phylogenetic versions of each. These models are useful for comparing different levels of each variable to 0, but do not control for any covariates. We then created a series of eight multivariate models incorporating our three fixed effects and used the deviance information criteria (DIC) to choose the best models. A phylogenetic and non-phylogenetic version of each model was run, and species and individual study were included as random factors in all analyses. Our series of models (see descriptions in Table 2.2) tested first for an overall relationship between CORT and fitness (M1 and M2, non-phylogenetic and phylogenetic respectively), then for a relationship within each fitness-related trait (M3 and M4), then for fitness-related trait relationships by study method (M5 and M6), and finally also including breeding stage as a fixed effect (M7 and M8).

For all models, we used the random effect prior of V = 1, nu = 0.02, which specifies an inverse Gamma distribution with a degree of belief of 0.02, widely used in the statistical literature (Gelman and Hill 2007). Each MCMC chain was run for 1.1 million iterations, with a burn-in of 100,000, and a thinning interval of 1,000, to produce a sample size (posterior distribution) of 10,000 samples. We checked convergence of model parameters using the potential scale reduction statistic (PSR; Gelman and Rubin 1992) and the multivariate potential scale reduction statistic (mvPSR; Brooks and Gelman 1998), calculated using the coda package (Plummer et al. 2006). To perform these tests, we ran 2 additional MCMC chains for each model (M1-M8), to produce a total of 3 chains per model (these additional chains were only used for convergence testing; all reported results are based on the first chain only). The potential scale reduction statistics compare among-chain and within-chain variance, and should be less than 1.1 if chains are converging well (Gelman and Rubin 1992). In all our models, the PSR values were less than 1.01 for all parameters, and the mvPSR values were less than 1.02. Additionally, we visually checked chain mixing and autocorrelation using trace and density plots produced in coda. In all cases, chains appeared to be mixing well and had low autocorrelation.

Meta-analytical results can be influenced by a publication bias towards studies with large effect sizes. To test for signs of publication bias in our dataset, we conducted a visual and statistical analysis based on the inspection of funnel plots and running Egger's regression (Egger and Smith 1997), respectively. To account for phylogenetic relationships when assessing publication bias, we followed the modified approach to Egger's regression outlined in Nakagawa and Santos (2012), which uses the residuals from meta-regression models as the input variable in the Egger's regression in order to account for heterogeneity due to phylogeny and the random effect structure when assessing publication bias. We used our best fit model (Model 3) to conduct the Egger's regression analysis. When the intercept of the Egger's regression is significantly different from 0, the analysis can be interpreted as showing evidence of publication bias. In our case, $\beta_0 = -0.04$, 95% CI [-0.19, 0.11], $p = 0.57$. Additionally, we visually assessed funnel plots for evidence of asymmetry and outliers (Appendix 4).

Results

In both the phylogenetic and non-phylogenetic univariate models, there were significant negative mean effect sizes for food availability (Fig. 2.3; non-phylogenetic meta-analytic mean Zr = -0.56, 95% CI [-0.96, -0.14]) and reproductive success (Fig. 2.3; non-phylogenetic meta-analytic mean Zr = -0.31, 95% CI [-0.50, -0.11]), but no strong correlation for any other fitness-related trait. There was no difference in correlation strength or direction between study method and breeding stage in the phylogenetic or non-phylogenetic models (Fig. 2.3). Overall, results indicate that baseline corticosterone was able to predict overall food availability and reproductive success, but not body condition, foraging effort or breeding effort (Fig. 2.3).

After comparing deviance information criterion (DIC) values between our eight models, M3-M6 were all within 2 DIC values and therefore were considered to be competitive models (Table 2.2). These four models all showed similar significant effects for food availability (Appendix 5; Zr around -0.5) and reproductive success (Appendix 5; Zr around -0.25). Models 5 and 6 both showed similar non-significant effects for the estimate of study method (Appendix 5; experimental around 0.19). While no individual model could be classified as the strongest, the set of top models all suggested similar results.

Discussion

To proactively monitor the health of wildlife, researchers and conservation managers are increasingly looking towards sensitive individual-level metrics (e.g., physiology, behaviour, movement) in lieu of slower-responding demographic measures (Berger-Tal et al. 2011; Cooke et al. 2013; Cooke et al. 2014; Madliger and Love 2015). Amongst the suite of physiological parameters proposed as biomarkers, GCs are often assumed to be reliable indicators of environmental impacts because they are closely tied to energetic management (Angelier et al. 2010) and food resources (Kitaysky et al. 2007), and therefore presumably to broader-scale environmental quality (Landys et al. 2006; Madliger et al. 2015). However, recent work has cautioned against the widespread use of GCs as biomarkers without first testing how well they relate to environmental variability and measures of fitness (Madliger and Love 2014; Madliger and Love 2016). We performed a systematic review and meta-analysis to examine the correlation between baseline CORT levels and fitness-related traits in seabirds (recognized as important sentinel species due to their high trophic position and worldwide distribution; Piatt et al. 2007b). The strength of relationships between baseline CORT and fitness varied by fitness trait. As predicted, food availability and reproductive success showed significant negative trends; however, body condition and effort at foraging and nesting showed no relationship. Moreover, our models including fitness trait as a fixed effect were much better supported than the null model, indicating that our fitness proxies were rooted in biological relevance and are therefore a practical means of grouping relationships between GCs and fitness in this taxonomic group.

Strength and Biological Relevance of CORT-Fitness Relationships

Body condition, which included measures such as body mass index, mass gain and fat level, did not generally correlate with baseline CORT. While individual studies did report significant results in these relationships (Appendix 3), trends were generally weak. Although body condition can relate strongly to environmental conditions and to reproductive success (Wendeln and Becker 1999; Balbontín et al. 2012), individuals may be able to sacrifice individual condition to benefit offspring to varying degrees (Jacobs et al. 2013). Moreover, some Alcid species with extreme wing-loading even exhibit adaptive mass loss (as a means to increase energetic efficiency) between the incubation and chick-rearing stages (Croll et al. 1991), potentially making relationships between body condition and fitness difficult to interpret. Variation in seabird life-history may also confound this relationship as seabird parents’ ability to maintain their own condition during breeding may depend on the manner in which they carry food to offspring (whole or semi-digested prey) and the ability of offspring to survive extended periods alone in the nest (i.e., need for constant feeding, predation risk, nest site dangers).

Neither effort during foraging, nor effort during nesting, correlated with baseline CORT, though both traits showed weak positive trends. Foraging effort included at-sea behaviours such as trip duration, amount of time diving for prey, and overall energy expenditure (i.e., daily energy expenditure – DEE). While these traits are predicted to relate to how well parents can care for their offspring and thus overall fitness (e.g., Weimerskirch et al. 2000), individual physiological management may obscure observable mean relationships with baseline CORT (Angelier et al. 2007b; Angelier et al. 2007c; Angelier et al. 2009; Love et al. 2014). More specifically, it may be necessary to measure baseline CORT levels both before and after a foraging trip to fully appreciate how physiology may predict foraging or nesting success (Madliger and Love 2014; Love et al. 2014). This is likely true for nesting effort traits as well given that time spent on the nest and chick feeding rate should relate to nesting success and fitness (e.g., Bukacinska et al. 2016).

In contrast to body condition and effort metrics, food availability showed a significant negative relationship with baseline CORT. Indeed, this was expected given baseline CORT's metabolic role and the fact that this pattern has been documented in other non-seabird avian species (e.g., barn swallow (*Hirundo rustica*): Jenni-Eiermann et al. 2008; white ibis (*Eudocimus albus*): Herring et al. 2011; zebra finch (*Taeniopygia guttata*): Lynn et al. 2010). Importantly, food availability has been proposed as one of the major drivers of changes in seabird populations (Kitaysky et al. 2007). Despite this, we were only able to include six studies of food availability in our analysis indicating that this is a potentially important area of research to expand upon in terms of pairing this data with the monitoring of circulating CORT levels (see below).

The strong relationship between baseline CORT and reproductive success could be similarly very important for proactively monitoring seabird populations and demographic trends. A review of the relationship between baseline GCs and reproductive success across multiple taxa (Bonier et al. 2009) reported mixed results (positive, negative and neutral), indicating that verification of the GC-fitness relationship is likely necessary in specific study systems (Bonier et al. 2009; Madliger and Love 2014). For example, one key consideration when testing relationships between GCs and fitness is life history (Crossin et al. 2016a). Patterns in baseline GCs differ between life-history strategies, stages and even within reproductive stages and favor different aspects of trade-offs (e.g., Love et al. 2004, Williams et al. 2008). Our quantitative analysis of relationships between baseline CORT and reproductive success revealed that this trend is strongly negative across seabirds (a long-lived group of species) and across breeding stages. It is possible that because many long-lived seabird species are able to forgo reproductive attempts during harsher years to instead favour investment in future offspring, baseline CORT levels may more strongly correlate to reproductive outcomes, and may be more likely to show a negative relationship (Hau et al. 2010). For example, such species may be less likely to possess mechanisms to resist social and environmental stressors in favour of successful breeding, leading to correlations between high GC levels and reproductive abandonment (Wingfield and Sapolsky 2003). In general, in longer-lived seabird species, there is great potential for GCs to relate food availability to reproductive success, making them a strong biomarker if deployed within the appropriate system (e.g., Piatt and Harding 2007).

We were careful to recognize potential biases in the current literature. First, our meta-analysis as a whole showed no publication bias from unpublished significant studies or overly strong results in certain studies (based on Egger's regression). Second, we found no significant effect of study method (experimental or correlational), though certain fitness traits are not represented evenly between methods. Most studies examining measures of foraging or nesting effort employed experimental methods to either increase the effort individuals faced (i.e., indirectly increase baseline CORT) or to increase baseline CORT directly. The lack of relationship with these effort-based traits and CORT, despite largely experimental methods, increases our confidence that CORT is not strong indicator of these traits overall. The opposite was true for the methodologies used in studies examining adult condition, food availability, and reproductive success where correlational methods characterized the majority of studies. Moving forward, additional studies employing experimental manipulations of CORT in the context of body condition, food resources, and reproductive outcomes will help to refine our appreciation of how baseline CORT may interact with the intrinsic and extrinsic environment to influence fitness in seabirds. Finally, we found no significant difference in mean effect size between correlational and experimental methods. Overall, we have confidence that the patterns we observed are not confounded by publication bias, or by a lack of consideration of methodological context.

Additional Recommendations for Using GCs as Seabird Biomarkers

It is clear from this meta-analysis and recent reviews (e.g., Bonier et al. 2009) that measurements of baseline GCs are not a perfect indicator for all fitness-related traits. Baseline GC levels are highly context-dependent because they can respond to both external environmental conditions and to internal changes in state; thus, fitness-related traits like condition and effort are likely to vary based on an individual's regulation of its physiology and its efficiency at gaining and using energetic resources (Busch and Hayward 2009; Madliger and Love 2015; Hennin et al. 2016). None of the studies completed in seabirds investigated how changes in baseline GCs over time (i.e., flexibility) related to fitness-related traits. However, there is growing evidence that the management of GCs over time may provide predictive capacity for fitness outcomes (Bonier et al. 2011; Ouyang et al. 2011; Ouyang et al. 2013; Love et al. 2014; Arlettaz et al. 2015). This may be particularly important to consider in seabird species that make extended foraging trips, requiring careful management of somatic resources while also tending to offspring. We urge future studies to consider how changes in CORT, rather than simply static measures, may provide information on foraging success and ultimately reproductive outcomes.

The large amount of CORT research in diverse seabird taxa is testament to the desire of researchers and managers for a simple, holistic monitoring technique for this at-risk group of birds. The five fitness traits investigated in this meta-analysis showed varying relationships with baseline CORT, indicating that some traits may be more sensitive or more easily monitored with baseline GCs, while other traits may require more in-depth study to adequately assess their potential connection with baseline GCs. Indeed, seabird biologists have not sampled all fitness-related traits equally. For example, harder-to-measure traits such as food availability were measured in only four of the studies in our analysis, while body condition and reproductive success were measured in 16 and 17 studies, respectively. Focusing on certain environmental and fitness-related traits such as food availability and reproductive success is important, not simply because these relationships showed significance in our meta-analysis, but because these traits can best link GCs to environmental (food) changes and population demography. Studies measuring reproductive success in this meta-analysis looked at laying, hatching, and fledging. While some of these early fitness traits (e.g., clutch size) may be strongly linked to reproductive output in certain seabird species, focusing on fitness during chick-rearing should take precedence in order to best predict chick survival and recruitment to assess population changes.

One of the primary studies linking food availability to baseline CORT in black-legged kittiwakes (*Rissa tridactyla*) employed multiple methods of prey-species sampling as well as experimental methods to rigorously test the relationship between average (population-level) CORT levels and food availability in the local ocean environment (Kitaysky et al. 2010). Although time consuming and often expensive, further testing of this relationship should ideally follow these types of broad prey sampling methods and work towards increasing experimental methods to further examine causal links between food availability and changing GC levels. Furthermore, recent evidence suggests that unpredictable food availability (as opposed to simply the total amount of food available) may influence baseline GCs, indicating the importance of not only quantifying total energetic constraints, but also temporal and spatial fluctuations in availability to fully understand how individuals may respond to changing resource levels (Fokidis et al. 2012). If the relationship remains strong between CORT and food availability across additional studies/species, CORT levels in seabirds may indeed emerge as a very effective tool for sampling large areas of ocean productivity.

The next step to explicitly testing the usefulness of baseline CORT as a relevant biomarker in seabirds is to scale up individual-level relationships to relate hormone levels to demographic patterns (adult/chick survival, breeding recruitment, population changes). If CORT predicts current year reproductive success, it will be worth testing how well it can predict future year success, though it will be important to appreciate possible time lags between baseline CORT and population changes, since baseline CORT levels in one year will likely relate to future population changes. Importantly, evidence is accumulating that elevated CORT levels may lead to carry-over effects, influencing patterns of migration, overwintering, and subsequent breeding. For example, Schultner et al. (2014) found that female black-legged kittiwakes exposed to a 3-day elevation of CORT during breeding left the breeding grounds earlier and spent a longer time at the wintering grounds than control females and CORT-treated males. In addition, Crossin et al. (2013, 2016b) found that feather CORT levels could successfully predict whether giant petrels (*Macronectes sp.*) and black-browed albatrosses (*Thalassarche melanophris*) would breed or defer breeding in the subsequent year. Paired with the experimental and correlational evidence in other avian and non-avian species indicating that GC measures can mediate carry-over effects (O’Connor et al. 2010; Mark and Rubenstein 2013; Sanderson et al. 2014), these patterns illustrate the potential for using GC measures to predict variation in future investment and success. Particularly in seabirds, which are comparatively long-lived, it will be important to determine whether CORT measures taken at different times may be able to forecast *multi-year* reproductive success across species (e.g. Angelier et al. 2010).

While GCs do play an important role in connecting an individual's environment to its energetic demands, they are not the only mechanism that relate these states. Importantly, other metrics can be easier to collect (e.g., ease of field collection, avoiding stress-induced samples) and less expensive to measure analytically. For example, energetic metabolites (triglycerides , beta-hydroxybutyrate, and non-esterified fatty acids; Guglielmo et al. 2013) and measures of thyroid hormone can reflect the energetic state of individuals (Guglielmo et al. 2002; Elliott et al. 2013) and may additionally provide key information on foraging success and energetic constraints. Importantly, physiological panels that combine multiple energetic metrics may provide the best indication of overall current state and therefore future reproduction or survival potential, and are one way in which physiological measures are currently contributing to tangible conservation success (Madliger et al. 2016). Finally, behaviour is increasingly studied in seabirds due to the continued development of small GPS units that can accurately collect behaviour in flight and on the water (Gaston et al. 2013; Ponchon et al. 2014; Weimerskirch et al. 2014). By pairing physiological metrics with behaviour, researchers can examine how changes in physiology may manifest as alterations in reproductive behaviour (Cooke et al. 2014; Madliger and Love 2015), thereby better understanding the mechanisms by which environmental change may influence seabird populations. Overall, pairing multiple metrics of physiology, behaviour and environmental quality (e.g., food availability) will be paramount to assessing baseline GC levels as monitoring tools for seabird fitness and, ultimately, population demographics.

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Tables

Table 2.1 - Descriptions and biological relevance of fitness-related traits used for grouping of effect sizes in meta-analysis examining relationships between CORT and fitness in seabirds.

Fitness-related trait	**Specific traits compared to CORT**	**Biological relevance**
Condition	body mass, body condition index, age	individual condition can be related to performance and fitness
Foraging effort	number of foraging trips or dives, time at sea, effect of handicap	altricial chicks and adult condition depend on parental foraging
Nesting effort	Attendance (time), chick feeding rate	altricial chicks depend on parental foraging
Food availability	sampled food abundance, fed vs. control individuals	environmental trait, parents and chicks rely on food sources
Reproductive success	number or percent of chicks hatched or fledged, clutch size, chick mass	metrics of reproductive output should relate to population level changes and individual fitness

Table 2.2 - DIC values and variance components (study, species, and phylogeny) for eight models compared to determine whether fitness-related traits relate to baseline corticosterone in seabirds. All models included random effects for study and species and were run with and without phylogenetic control.

Model	**Fixed effects**	**DIC**	**Variance Components** **Study**	**Species**	**Phylogeny**
M3	Fitness-related trait	150.022	0.176	0.166	--
M5	Fitness-related trait and study method	150.458	0.168	0.179	--
M4	Fitness-related trait	151.655	0.156	0.155	0.185
M6	Fitness-related trait and study method	152.007	0.144	0.164	0.205
M7	Fitness-related trait, study method, and breeding stage	155.339	0.167	0.161	--
M8	Fitness-related trait, study method, and breeding stage	156.709	0.148	0.153	0.199
M1	intercept	157.758	0.238	0.166	--
M2	intercept	159.452	0.217	0.150	0.174

Figures

Figure 2.1 - Diversity of seabird species studied worldwide. a) black-legged kittiwake (*Rissa tridactyla*), S. Descamps b) african penguin (*Spheniscus demersus*), K. Hick c) thick-billed murre (*Uria lomvia*), G. Sorenson d) northern fulmar (*Fulmarus glacialis*), M. Mallory e) antarctic petrel (*Thalassoica Antarctica*), S. Descamps f) tufted puffin (*Fratercula cirrhata*), K. Elliott.

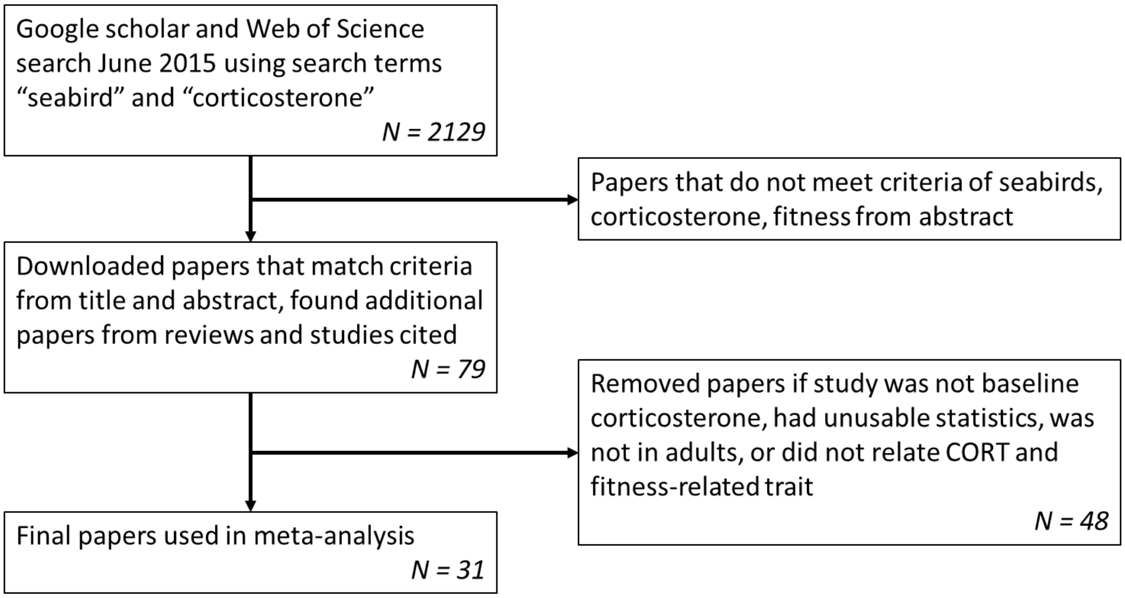

Figure 2.2 - Flow chart showing process of finding, selecting, and removing studies in meta-analysis.

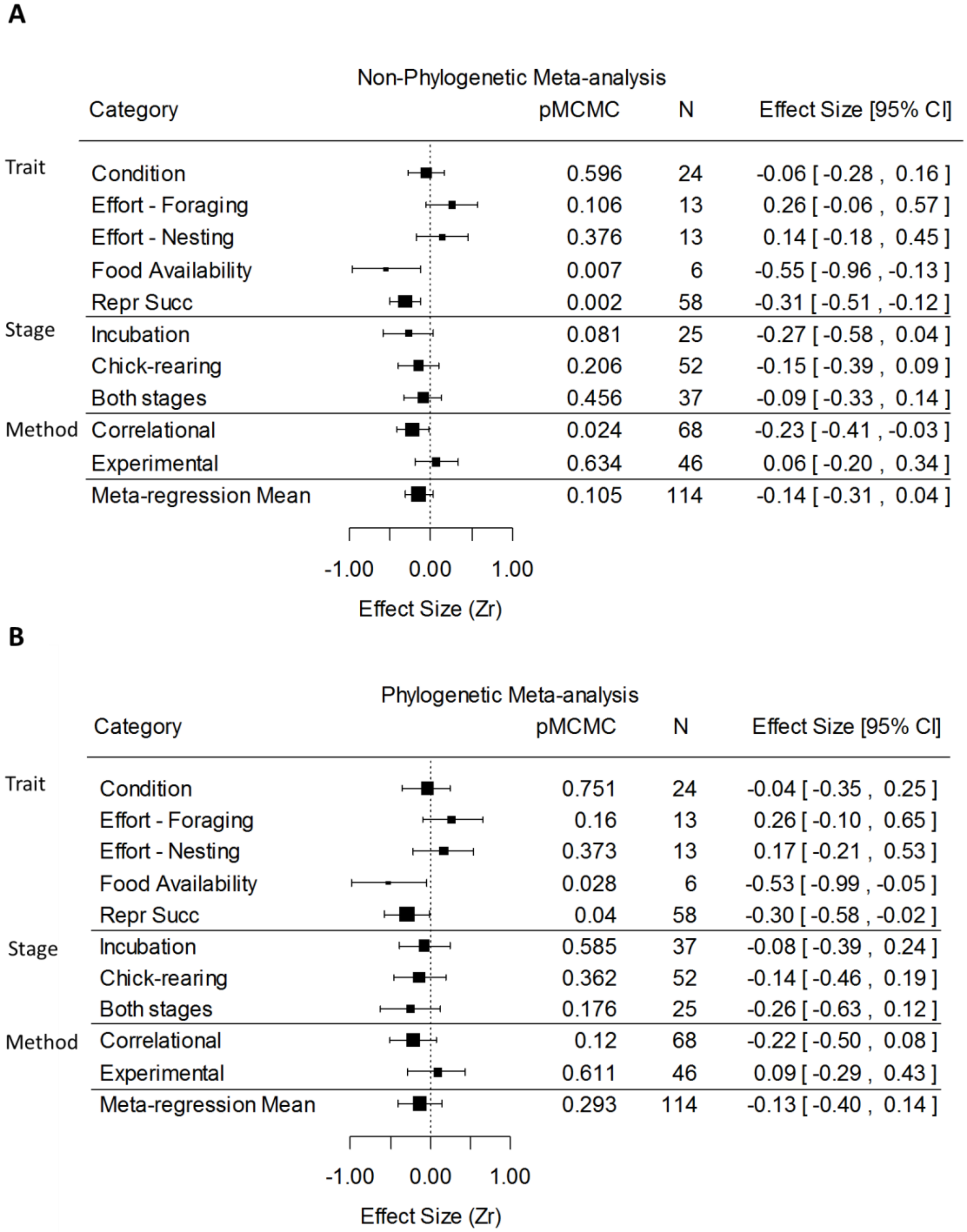

Figure 2.3 - Mean effect sizes from four models run with fixed effects for trait, stage, method, and intercept only. Both non-phylogenetic (A) and phylogenetic models (B) are presented.

CHAPTER 3

Integrating foraging behaviour and energetic physiology reveals impacts of low ice conditions on an Arctic seabird

Chapter Summary

Due to broad-scale environmental change, polar species may be at significant risk of decline in some of the most rapidly changing ecosystems. Traditional methods of monitoring population health and/or condition (i.e., through demographics) may not be responsive enough and have the capacity to predict population declines before they can be mitigated. An integrative, mechanistic (i.e., physiological, behavioural) approach linking environmental patterns to population change at multiple scales may provide a more rapid and predictive solution. Using emerging technologies and techniques we measured behavioural, physiological, and energetic responses of individuals to a natural "climate experiment" to assess how a sensitive, ice-dependent, declining Arctic-breeding seabird (thick-billed murre, *Uria lomvia*) responds phenotypically in the face of rapid environmental change. We evaluated these relationships across multiple biological scales (population, across individuals, within-individuals) to determine how best to assess these responses and inform future predictive models. Using the second largest Canadian breeding colony of this species at Digges Island, Nunavik, we combined the deployment of miniature GPS units, measures of baseline energetic physiology (corticosterone (CORT), triglycerides (TRIG), beta-hydroxybutyrate (BOH), non-esterified fatty acids (NEFA)), body mass changes and estimated daily energetic expenditure (eDEE) to compare murre responses across two years of dramatically different ice conditions. Behavioural results initially suggest that birds faced fewer foraging costs in the low ice year with shorter maximum foraging distances and shorter mean trip distances and durations. However, birds also undertook more frequent foraging trips in low ice conditions resulting in the same average daily foraging distance and eDEE across years. Moreover, pairing these results with physiological metrics revealed apparent foraging costs within the low ice year (2014): chick-rearing birds had higher baseline CORT and NEFA levels and lost significantly more body mass during foraging. However, the lack of year differences for TRIG and BOH levels indicated that murres appeared to still be able to maintain resource intake in the face of changes in ice conditions. Our inter-individual analyses further indicated that changes in foraging strategy during the low ice year had mixed results on the energetic condition of individuals, though increased foraging effort related to better energetic condition. Overall our results provide strong mechanistic support for the prediction that Arctic-breeding seabirds, especially those at the southern edge of their range, may be negatively impacted by the direct effects of climate change and warming oceans. Our results confirm that combining physiology, especially sensitive (labile) traits such as CORT and NEFA, and measures of foraging behaviour provides key underlying information on how environmental variation influences population- and individual-level energetic stress in species of concern.

Introduction

While it is difficult to find an ecosystem not impacted to some degree by global environmental change (Parmesan 2006; Bellard et al. 2012), effects are occurring most rapidly in polar regions and especially in the Arctic (Mauritsen 2016; Navarro et al. 2016). Specifically, global climate change is driving increases in Arctic ocean temperatures (Timmermans and Proshutinsky 2015) and causing dramatic shifts in ice dynamics both within and across years (Perovich et al. 2015). Many Arctic species have evolved to be highly dependent on temporally- and spatially-stable ice conditions to optimize foraging patterns in order to maximize breeding success (Moore and Huntington 2008; Mallory et al. 2010). As a result, these species are expected to be at significant risk of decline due to rapid changes in climatic and hence ice patterns (Post et al. 2009).

Demographic techniques are commonly used to connect population patterns to surrounding environmental variation across diverse taxa (Parr et al. 2003; Magurran et al. 2010) and have been used to assess whether climate patterns are imposing negative consequences on populations of interest (Croxall et al. 2002; Van de Pol et al. 2010; Baylis et al. 2012; Descamps et al. 2013; Merkel et al. 2014). However, while long-term demographic studies provide strong correlative trends that can be projected into the future (Dommasnes 2010; Trathan et al. 2012; Frederiksen et al. 2013), they nonetheless can have several disadvantages within the perspective of a rapidly changing environment. First, population data often show a delayed response to sudden changes in environmental factors (Ewers and Didham 2006), especially in long-lived species with a slow pace of life (i.e., low annual fecundity rates, delayed adult maturation, low annual reproductive success; Forcada et al. 2008). Second, to monitor changes within a given population, demographic studies require long-term population monitoring and fairly significant and consistent changes in size to statistically recognize trends (Crick 2004; Forcada et al. 2008; Descamps et al. 2013). These two major drawbacks can make demographic studies challenging for aiding immediate conservation efforts, especially in species where historical data on the relationship between environmental variation and population changes are unavailable.

In an attempt to increase the efficiency, accuracy and timeliness of detecting environmental challenges facing populations, there has been a recent focus on individual-based studies within environmental ecology (e.g., Janin et al. 2011). By narrowing the scale from population-level demography to mechanisms and fitness at the level of the individual it may be possible to both assess and predict how well certain populations will respond to rapid environmental change. Importantly, traits such as body condition, behaviour and energetic physiology all have the ability to react to environmental change on a short time scale (Cockrem et al. 2006; Toïgo et al. 2006; Harding et al. 2007; Angelier et al. 2011) and therefore provide key information on the relative success or status of the individual (Shoji et al., 2013). For example, body condition (e.g, body mass, fat level) is a simple and widely-used measure to gauge the general health of an individual (Harding et al. 2011) and environmental challenges directly impact the condition of an individual (Toïgo et al. 2006). Moreover, state-related metrics are often correlated with reproductive success (Balbontín et al. 2012) making them potentially useful metrics for predicting how environmental challenges may translate into population change. Nonetheless, it is increasingly appreciated that to reveal the underlying (causal) mechanisms linking individuals and populations to their environment studies must be highly integrative (Madliger and Love 2015). As such, they should ideally span multiple techniques (i.e., physiology, behaviour, genetics), biological scales (i.e., within- and across-individual variation) and methodological approaches (i.e., correlative vs. experimental) (Collins and Storfer 2003; Bolger et al. 2008; Madliger and Love 2015).

Behaviour responds rapidly to environmental change at many scales (Westhus et al. 2013) and individual variation in behavioural metrics (e.g., foraging behaviours) can indicate energetic demands, investment and the ability to cope with change (Ropert-Coudert et al. 2009; Houston and McNamara 2014). Furthermore, behavioural responses to environmental variation can be used to project population trends (Dolman and Sutherland 1995) and flexibility in foraging behaviour can help predict seabird resilience (Ponchon et al. 2014). Likewise, measures of energetic physiology encompass multiple traits that are increasingly thought of as valuable indicators of individual health with direct correlations to environmental variability and ensuing resource availability (e.g., glucocorticoids: Kitaysky et al. 1999; Angelier et al. 2008; Hennin et al. 2015, energetic metabolites: Seaman et al. 2006, Williams et al. 2007, fatty acids: Iverson et al. 2004, 2007, daily energetic expenditure: Welcker et al. 2009b, Elliott et al. 2013a). These metrics can provide clear insights into the dietary and energetic demands of an individual (Anteau and Afton 2008; Hennin et al. 2016), and can indicate differences in the quality of foraging locations or available resources (Seaman et al. 2006; Kitaysky et al. 2007). For example, glucocorticoids (corticosterone and cortisol) are responsible for managing and inducing feeding behaviour, and can be used as proxies of an individual's need for energetic refueling (Angelier and Wingfield 2012) and food availability (Kitaysky et al. 2007; Benowitz-Fredericks et al. 2008). In addition, energetic metabolites (triglycerides, beta-hydroxybutyrate, and non-esterified fatty acids) can indicate an individual's current use of or addition to fat stores (Guglielmo et al. 2005), and a single time point measure can provide the same information as repeated measures of body mass change (Jenni-Eiermannm and Jenni 1994; Williams et al. 1999; Anteau and Afton 2008).

Here we take an integrative approach that combines physiology, behaviour and estimated energetic expenditure across multiple biological scales (population, among-individual, within-individual) to assess the impacts of rapid environmental change on an ice-dependent Arctic-breeding seabird, the thick-billed murre (*Uria lomvia*). Our overall goal was to assess which of these phenotypic metrics (i.e., biomarkers) were most sensitive to variation in ice conditions or foraging effort at multiple scales to provide researchers with biologically-relevant metrics with which to assess environmental change. We were fortunate to take advantage of a 'natural experiment' by collecting data across two years with highly contrasting ice conditions (2014 low concentrations and 2015 high concentrations, Figure 3.1). Our two-year study encompasses ice extent similar to historic norms and more recent record lows in the Hudson Bay region (Gaston et al. 2005, Figure 3.2). We carefully chose a series of individual response metrics known for their sensitivity to environmental change and commonly used to assess the foraging success of seabirds: baseline corticosterone, energetic metabolites (triglycerides, beta-hydroxybutyrate, and non-esterified fatty acids), body mass, estimated daily energetic expenditure and metrics of foraging behaviour using GPS technology. We began by examining the relative sensitivity of the individual response metrics and behavioural predictors to year-differences in ice conditions to detect the best metrics for assessing population-level sensitivity to a change in environmental quality. Since this species' foraging behaviour should be significantly impacted by varying ice conditions (Gaston and Hipfner 1998; Gaston et al. 2005; Gaston et al. 2009), we then assessed whether physiological metrics alone (both single-time point and changes within an individual across a foraging bout) could be used to predict variation in foraging behaviour in response to environmental variability for the purpose of examining whether physiology can simultaneously inform on broad environmental differences and the behaviour exhibited. We predict murres would exhibit exaggerated behavioural and physiological metrics indicative of elevated energy use or a lack of resources during the low ice year since this species has evolved to be ice-dependent during early breeding.

Methods

Study System and Sites

Primary fieldwork was conducted at Digges Island, Nunavut, Canada (62° North) from early July to mid-August of 2014/2015. The thick-billed murre colony surrounding Digges Sound is the second largest murre colony in the Canadian Arctic (300,000 birds on Digges Island, 700,000 birds on Cape Wolstenholme). Thick-billed murres breed once per year on rocky cliffs where both parents care for a single offspring by alternating incubation periods and foraging bouts for the chick (Gaston and Hipfner 2000). Thick-billed murres are an extreme of the family *Alcidae* due to their extremely high wing-loading in flight (Elliott et al. 2013b). They are considered an ice-dependent species making long foraging trips in their North American range to capture Arctic cod, sandlance, capelin, and as well as some crustaceans and deep water fish (Springer et al. 1986; Gaston and Hipfner 1998). Research in Digges Sound by Environment Canada has been conducted since 1980 to monitor population changes (Gaston et al. 2000). Selected sites (one on Cape Wolstenhome and four on Digges Island) were chosen for accessibility to adequate numbers of murres. We sampled 97 murres in 2014 and 120 murres in 2015 over four sites. All work was conducted under a University of Windsor Animal Use Care permit (15-04) and Environment Canada collection and Animal Care permits (NUN-SCI-14-11, EC-PN-14-017, EC-PN-15-017), respectively.

Ice Data

We used daily AMSR2 sea ice maps from the University of Bremen to compare the variation in sea-ice extent between the two study years. Specifically, we measured the percent cover of sea ice within a 300-kilometer radius of Digges Island (the approximate furthest straight-line foraging trip of murres on Digges Island) on each day from June 15 to August 15 in both years. We chose June 15 as it is just before the first eggs are laid on Digges Island, and as such represents the conditions during which murres begin breeding. By August 15, sea ice in the Hudson Straight and Hudson Bay is largely gone, meaning that ice differences between the years are negligible by this point.

Individual Metrics and GPS Deployment

Breeding thick-billed murres were targeted for capture during both incubation and chick-rearing periods. Only breeding individuals were selected for behavioural measures to ensure the individual would be returning to the same nest ledge. Targeted individuals were spaced out on the ledges so as not to overly disturb the sites or allow predators (gulls and ravens) an opportunity to take eggs or young. Birds were captured using a noose pole.

Upon capture, blood samples were taken within 3-5 minutes to ensure that baseline corticosterone levels could be measured (Romero and Reed 2008). Approximately 1.0-2.0 mL of whole blood was taken from the brachial vein using 26-

gauge needles and heparinized capillary tubes. Blood was kept on ice for up to 8 hours and then centrifuged at 10,000 rpm for 10 minutes. Plasma was separated using a micropipette, and both the plasma and red-blood cells were stored in a cryo-shipper (-75˚C) for the duration of the field season. Upon return to the lab, samples were stored in a -80˚C freezer. Following blood sampling, each bird was banded on its right leg with a numbered Fish and Wildlife Service aluminum band. Wing, tarsus and bill measurements were taken (nearest mm) and body mass was recorded (nearest g). Individuals were then fitted with a GPS tracking device (either CatTracks, 10 g, 1.1% of body mass or Ecotone Ltd., 14 g, 1.5% of body mass). GPS devices were deployed using Tesa tape to attach the devices to the feathers on the lower back (Paredes et al. 2005). The GPS units were programmed to collect location data every 5 minutes and to turn off when at the colony (near an Ecotone base station). Birds were then marked on their chests with colored permanent marker to increase the ease of recapture. After 2-9 days from the initial deployment, returning birds were recaptured, blood sampled within 3-5 minutes, and GPS devices were removed and body mass was re-measured.

Laboratory Assays

For the measurement of baseline corticosterone (CORT), plasma samples were extracted prior to assay (Guindre-Parker et al. 2012). Tubes containing 20 uL of plasma, 1 mL of distilled water and 5 mL of dichloromethane were vortexed and then left to separate for two hours. The dichloromethane phase was removed into scintillation vials and left in a fume hood to evaporate. Samples were rehydrated with assay buffer and vortexed for 30 seconds to reconstitute the sample. Samples were assayed in triplicate at a dilution of 1:40 using a previously optimized protocol for seabirds (see Hennin et al. 2015) using a commercial EIA kit (Assay Designs Inc.). All samples were run with a control to obtain coefficients of variation for intra- and inter-assay (plate) variation (2015: intra = 4.99%, inter = 8.52%, 2014: intra = 5.16%, inter 3.88%). Triglycerides (TRIG) and free glycerol were measured in duplicate with a commercially available kit (TRIG; #TR0100-1KT; Sigma Aldrich, USA; Williams et al. 2007). Each plate was run with a laying hen control plasma (Sigma-Aldrich, USA) and a standard curve of the kit-provided glycerol standard (Hennin et al. 2015) where the difference in total and free glycerol provides the total TRIG concentration (mmol L^{-1}). All samples were run with a control to later obtain coefficients of variation for intra- and inter-assay (plate) variation (2015: intra = 2.94%, inter = 2.48%, 2014: intra = 3.27%, inter 3.30%). Beta-hydroxybutyrate (BOH) was measured by kinetic assay (SIGMA, Guglielmo et al. 2013). Samples were run in triplicate by reacting eleven microliters of standard or plasma sample with two microliters of BOH-butyrate dehydrogenase reagent and reagent buffer. The absorbance was then monitored by spectrophotometer. Coefficients of variation for intra- and inter-assay (plate) variation were 2015: intra = 4.96%, inter = 5.12% and 2014: intra = 4.06%, inter 3.50%. Non-esterified fatty acids (NEFA) were measured using a commercial assay kit (Wako NEFA-HR(2)) (Smith et al. 2007; Jeanniard du Dot et al. 2009). Samples were run in duplicate by reacting five microliters of plasma with acyl-CoA synthetase along with adenosine triphosphate and CoA to form acyl-CoA. This product is then oxidized and condensed to form a purple end product with maximum absorbance at 550 nm. Absorbance of the final solution is measured at 550 nm by spectrophotometer to obtain NEFA concentration. Coefficients of variation for intra- and inter-assay (plate) variation were 2015: intra = 3.34%, inter = 3.88% and 2014: intra = 2.97%, inter 4.13%).

Data Analysis

Spatial analysis of GPS tracking data provided the metrics of foraging distance and effort used for analyses. Tracking data from each device was analyzed in R v4.1.2 to extract variables for the foraging period (maximum distance from the colony, daily average distance, total distance, average trip distance, number of trips, and the percent time flying, on water and at the colony). Any trip greater than one kilometer from the colony was considered an individual foraging trip. All distances were calculated using the Haversine formula (WGS-84 ellipsoid) from the R package "geosphere" and the distHaversine function. Activity budgets of birds (percent time flying, on water or at the colony) were calculated based on flight speed and presence of GPS at the colony. Birds travelling at over 4 m/s (14.4 km/h) were considered flying, while birds away from the colony moving under this speed were considered on the water (diving or drifting on the surface). GPS data were quality checked by removing all sets of tracks that did not include data from at least 50% of the duration the GPS unit was deployed (4 of 63 tracks removed from 2014). Each GPS deployment included one or more individual foraging trips, and changes in body mass or physiology over a foraging trip were calculated as the pre-deployment sample subtracted from the post-deployment sample (i.e., a positive change in a trait indicates the level of that trait increased from the first to the second measurement).

Daily energetic expenditure was calculated from the activity budgets using values calculated in Elliott et al. (2013a). These values (energetic expenditure in flight = 533 kJ/hr, on water = 99 kJ/hr, at nest = 32 kJ/hr) are calculated based on energetic measurements using doubly-labelled water and miniature accelerometers attached to thick-billed murres (Elliott et al. 2013a). Percent time activity budgets can be converted to daily energetic expenditure for the duration of GPS deployment based on these values (Gaston et al. 2013).

Principle component analysis was conducted on foraging behaviour data to condense multiple variables into more concise, biologically meaningful variables. Foraging behaviour data (maximum trip distance, average daily distance, trips per day, mean trip distance, and mean trip duration) were normalized via log-transformation prior to the principal component analysis. The analysis resulted in two eigenvalues over 1.0 and to simplify interpretation, we conducted a factor analysis using a Varimax rotation for two principle factors (Table 3.1, Abdi 2003). The number of trips per day (negative loading) and the mean distance per trip (positive loading) both load heavily onto Factor 1 and maximum foraging distance and mean trip duration also positively loaded on Factor 1. Average daily foraging distance (positive loading), but also maximum foraging distance (positive loading, slightly stronger than in factor 1) loaded onto Factor 2. Based on these loadings, we considered factor 1 to represent foraging strategy with larger values corresponding to trips of longer distance and duration, with lower frequency. For the remainder of our analyses, PC factor 1 was used in place of trips per day, mean trip distance, mean trip duration and maximum trip distance, and is hereafter termed "foraging strategy PC". Since PC factor 2 was dominated by average daily foraging distance, we used average daily foraging distance independently to represent overall foraging effort.

We began our analyses at a broad population level to first examine impacts of between-year ice conditions on biomarker metrics, and then focused in at the individual and within-individual level to determine the relevance of using individual-based metrics to predict variation in foraging behaviour/effort. To compare the two climactic years, we ran comparisons of foraging behaviour and baseline physiology values across the years within each breeding stage (incubation or chick-rearing). We took this approach because murres are known to behave differently across these two breeding stages (Croll et al. 1991; Gaston and Hipfner 2006) and therefore it was important to assess whether our chosen biomarkers were more sensitive to changes in ice conditions within a given stage. All analyses were completed on raw data, except those for baseline CORT, TRIG, BOH, and NEFA in both stages, and foraging strategy PC during chick-rearing performed on log-transformed data. We used t-tests except for comparisons of NEFA and average daily distance during incubation, which were Wilcoxon/ Kruskal-Wallis tests for non-parametric data. We controlled for false discovery rate (Benjamini and Hochberg 1995) using the classical one-stage method (Pike 2011) for the series of analyses on multiple traits. We used a maximum false discovery rate (d) of 0.05 on our p-values, and separated these false discovery rate calculations by our two breeding stages (e.g., Madliger and Love 2016). We calculated FDR-adjusted p-values (q-values) as per Pike (2011) (Benjamini and Hochberg 1995; Benjamini and Hochberg 2000; Benjamini et al. 2006). All population level analyses and the principal component analysis were completed in JMP 12.

To assess which physiological metric(s) best predicted foraging behaviour and effort at the individual level, we examined the relationship between foraging behaviour and physiological traits from both the post-foraging sample as well as the change in a given trait across the foraging trip. Growing evidence indicates that changes in physiology over key time periods may better predict fitness and behavioural outcomes compared to single-point measures and it was therefore important to assess which type of metric may be most useful at reflecting broad-scale environmental differences. Specifically, we ran a series of linear mixed effects models in R to examine relationships between our two foraging metrics (foraging strategy PC and average daily distance) and our four physiological metrics (CORT, TRIG, BOH, NEFA). As outlined previously, we separated our analyses by breeding stage to take into account the specific physiological challenges expected to be associated with the energetic demand of each life-history stage. Year was included in all models as a random effect and each model was estimated using maximum likelihood (Zuur et al. 2009). We compared models within breeding stages and foraging metrics using AIC_c (Akaike's Information Criterion adjusted for small sample size) obtained from the R package *AICcmodavg*. We also calculated the weight of each model to compare their relative strength (Burnham et al. 2011). All models within 2 AIC units of the top model were considered competitive (Burnham and Anderson 2010; Girard et al. 2014).

Results

Inter-Annual Differences in Sea Ice

The extent of sea ice in a 300-kilometer span of our study site was significantly less in 2014 compared to 2015 (means: 2014: 11.47%, 2015: 26.00%; paired t-test: t-ratio = 9.12, $p < 0.0001$, Figure 3.3). Historically (e.g., 1971-1985) ice extent in the Hudson Bay region during the murre breeding period remained fairly consistent at approximately 25%

(Gaston et al. 2005, Figure 3.2). However, Gaston et al. (2005) demonstrate the ice decline over the two decades following this period (e.g., 1986-2003) and this decrease has continued (Figure 3.2) to recently hit historic lows (Post et al. 2013; National Snow & Ice Data Center 2016). Therefore, our two study years essentially spanned from the contemporary norm of climate-change induced ice-cover (11.47% in 2014) to the historical norm of ice cover (26.00% in 2015).

Sensitivity of Biomarkers to Inter-Annual Variation in Ice Conditions

Foraging strategy PC was lower in the low ice year (2014) during incubation, but not chick-rearing (Table 3.2), indicating that birds undertook more short-distance trips during incubation in the low ice year (2014). Interestingly however, the average daily distance travelled (i.e., average effort) did not differ between ice conditions (Table 3.2). Estimated daily energetic expenditure (eDEE) also did not differ between years and breeding stages (Table 3.2). Average daily distance travelled and the estimated daily energetic expenditure were strongly correlated ($R^2 = 0.72$) due to the fact that total distance travelled during GPS deployment should be strongly related to the percent of time spent flying (the behaviour that most greatly influences eDEE). Baseline CORT levels were higher in the low ice year (2014) across both breeding stages (Table 3.2), while NEFA levels were higher in the low ice year (2014) during incubation (Table 3.2). However, plasma TRIG and BOH levels did not differ between ice conditions in either stage (Table 3.2). Effects on body mass were complex, where mass before the foraging trip during incubation (but not chick-rearing) was significantly higher in the low ice year (2015) (Table 3.2), although birds lost more body mass during chick-rearing in the low ice year (2014) (Table 3.2).

Predicting Foraging Behaviour with Physiology

Three models were identified as plausible in explaining variation in foraging strategy PC during the chick-rearing stage: plasma TRIG, change in NEFA and change in body mass (Table 3.3). Essentially, during chick-rearing, lower levels of plasma TRIG, higher NEFA and greater body mass loss were associated with fewer foraging trips per day and greater mean trip distances, mean trip durations, and maximum trip distances (TRIG: β=-0.65, SE=0.32; NEFA : β=0.50, SE=0.25; change in body mass: β=0.0039, SE=0.0028). Two models were effective at explaining variation in average daily distance during chick-rearing: change in CORT ($w = 0.32$) and NEFA ($w = 0.27$), with greater decreases in baseline CORT over the foraging trip and lower NEFA levels at the end of the foraging trip being associated with higher average foraging distances (change in baseline CORT: β=-1.99, SE=1.35; NEFA: β=-33.12, SE=14.39). However, no metrics were predictive of foraging behaviour during incubation, with the best supported model being the null model for both foraging metrics (foraging strategy PC and average daily distance, Table 3.3).

Discussion

We took advantage of an ideal ‘natural experiment’ in ice-cover variation to assess the relative sensitivity of multiple energetically-related behavioural and physiological biomarkers in an ice-dependent, Arctic-breeding species, the thick-billed murre. Our two study years spanned from the historical norm of ice cover (26.00% in 2015) to the current norm of climate-change induced ice-cover (11.47% in 2014). We found that birds altered both behavioural and physiological traits in response to the observed variation in ice conditions. On the surface, behavioural results initially suggest that birds faced fewer foraging costs in the low ice year: they had shorter maximum foraging distances, shorter mean trip distances and shorter mean trip durations. However, birds also undertook more foraging trips per day in low ice conditions resulting in the same average daily foraging distance across years and the same eDEE, both strong measures of mean foraging effort. Moreover, pairing these results with physiological metrics revealed apparent foraging costs within the low ice year (2014) compared to a historically normal ice year (2015): chick-rearing birds had higher baseline CORT and NEFA levels and lost significantly more body mass during foraging in the low ice year, all of which are considered robust indicators of higher energy usage during foraging (see Introduction). Despite these apparent short-term costs, birds appeared to be able to maintain resource intake given that we did not detect any year differences in either plasma TRIG or BOH. Our results further indicated that changes in foraging strategy during the low ice year had mixed effects on the energetic condition of individuals, though increased foraging effort related to better energetic condition. Taken together our work suggests that, compared to ‘normal’ historical ice conditions (as seen in 2015) thick-billed murres have presumably evolved in conjunction with, this species shows evidence of physiological costs in response to low-ice conditions despite individuals attempting to maintain a consistent daily energy expenditure and resource intake across very different environmental conditions.

Relevance of Biomarker Variation in Relation to Ice Conditions

The large difference we observed in ice conditions were reflected in a number of physiological traits. First, baseline CORT was higher in the low ice year (2014) across both breeding stages which we interpret as greater energetic demand in the year with lower ice concentration (Angelier et al. 2008). Elevated baseline corticosterone levels have been directly related to lower food availability and quality (Kitaysky et al. 1999; Kitaysky et al. 2001; Kitaysky et al. 2007) and used as a proxy for food availability in thick-billed murres and other related auk species (Benowitz-Fredericks et al. 2008). Elevated levels are also found in individuals working harder during reproduction to maintain overall effort or performance in the face of environmental change (Love et al. 2014; Madliger et al. 2015; Rivers et al. 2016). Therefore, elevated baseline CORT in murres is expected to indicate lower food availability or greater overall energetic demand in the year with lower ice concentration. Indeed, Gaston and Hipfner (1998) found both Arctic cod (*Arctogadus glacialis*) and capelin (*Mallotus villosus*) in the diet of murre chicks to be positively related to ice extent, providing further evidence that food availability was lower in the low ice year. Earlier sea ice breakup over the last several decades has changed fish communities (Gaston et al. 2003; Gaston et al. 2005), and our results indicate these shifts are possibly negative for murres during warmer, more ice-free years. In support of our interpretation for baseline CORT, we also observed higher mean NEFA levels during chick-rearing in the year with low ice concentration. Elevated NEFA in the blood indicates a negative energy balance (Williams and Buck 2010), suggesting the higher NEFA levels observed in the low ice year are indicative that murres were working harder energetically, or not feeding enough for a given behaviour level. Murres also lost more mass over foraging trips during chick-rearing in the low ice year, though mean mass was greater during this period, possibly because the long foraging trips in the high ice year are less with reducing wing-loading (Croll et al. 1991).

Plasma TRIG and BOH did not differ across years in response to variation in ice conditions suggesting that murres were able to meet their resource demands during foraging. However, combined with the other physiological traits these results indicate that while murres were able to find similar quality food resources across ice conditions (i.e., similar TRIG/BOH levels between 2014/2015, Seaman et al. 2006), birds were working harder to find those resources (i.e., higher CORT/NEFA levels and greater mass loss) in the low ice year. As such, combining information on energy intake (i.e., TRIG and BOH) with energy use (i.e., CORT and NEFA) provides a much more accurate and global picture of how ice extent impacts this species. These integrated results underscore the importance of combining multiple, carefully-chosen physiological parameters when evaluating the influence of environmental change (Madliger and Love 2015). Similarly, ice-related changes in behaviour are also difficult to interpret in isolation. Shifts during the low ice year to a foraging strategy of frequent, shorter trips does not necessarily reveal costs or challenges that individuals or species may be facing (Paredes et al. 2014), and lack of difference in average daily foraging and eDEE appear to indicate that birds are maintaining their overall energy use in the face of ice variation although potentially paying an underlying physiological costs (elevated CORT and NEFA) to do so. Ultimately, working harder but maintaining energy intake appears to have resulted in a greater mass loss during foraging attempts in the low ice year. A greater mass loss, while not always considered negative (adaptive mass loss hypothesis) is nonetheless consistent with lowered success and poorer fitness outcomes in seabirds (Wendeln and Becker 1999; Chapter 2).

Foraging Flexibility Involves Physiological Costs

Models relating physiological traits with foraging behaviour are important for helping to interpret whether the year differences in foraging behaviour patterns we observed indicate whether birds were working harder under low ice conditions. During chick-rearing, individuals making longer foraging trips had lower TRIG levels after foraging, and more positive increases in NEFA and body mass across the foraging trip, indicating a complicated relationship between variation in foraging strategy (i.e., short vs. long trips) and associated energetic payoffs. Plasma TRIG and NEFA levels could relate to differences in the energetic demand that each strategy requires - long trips require more energy, while less mass loss with longer trips may relate to birds spending more time feeding for their own self-maintenance (Weimerskirch 1998). Average daily distance (foraging effort) was negatively related to both the change in CORT and NEFA (i.e., greater distances equated to a larger reduction in both CORT and NEFA) indicating that birds putting more effort into their daily foraging appeared to gain a benefit (i.e., they were in a better energetic state).

Our behavioural work suggests that the foraging strategy of thick-billed murres appears to be highly flexible in response to changing ice conditions and that this flexibility may have evolved to maintain the overall effort individuals are investing in foraging (i.e., mean daily trip distance and eDEE did not differ across years). Across ice conditions, birds altered the frequency, distance and duration of individual foraging trips, as well as the maximum foraging distance. Common murre (*Uria algae*) foraging behaviour has also been shown to be flexible in response to food availability, with the apparent ‘goal’ of maintaining chick-feeding rates (Harding et al. 2007). In fact, flexibility in trip length (alternate long and short foraging trips) is well known in several *Procellariiform* species (tubenose seabirds) when foraging areas near the colony are depleted (Chaurand and Weimerskirch 1994; Weimerskirch et al. 1994; Welcker et al. 2009a). Other northern ocean seabird species have been shown to respond to altered food conditions surrounding the colony by changing their foraging behaviour (common murre; Burke and Montevecchi 2009, northern gannet (*Sula bassana*); Montevecchi et al. 2009), using alternating foraging strategies in response to challenging conditions (little auk (*Alle alle)*; Welcker et al. 2009a), or varying their foraging strategies based on local environmental cues (razorbills (*Alca torca*); Shoji et al. 2014). Marine prey sources are constantly fluctuating spatially and temporally, which has given rise to a diversity of foraging strategies between and within species (Weimerskirch 2007). However, despite the well-documented flexibility in the foraging strategies of seabirds to this environmental heterogeneity, few studies have been able to focus on measuring potential costs associated with different behaviours. Our results indicate that variation in the foraging strategy has mixed energetic or state-dependent costs that are not apparent from examining measures of behaviour alone. Our estimated daily energetic expenditure metric also showed no differences between years at either breeding stage, indicating that thick-billed murres appear to regulate their overall level of effort, despite variation in conditions they face during breeding. Food availability and DEE relate oppositely in two studies on kittiwakes (Kitaysky et al. 2000; Jodice et al. 2006), and Welcker et al. (2009b) explain two hypotheses for these mixed results: low food availability forces higher energetic expenditure due to increased foraging effort, or high food availability enables increased energy towards breeding, self-maintenance, or foraging. The high levels of CORT and NEFA in our low ice year potentially indicate low food supply, yet the consistent eDEE levels between years indicates both hypotheses may apply within the same species.

While physiology and state-dependent variables such as body condition can indicate some of the costs of differing foraging strategies and environmental variation, the ultimate measure of these potential costs is fitness at the individual level, which eventually impacts population size and productivity. CORT has received the most attention in seabirds, and studies have connected behaviour, CORT levels, and measures of fitness (for review see Chapter 2). Nonetheless, more work is needed in connecting physiology, behaviour and fitness, especially in relation to environmental variation.

Relevance of Findings to Future Work

While physiology and state-dependent variables such as body condition can indicate some of the costs of differing foraging strategies and environmental variation, the ultimate measure of these potential costs is fitness at the individual level, which eventually impacts population size and productivity. Baseline CORT and NEFA both varied at the population level in response to environmental variation and also at the individual level in response to foraging effort and behaviour. A strong biomarker should relate to environmental quality (Madliger et al. 2015), and to success of individuals and the population (Cooke and O’Connor 2010). CORT has received the most attention in seabirds, and studies have connected behaviour, CORT levels, and measures of fitness (for review see Chapter 2). Nonetheless, more work is needed in connecting physiology, behaviour and fitness, especially in relation to environmental variation. Further work to relate NEFA levels to reproductive success at the individual or population level would increase its strength as a physiological biomarker.

The results also indicate that the change in a physiological trait over time is needed to predict some of the foraging relationships. Collecting this data is more challenging because it requires capturing the animal twice, which has implications for the ease of collecting this sort of data. However, our results suggest the strengths of repeated measures compared to single time point measures. For example, CORT has been shown to change predictably with foraging behaviour (Angelier et al. 2008), showing the potential for the change in a physiological trait to provide more information about the foraging trip or the environment experienced (Dingemanse et al. 2010). Scaling this information on the flexibility of traits up to the population level is also important towards recognizing how a population will fair under environmental change (Madliger and Love 2014).

We found stage-specific trends in our data, both when comparing between year differences and in foraging behaviour and physiology relationships. Stage specific differences have been observed previously in physiological data (e.g., Lanctot et al. 2003), and are very important to consider when using physiology as a biomarker (Madliger and Love 2014). CORT differed consistently between years in both breeding stages, while foraging strategy PC only differed during incubation and NEFA, mass, and mass change only differed during chick-rearing. We are unable to draw conclusions about relationships between physiology and foraging behaviour during incubation because our null model was the strongest. Further work to test if relationships are tighter during chick-rearing will help establish the importance of timing in measuring certain biomarkers.

The relative strength of biomarkers is most important when considering use, however the ease of use and cost of different biomarkers is also important to consider. Measuring baseline CORT for example can be challenging in some species due to the rapid increase in stress-induced levels after 3 minutes of capture (Romero and Reed 2005). Other physiological measures are less sensitive to the bleed time, making them potentially better suited for hard-to-capture study species. Assay or device cost is also necessary to consider to effectively use research resources, for example physiological assays range in cost per sample (CORT $17.50 CAD, TRIG $3.75, BOH $1.68, NEFA $3.26) which may be important in choosing a practical biomarker. Finally, as our results demonstrated, integrating techniques and multiple biomarkers is necessary to capture the entirety of responses to the environment.

Conclusions

Our results demonstrate the impacts warming and changing Arctic temperatures can have on polar-breeding species. Negative effects of environmental warming and ice loss are not new discoveries in the Arctic, however, the mechanisms we use to document these effects are important for future work. While behaviour alone has appeal to researchers as a simple metric to relate environmental variation to the success of individuals, our study demonstrates that behaviour may not reveal all the costs experienced by changing environments. Sensitive physiological traits (CORT, NEFA, mass change) provide information on the costs of different behavioural decisions, and reveal challenges from large-scale environmental variation furthering support for these traits as strong environmental biomarkers.

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Tables

Table 3.1 - Rotated factor loading from foraging behaviour principal component analysis.

	Factor 1	Factor 2
Log10 Maximum Distance	0.605	0.648
Log10 Average Daily Distance	0.025	0.986
Log10 Trips/ Day	-0.980	0.125
Log10 Mean Distance/ Trip	0.822	0.528
Log10 Mean Trip Duration	0.575	0.387

Table 3.2 - Trait means (+/- SE) and sample size (N) for each year and test statistics (t/Z, q-value, DF) between years for both breeding stages (incubation and chick-rearing). All statistics based on raw data, except statistics for CORT, TRIG, BOH, and NEFA in both stages, and foraging strategy PC during chick-rearing performed on log-transformed data. NEFA and average daily distance during incubation are from Kruskal-Wallis test. Q-values represent false discovery rate-adjusted p-values.

Stage			**Incubation**				
Year	2014		2015		Stats		
Value	**Mean +/- SE**	**N**	**Mean +/- SE**	**N**	**T/ Z**	**q-value**	**DF**
CORT (ng/mL)*	9.57+/-1.05	28	5.62+/-0.64	44	-3.241	0.013	57.463
CORT change (ng/mL)	0.05+/-1.48	18	2.9+/-1.36	26	1.414	0.239	39.022
TRIG (mmol/L)	0.74+/-0.06	27	0.88+/-0.05	48	1.900	0.165	46.587
Trig change (mmol/L)	-0.19+/-0.09	18	-0.13+/-0.08	26	0.533	0.777	35.819
BOH (mmol/L)	1.09+/-0.08	26	1.17+/-0.09	46	0.233	0.885	59.136
BOH change (mmol/L)	0.18+/-0.13	18	0.66+/-0.17	26	2.240	0.119	41.628
NEFA (mmol/L)	0.72+/-0.07	27	0.56+/-0.04	45	1.681	0.201	
NEFA change (mmol/L)	-0.02+/-0.1	17	0.2+/-0.09	25	1.637	0.201	37.267
Mass (g)	1003.53+/-9.8	34	977.55+/-7.23	53	-2.134	0.119	66.225
Mass change (g)	-43.5+/-17.4	20	-42.1+/-9.93	31	0.070	0.945	31.282
Average Daily Distance (km)	150.29+/-12.78	21	142.75+/-8.46	22	0.316	0.885	
DEE (kJ/day)	2480.8+/-103.29	21	2692.37+/-86.22	22	1.572	0.201	39.376
ForagingStrat PC1*	0.34+/-0.13	21	1.13+/-0.18	22	3.537	0.013	37.056

Stage	**Chick-rearing**						
Year	2014		2015		Stats		
Value	**Mean +/- SE**	**N**	**Mean +/- SE**	**N**	**T-test**	**q-value**	**DF**
CORT (ng/mL)*	10.31+/-0.93	55	5.67+/-0.71	69	-5.150	0.0013	121.400
CORT change (ng/mL)	5.3+/-1.84	18	1.67+/-0.9	39	-1.770	0.192	25.519
TRIG (mmol/L)	0.94+/-0.06	54	1.02+/-0.05	68	1.442	0.282	106.922
Trig change (mmol/L)	-0.12+/-0.19	15	-0.31+/-0.08	39	-0.894	0.497	19.106
BOH (mmol/L)	1.52+/-0.1	55	1.65+/-0.1	67	1.370	0.282	101.985
BOH change (mmol/L)	0.01+/-0.27	16	0.13+/-0.18	36	0.357	0.724	29.122
NEFA (mmol/L)*	0.74+/-0.04	55	0.57+/-0.04	57	-3.062	0.012	108.633
NEFA change (mmol/L)	0.28+/-0.14	17	0.16+/-0.08	35	-0.783	0.521	26.292
Mass (g)*	975.64+/-8.92	55	942.3+/-7.88	74	-2.801	0.020	117.991
Mass change (g)*	-86.11+/-7.79	18	-45.75+/-9.51	40	3.284	0.012	53.554
Average Daily Distance (km)	154.57+/-7.51	37	150.7+/-7.29	47	-0.370	0.724	80.118
DEE (kJ/day)	2613.04+/-87.36	37	2760.75+/-75.63	47	1.278	0.296	76.538
ForagingStrat PC1	-0.59+/-0.1	37	-0.21+/-0.15	47	2.122	0.096	77.031

Table 3.3 - Results of multiple AICc analyses of models relating physiological measures to foraging behaviour. Each null model had one parameter, regular models had 2. Values presented are the AICc, the difference in AICc, model weight (w), evidence ratios (ER), and conditional R^2 values.

Group	Model	AICc	ΔAICc	w	ER	R^2 (cond.)
Incubation						
Foraging Strategy	null (1|Year)	50.54	0.00	0.29	1.00	0.20
	chNEFA	52.29	1.75	0.12	2.40	0.25
	chTRIG	52.52	1.98	0.11	2.69	0.21
Average Daily Distance	null (1|Year)	226.31	0.00	0.27	1.00	0.00
	NEFA	227.24	0.93	0.17	1.59	0.11
	CORT	228.19	1.88	0.10	2.56	0.07
Chick-rearing						
Foraging Strategy	TRIG	87.00	0.00	0.27	1.00	0.11
	chNEFA	87.23	0.23	0.24	0.89	0.11
	chMass	88.98	1.98	0.10	0.37	0.06
Average Daily Distance	chCORT	350.02	0.00	0.32	1.00	0.15
	NEFA	350.40	0.38	0.27	1.21	0.14

Figures

Figure 3.1 - Inter-annual variation in ice conditions during the height of incubation at the murre colony at Digges Island, Nunavik, Canada (2014 - July 15; 2015 - July 13).

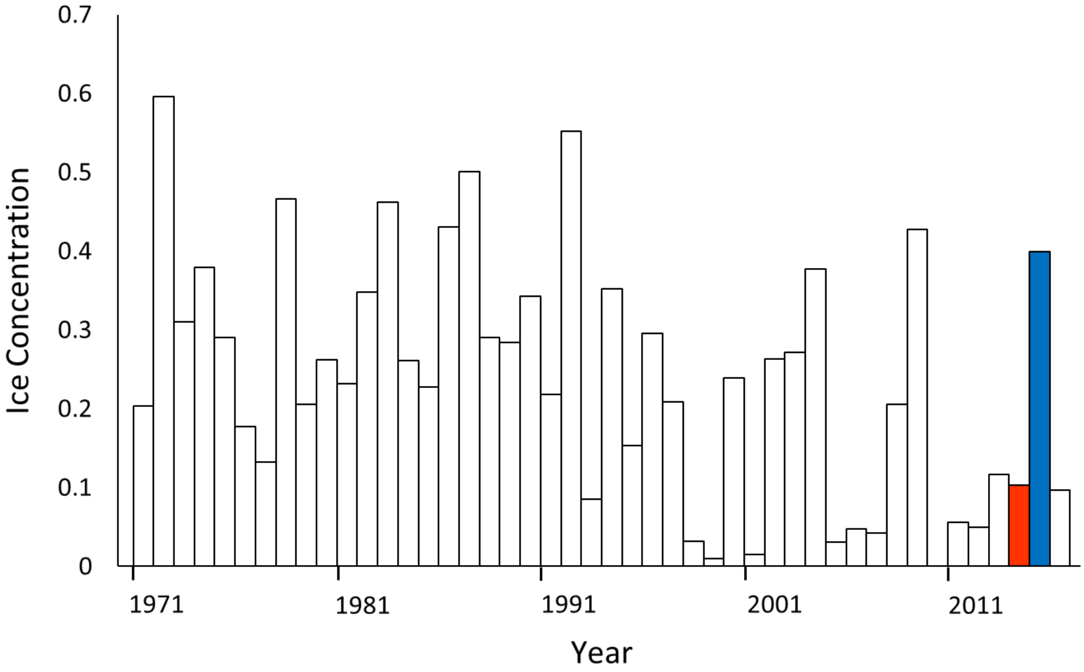

Figure 3.2 - Ice cover variation in Hudson Bay, Canada on July 16 from 1971-2016. Data from Canadian Ice Service, partially based on figure from Gaston et al. (2005). Current study years of 2014 (red) and 2015 (blue) are shown specifically.

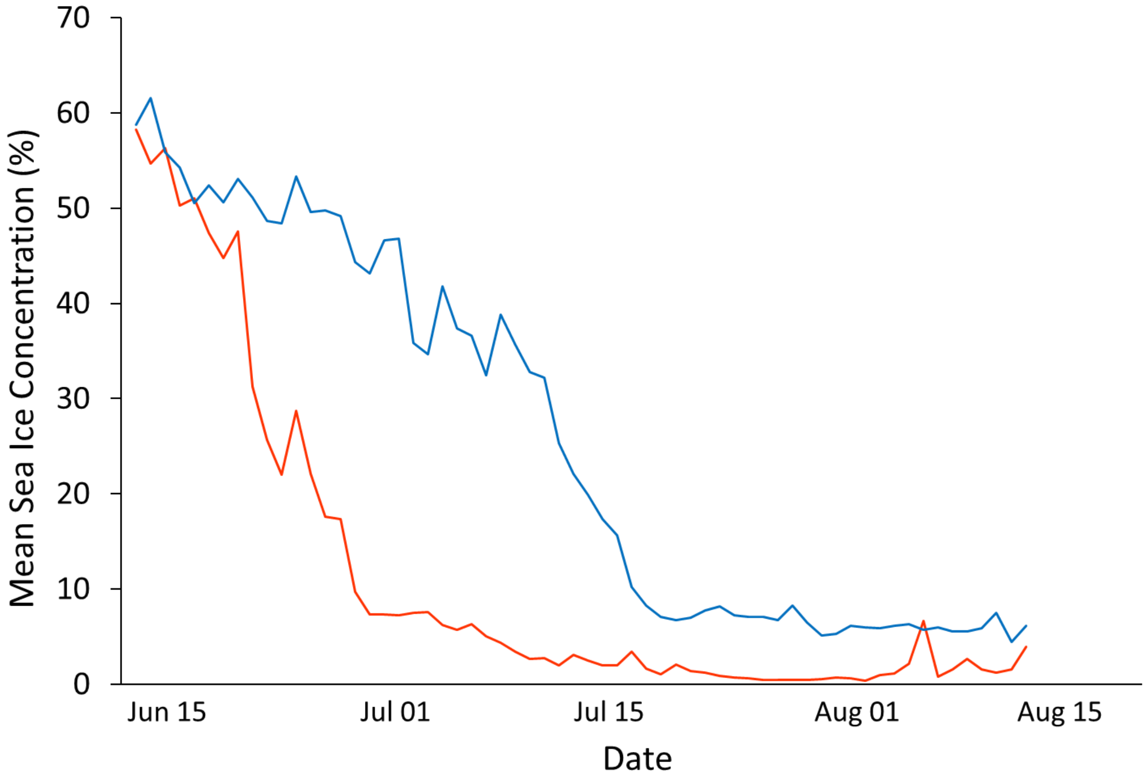

Figure 3.3 - Significant inter-annual differences in ice conditions during the early breeding period (i.e., incubation) of thick-billed murres breeding at Digges Island, Nunavik, Canada (2014: red; 2015: blue).

CHAPTER 4

General Discussion

In our rapidly changing world, strong biomarkers that indicate population fitness and reflect environmental change are increasingly sought-after, making verification of the effectiveness of these biomarkers an important area of study. In this thesis, my overall goal was to assess the effectiveness of several potential physiological and behavioural biomarkers across multiple biological scales. To do so, I first investigated whether a commonly-used individual metric (baseline levels of the glucocorticoid, corticosterone - CORT) correlates with fitness-related traits by reviewing current literature across seabirds that attempts to link CORT to fitness and environmental variation. I then used a model seabird study system – the thick-billed murre (*Uria lomvia*) – to assess several individual metrics for their relative strength as biomarkers across environmental variation and biological scales (population, between individual, and within individual). Combined, the results of these two chapters provide strong evidence of the relative effectiveness of several individual physiological metrics proposed as biomarkers. Importantly, these results were consistent across environmental contexts, fitness metrics, and species. While previous studies have supported the use of CORT as a biomarker in marine systems (Kitaysky et al. 2007) and have demonstrated the use of seabirds as environmental indicators (Piatt et al. 2007a), my thesis specifically tests these ideas by: 1) validating the use of a CORT as a biomarker of fitness and broad environmental quality across seabird species, and 2) integrating multiple physiological traits and behaviour to determine the most effective metrics of environmental change in a model study system.

Baseline Corticosterone as a Biomarker for Fitness Variation in Seabirds

Baseline corticosterone is widely used in seabird research as a means to estimate environmental variation and attempt to predict fitness outcomes. While one review has examined these links in vertebrates in general (Bonier et al. 2009), no review in this field has been conducted to test the validity of these assumptions in long-lived, declining seabirds. Seabirds rely on relatively large areas of ocean, and thus in a time of rapid climate change, are very useful bio-indicator species of entire marine environments (Frederiksen et al. 2007; Piatt et al. 2007b), making the validation of CORT as a biomarker timely in this avian group. My systematic review and meta-analysis of the seabird literature revealed that CORT levels do not predict foraging effort, nesting effort or body condition. However, strong relationships existed between baseline CORT and both food availability and reproductive success, indicating the potential for CORT to serve as a robust biomarker of environmental quality and fitness for seabirds. An important future step towards conservation efforts is being able to scale individual CORT levels up to the population by using longer-term studies relating population baseline CORT to predict one or multi-year changes in demography (e.g., survival, reproductive output, population growth/decline). Although the data necessary to examine this relationship requires a full year of demography and physiology data to produce a single data point, accounting for delays between elevated baseline CORT and population changes may require at least several years of collected data per data point. Nonetheless, continuing long-term studies that both measure CORT and estimate population demography will enable conservation physiologists to examine these relationships for seabirds, and perhaps even within other at-risk taxonomic groups. Seabird colonies will likely remain as research priorities as they are perfect systems for the study of broad-scale climate change, meaning these investigations are likely to continue into the future.

Behavioural and Physiological Biomarkers of Environmental Variation in Murres

Thick-billed murre populations are in decline globally (Gaston et al. 2012; Descamps et al. 2013; Merkel et al. 2014) as a result of changing oceanic patterns and ice concentration (Descamps et al. 2013). However, we are in need of tools to more rapidly assess the disturbance level and health of birds and colonies in cases where population demography is too slow to respond. To examine these issues, my second data chapter took advantage of a natural climate experiment to examine environmental impacts on the physiological and behavioural phenotype of ice-dependent thick-billed murres breeding within Digges Sound, Nunavut/Nunavik. Comparison across two years with differing sea ice conditions and across biological scales served two purposes: i) to measure the effects of changing ocean patterns on a widespread Arctic species, and ii) to test the relative effectiveness of multiple individual physiological and behavioural metrics as biomarkers of change or challenging environments. It is not uncommon for studies to link single metrics to environmental variation, but the strength of my study lies in the comparison of a range of important traits within the same individuals, population and study years.

In terms of ice coverage during the breeding period, the two study years ranged from the historic norm (20-25% seen in 2015) to very low (5-10% seen in 2014), which is now becoming more and more common for these populations. The low ice year was characterized by foraging strategies involving shorter and more frequent foraging trips, yet average daily foraging distance and daily energetic expenditure were maintained across ice conditions. Plasma baseline CORT and non-esterified fatty acids (NEFA) were both higher in the low ice year, indicating higher energetic demand (CORT) and increased exercise level or fasting (NEFA), but this apparent cost came at the benefit of maintaining resource intake (year-consistent values of both plasma TRIG and BOH). Combined, the results of my second chapter indicate that low ice years likely represent more challenging conditions and suggest that foraging behaviour, CORT and NEFA are all sensitive enough biomarkers at the population level to highlight mechanistic impacts of environmental variation.

Relevance of these Results for Seabird Conservation

Taken together, my thesis highlights the strength of using energetic physiology (e.g., baseline CORT, NEFA, TRIG and BOH) as biomarkers of environmental and possibly fitness-related variation. Combining the information from the meta-analysis that baseline CORT can represent a biomarker of food availability and reproductive success with the between year differences in CORT seen in my single species chapter may indicate that significant reductions in food availability and reproductive success occur in low ice years. Overall, my thesis supports the premise that baseline CORT measures can connect large-scale environmental variation to fitness-related traits. Measures of CORT from a few years in a population may therefore be able to indicate which years or conditions were more challenging for birds, and suggest population health. NEFA shows similar potential to be a strong biomarker of environmental variation, though investigations assessing its ability to predict fitness metrics are yet to be completed. Nonetheless, this would be an important avenue to follow given that in my study on murres NEFA predicted between-year variation in the environment and related strongly to foraging behaviour and effort. This thesis indicates possible challenges of using behaviour alone as a relevant biomarker of environmental change due to the fact that it does not necessarily convey the costs an individual is experiencing. Ultimately fitness is the most important cost with which a biomarker should correlate in order to predict demography, yet measuring fitness and relating biomarkers to demography relies on long-term datasets that need at least several years to provide data.

Future directions

While baseline CORT has strong support in both my thesis and the literature as a biomarker of environmental change and fitness in seabirds, the additional energetic physiology (NEFA, TRIG, BOH, body condition) metrics and behavioural (foraging) metrics I have measured suggest that individuals may be adjusting in complex ways in the face of environmental change in an attempt to maintain performance. Importantly, while many behavioural and physiological traits have been related to environmental variation (Seaman et al. 2006; Harding et al. 2007b), relationships with fitness have rarely been investigated (Hennin et al. 2016) and the current murre chapter is no exception (see discussion below). Examining these relationships will be an important next step, especially in metrics that already show complex responses to environmental variation such as NEFA, TRIG/BOH, and foraging behaviour. While further testing of the relationships between single-point physiological or behavioural metrics and fitness relationships is important, flexibility in traits should also be considered given that flexibility at the individual or population level may be important for examining how well species respond to environmental change. This idea of within individual flexibility in foraging strategy, hormone regulation, or effort may provide greater insights into why certain individuals or populations are more successful under environmental challenges

(Williams 2008). Certain responses will have differing effects on fitness, and individuals that can respond appropriately may have greater fitness and populations with more of these individuals may have increased productivity (Williams 2012). Within my study years, foraging strategy varied while foraging effort remained constant, demonstrating flexibility in foraging behaviour at the population level (Chapter 3, Table 2). Foraging flexibility has been demonstrated among other seabirds (e.g., Welcker et al. 2009), but researchers have not yet demonstrated repeatable behaviours that relate to environmental variation or ultimately link to variation in fitness. Although trait flexibility among individuals can reduce the ability to recognize mean fitness outcomes within a population (Dingemanse et al. 2010; Madliger and Love 2014), if the degree of individual flexibility predicts fitness outcomes it has the potential to relate to population-level success (Reed et al. 2009). Although examining individual flexibility in phenotypic traits in response to environmental variability is considered a key step in determining how and why certain individuals contribute to population changes (Forsman 2014), and while capturing flexibility in phenotypic markers in the same individuals across years was an initial central goal of my thesis, my field-work demonstrated the challenges of collecting this data. For example, of the several hundred birds captured across my two years of field-work, only 20 individuals were caught in both years, and only 10 of these had both GPS and physiology data. Nonetheless, preliminary data from my murre work suggests that both energetic physiology (Figure 4.1) and foraging behaviour (Figure 4.2) has the potential to show flexibility at the individual level. While population averages of physiology and foraging behaviour either changed or remained constant across years in my study, determining whether all individuals changed similarly, or varied in their response across the years, would demonstrate whether i) flexibility within populations will enable populations to respond to environmental change (Figure 4.3a), or whether ii) certain individuals within the population are expected to succeed over others in the face of rapid environmental change (Figure 4.3b).

Recognizing and testing the expected links between environmental variation, biomarkers and fitness across a diversity of taxa with varying life-histories is also important as life-history can strongly influence species' responses to environmental change (Catry et al. 2013). For example, both a recent review of the strength of baseline CORT-fitness relationships across diverse taxa (Bonier et al. 2009) and my review of CORT as a predictor of fitness-related traits in seabirds in Chapter 2 showed mixed results, although food availability and reproductive success showed strong relationships in my meta-analysis. We would predict that most of the currently-used individual-level biomarkers are likely to vary across taxa at the absolute levels of the biomarkers. Even more importantly, the relationships with fitness may vary due to differing tolerance for change between species (Beaulieu and Costantini 2014), making verification of relationships important, especially when studying new families or orders of species. Although our original plan for my study of thick-billed murres included quantification of fitness metrics (e.g., hatching/fledging success), constraints in the field made this goal impossible. Nonetheless, testing the ability of biomarkers to respond to environmental variation and then relating the strength of this relationship to variation in fitness is necessary to truly validate environmental biomarkers, and drawing conclusions without fitness correlates should be done with caution (Madliger and Love 2016).

Seabirds are an important group of species for their role as top marine predators, their global distribution, their sensitivity to environmental change, and their widespread decline in population numbers. These factors have all contributed to the high rate of study of this group, as have the practical aspects of studying seabirds; most are colony breeders making them accessible in large numbers and being generally larger birds they are able to tolerate handling, sampling, and GPS deployment. While several biomarkers have been used individually in seabird species (Harding et al. 2007a; Kitaysky et al. 2007; Satterthwaite et al. 2012), my field-work has shown that combining multiple biomarkers may make predictions and relationships much stronger. In my work and the recent work of others, behaviour appears to relate strongly to environmental variation (Harding et al. 2007b; Burke and Montevecchi 2009), while physiology may relate to both fitness and environmental variation (Satterthwaite et al. 2012).

While examining these relationships using correlational approaches is important to test the responsiveness of biomarkers to actual environmental variation, experimental methods are also needed to confirm causal relationships. Correlational methods may provide baseline information on which biomarkers are more sensitive to minor environmental changes or predictive of short-term fitness variation. However, experimental techniques involving large-scale alteration of the environment an individual is experiencing will provide clearer, causal indications of how environmental variation ultimately influences biomarkers (i.e., increase hormone level, alter foraging behaviour/ effort) and fitness. We were fortunate during my thesis to experience a natural environmental experiment enabling us to test biomarkers across contrasting environmental conditions. However, these large-scale dichotomous events are of course rare, unpredictable, and hard to capture over short periods of time such as that associated with a thesis. An alternative would be to experimentally alter the individual metric used as a biomarker and then measure individual fitness to examine the relative strength of a given biomarker for linking environmental variation and fitness (i.e., increase CORT level and follow an individual's changes in foraging behaviour and reproduction).

Conclusions

My thesis provides a strong framework for validating the use of CORT as a biomarker of environmental variation and fitness in seabirds, and provides a thorough foundation for validating the power of integrating multiple physiological and behavioural metrics within a natural climate experiment. As conservation relies more on rapidly recognizing changes in population health, comparative studies employing multiple biomarkers are important to verifying sensitive biomarkers that are also practical and cost-effective. Ultimately, our long-term goal is to scale individual-level phenotypic responses and resultant variation in fitness up to the population level as a predictive tool for estimating the expected responses of different species to global change.

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Gaston AJ, Mallory ML, Gilchrist HG (2012) Populations and trends of Canadian Arctic seabirds. Polar Biol 35:1221–1232. doi: 10.1007/s00300-012-1168-5

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Kitaysky AS, Piatt JF, Wingfield JC (2007) Stress hormones link food availability and population processes in seabirds. Mar Ecol Prog Ser 352:245–258. doi:

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Figures

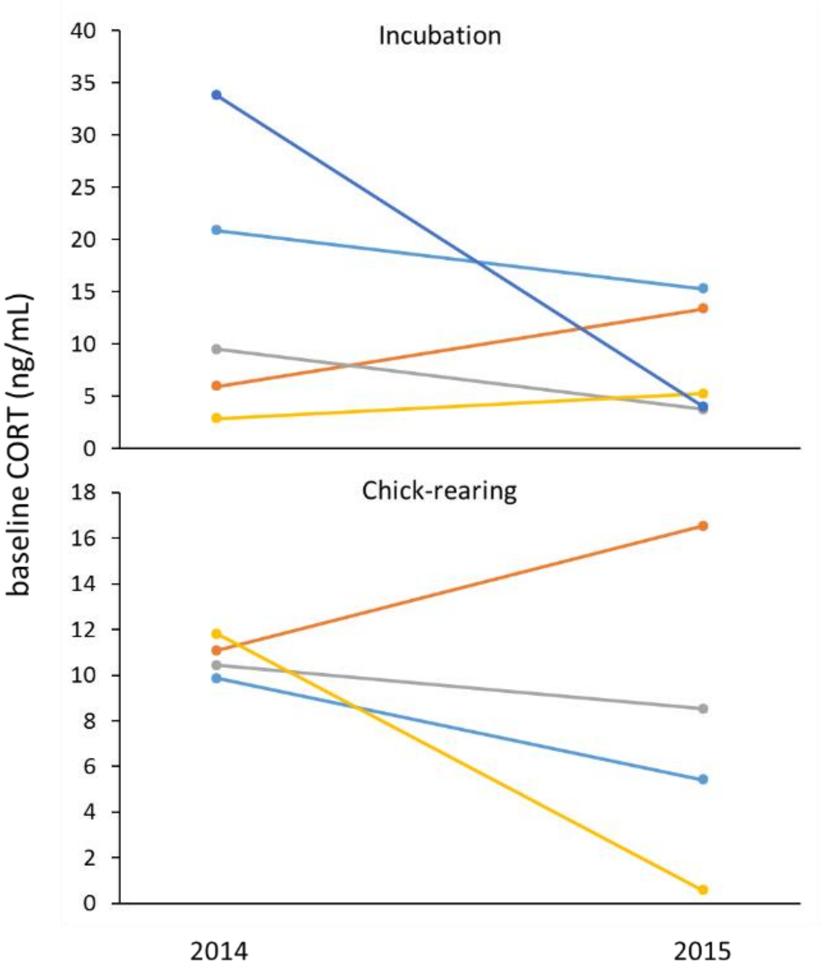


Figure 4.1 - Individual flexibility in baseline CORT levels between years for 9 individual thick-billed murres (*Uria lomvia*) during incubation and chick-rearing from Digges Sound, Nunavik/Nunavut.

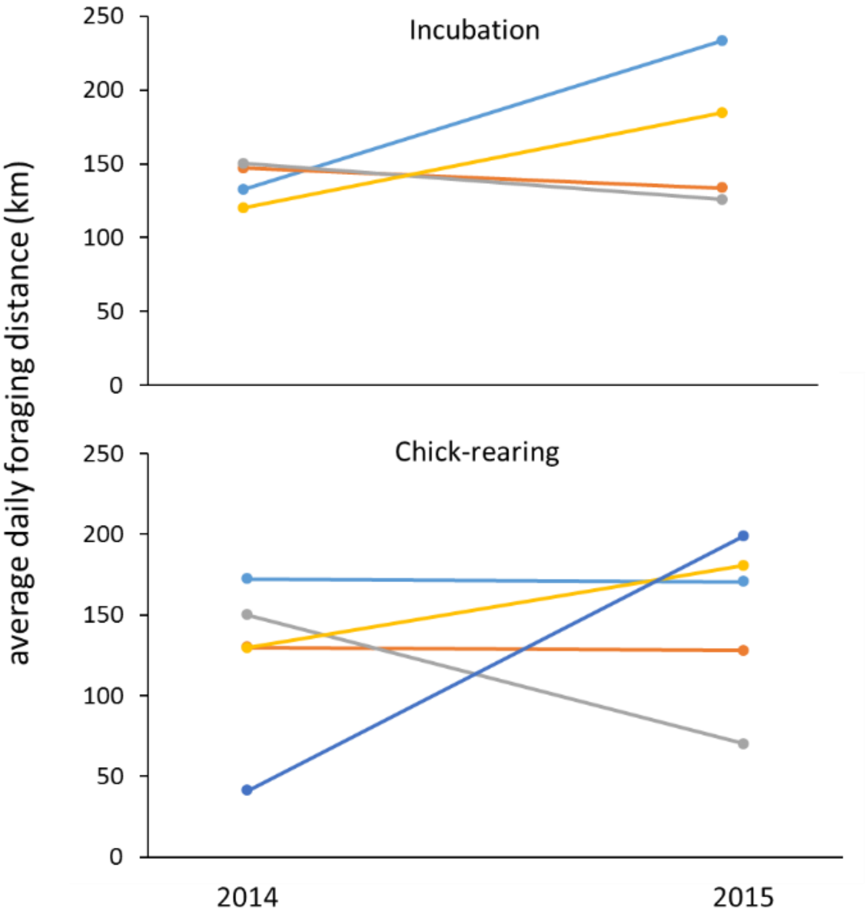


Figure 4.2 - Individual average daily distance travelled change between years for 9 individual thick-billed murres (*Uria lomvia*) during incubation and chick-rearing from Digges Sound, Nunavik/Nunavut.

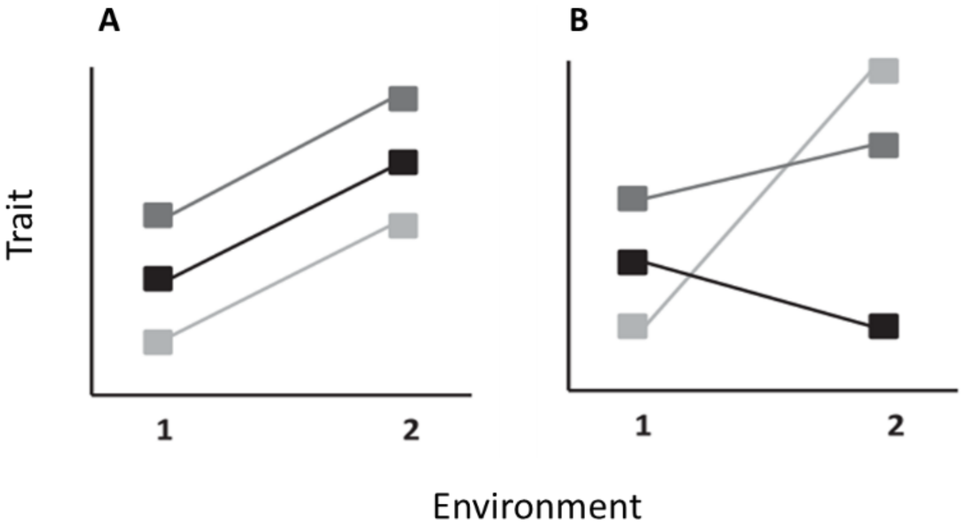
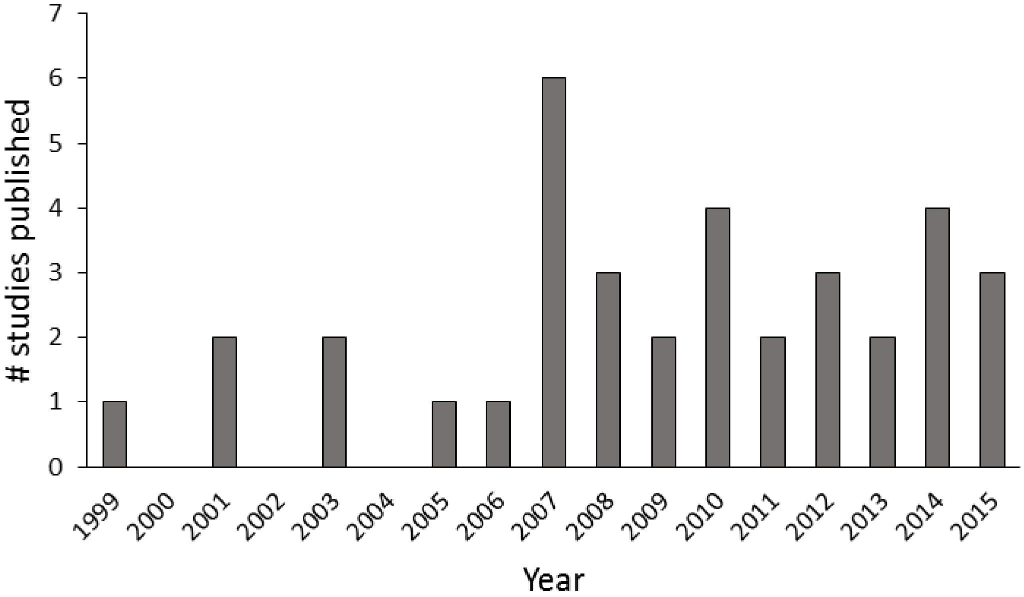


Figure 4.3 - Figures adapted from Madliger and Love (2014) showing (A) similar response of all individuals (i.e., population flexibility) to environmental change and (B) varied responses of individuals (i.e., individual flexibility) to environmental change.

APPENDICES

Appendix 1 - Publishing history (1999-2015) of papers relating baseline CORT to fitness-related traits in adult seabirds.



Appendix 2 - Complete list of references accumulated to generate effect size data for meta-analysis on relationship between seabird corticosterone level and fitness-related traits.

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Crossin GT, Trathan PN, Phillips R a., et al (2012) Corticosterone Predicts Foraging Behavior and Parental Care in Macaroni Penguins. Am Nat 180:E31–E41. doi: 10.1086/666001

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Appendix 3 - Studies and effect size data included in meta-analysis examining whether baseline corticosterone predicts fitness-related traits in seabirds from a systematic review of literature. Method: C = correlational; E = experimental. Breeding stage: B = both stages together; C = chick-rearing; I = incubation. RES: calculated or extracted correlation coefficient (r) effect sizes.

Species	Trait	Description of Trait	Method	Stage	N	RES	Study
Black-legged Kittiwake (*Rissa tridactyla*)	Condition	Body condition	C	B	9	-0.316	(Angelier et al. 2007a)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Fledged vs lost broods (males)	C	B	11	-0.613	(Angelier et al. 2007a)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Fledged vs lost brood (females)	C	B	15	-0.046	(Angelier et al. 2007a)
Black-legged Kittiwake (*Rissa tridactyla*)	Condition	Mass gain between treatments	E	C	32	0.38	(Angelier et al. 2007b)
Black-legged Kittiwake (*Rissa tridactyla*)	Effort - Foraging	Time spent flying	E	C	21	0.186	(Angelier et al. 2007b)
Black-legged Kittiwake (*Rissa tridactyla*)	Effort - Nesting	Time spent on nest	E	C	21	-0.1	(Angelier et al. 2007b)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Probability of losing chick	E	C	41	-0.24	(Angelier et al. 2007b)
Black-browed Albatross (*Thalassarche melanophrys*)	Condition	Individual quality	C	B	24	0.318	(Angelier et al. 2007c)

Black-browed Albatross (*Thalassarche melanophrys*)	Condition	Breeding experience	C	B	36	0.383	(Angelier et al. 2007c)
Black-browed Albatross (*Thalassarche melanophrys*)	Reproductive success	Fledging success	C	B	59	-0.34	(Angelier et al. 2007c)
King Penguin (*Aptenodytes patagonicus*)	Condition	Body condition	C	C	58	-0.013	(Angelier et al. 2009a)
King Penguin (*Aptenodytes patagonicus*)	Effort - Foraging	Handicap experiment	E	C	58	-0.084	(Angelier et al. 2009a)
Black-legged Kittiwake (*Rissa tridactyla*)	Effort - Nesting	Experimental CORT increase to nest attendance	E	I	36	0.149	(Angelier et al. 2009b)
Black-browed Albatross (*Thalassarche melanophrys*)	Condition	Individual quality (males)	C	B	35	-0.545	(Angelier et al. 2010)
Black-browed Albatross (*Thalassarche melanophrys*)	Condition	Individual quality (females)	C	B	29	-0.049	(Angelier et al. 2010)
Common Murre (*Uria aalge*)	Food Availability	Mean mass of larvae (mg)	C	C	110	-0.421	(Barrett et al. 2015)
Black-legged Kittiwake (*Rissa tridactyla*)	Condition	Body condition index	C	B	184	-0.0633	(Buck et al. 2007)
Black-legged Kittiwake	Reproductive	Number of fledglings/	C	B	184	-	(Buck et al. 2007)

(*Rissa tridactyla*)	success	nesting attempt				0.8775	
Black-legged Kittiwake (*Rissa tridactyla*)	Effort - Nesting	Chick-rearing parent vs failed parent	C	C	28	0.455	(Chastel et al. 2005)
Macaroni Penguin (*Eudyptes chrysolophus*)	Condition	Experimental CORT increase to mass gain	E	B	15	0.6245	(Crossin et al. 2012)
Macaroni Penguin (*Eudyptes chrysolophus*)	Effort - Foraging	Experimental CORT increase to total dives	E	B	15	0.565685	(Crossin et al. 2012)
Macaroni Penguin (*Eudyptes chrysolophus*)	Effort - Foraging	Experimental CORT increase to dive depth	E	B	15	0.565685	(Crossin et al. 2012)
Macaroni Penguin (*Eudyptes chrysolophus*)	Effort - Foraging	Experimental CORT increase to dive duration	E	B	15	0.6	(Crossin et al. 2012)
Macaroni Penguin (*Eudyptes chrysolophus*)	Effort - Foraging	Experimental CORT increase to prey wiggles	E	B	17	0.336	(Crossin et al. 2012)
Macaroni Penguin (*Eudyptes chrysolophus*)	Reproductive success	Experimental CORT increase to chick mass	E	B	15	0.655744	(Crossin et al. 2012)
Southern Giant Petrel (*Macronectes giganteus*)	Reproductive success	Failed vs still chick-rearing birds	C	B	23	0.123	(Crossin et al. 2013)
Southern Giant Petrel (*Macronectes giganteus*)	Reproductive success	Failed vs still chick-rearing birds	C	B	19	-0.012	(Crossin et al. 2013)
Northern Giant Petrel (*Macronectes halli*)	Reproductive success	Failed vs still chick-rearing birds	C	B	17	-0.308	(Crossin et al. 2013)

Northern Giant Petrel (*Macronectes halli*)	Reproductive success	Failed vs still chick-rearing birds	C	B	23	-0.056	(Crossin et al. 2013)
Common Murre (*Uria aalge*)	Condition	Between year mass change	C	C	12	-0.63	(Doody et al. 2008)
Common Murre (*Uria aalge*)	Effort - Nesting	Chick feeding rate (prey mismatch)	C	C	23	0.288	(Doody et al. 2008)
Common Murre (*Uria aalge*)	Effort - Nesting	Chick feeding rate (prey mismatch)	C	C	25	0.023	(Doody et al. 2008)
Common Murre (*Uria aalge*)	Effort - Nesting	Chick feeding rate (prey match)	C	C	22	0.4	(Doody et al. 2008)
Yellow-eyed Penguin (*Megadyptes antipodes*)	Reproductive success	Fledging chick weight (tourists)	C	C	5	-0.906	(Ellenberg et al. 2007)
Yellow-eyed Penguin (*Megadyptes antipodes*)	Reproductive success	Fledging chick weight	C	C	6	-0.828	(Ellenberg et al. 2007)
Yellow-eyed Penguin (*Megadyptes antipodes*)	Reproductive success	Month-old chick weight	C	C	6	-0.233	(Ellenberg et al. 2007)
Yellow-eyed Penguin (*Megadyptes antipodes*)	Reproductive success	Month-old chick weight (tourists)	C	C	5	0.355	(Ellenberg et al. 2007)
Thick-billed Murre (*Uria lomvia*)	Condition	Adult mass	C	B	7	-0.737	(Elliott et al. 2015)
Thick-billed Murre (*Uria lomvia*)	Effort - Foraging	Daily energy expenditure (kJ/d)	C	B	7	0.667	(Elliott et al. 2015)

Thick-billed Murre (*Uria lomvia*)	Effort - Foraging	Diving (min/d)	C	B	7	0.58	(Elliott et al. 2015)
Thick-billed Murre (*Uria lomvia*)	Reproductive success	Chick mass at 14 days	C	B	6	-0.851	(Elliott et al. 2015)
Thick-billed Murre (*Uria lomvia*)	Reproductive success	Fledging	C	B	7	0.128	(Elliott et al. 2015)
Snow Petrel (*Pagodroma nivea*)	Condition	Pre-laying condition	C	I	56	-0.01	(Goutte et al. 2010)
Snow Petrel (*Pagodroma nivea*)	Reproductive success	Hatching success	C	I	40	-0.475	(Goutte et al. 2010)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Clutch size (female)	E	I	21	0.041	(Goutte et al. 2011)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Clutch size (male)	E	I	22	0.06	(Goutte et al. 2011)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Lost eggs (female)	E	I	21	0.437	(Goutte et al. 2011)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Lost eggs (male)	E	I	22	-0.447	(Goutte et al. 2011)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Number chicks reached 12 days old (female)	E	C	21	-0.592	(Goutte et al. 2011)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Number chicks reached 12 days old	E	C	22	0.369	(Goutte et al. 2011)

		(male)					
Black-legged Kittiwake (*Rissa tridactyla*)	Condition	Body condition	C	B	48	-0.387	(Kitaysky et al. 1999)
Black-legged Kittiwake (*Rissa tridactyla*)	Effort - Foraging	Experimental CORT increase to number of trips	E	B	12	0.712	(Kitaysky et al. 2001)
Black-legged Kittiwake (*Rissa tridactyla*)	Effort - Foraging	Experimental CORT increase birds to number trips	E	B	12	0.905	(Kitaysky et al. 2001)
Black-legged Kittiwake (*Rissa tridactyla*)	Effort - Nesting	Experimental CORT increase to provisioning level	E	C	12	0.1	(Kitaysky et al. 2001)
Black-legged Kittiwake (*Rissa tridactyla*)	Effort - Nesting	Experimental CORT increase to attendance level	E	B	24	-0.623	(Kitaysky et al. 2001)
Black-legged Kittiwake (*Rissa tridactyla*)	Effort - Nesting	Experimental CORT increase to nest guarding amount	E	C	12	-0.731	(Kitaysky et al. 2001)
Common Murre (*Uria aalge*)	Food Availability	Current 2 week food level	C	B	23	-0.748	(Kitaysky et al. 2007)
Common Murre (*Uria aalge*)	Reproductive success	Egg-laying CORT level and hatching success	C	I	8	-0.73	(Kitaysky et al. 2007)
Common Murre (*Uria*	Reproductive	Egg-laying CORT	C	I	8	-0.87	(Kitaysky et al. 2007)

aalge)	success	level and Fledging success					
Common Murre (*Uria aalge*)	Reproductive success	Egg-laying CORT level and productivity	C	I	9	-0.76	(Kitaysky et al. 2007)
Common Murre (*Uria aalge*)	Reproductive success	Incubation CORT level and hatching success	C	I	9	-0.82	(Kitaysky et al. 2007)
Common Murre (*Uria aalge*)	Reproductive success	Incubation CORT level and Fledging success	C	I	9	-0.8	(Kitaysky et al. 2007)
Common Murre (*Uria aalge*)	Reproductive success	Incubation CORT level and productivity	C	I	10	-0.8	(Kitaysky et al. 2007)
Common Murre (*Uria aalge*)	Reproductive success	Early chick-rearing CORT level and hatching success	C	C	9	-0.79	(Kitaysky et al. 2007)
Common Murre (*Uria aalge*)	Reproductive success	Early chick-rearing CORT level and Fledging success	C	C	9	-0.82	(Kitaysky et al. 2007)
Common Murre (*Uria aalge*)	Reproductive success	Early chick-rearing CORT level and productivity	C	C	10	-0.79	(Kitaysky et al. 2007)
Common Murre (*Uria aalge*)	Reproductive success	Late chick-rearing CORT level and hatching success	C	C	8	-0.34	(Kitaysky et al. 2007)

Common Murre (*Uria aalge*)	Reproductive success	Late chick-rearing CORT level and Fledging success	C	C	8	-0.45	(Kitaysky et al. 2007)
Common Murre (*Uria aalge*)	Reproductive success	Late chick-rearing CORT level and productivity	C	C	9	-0.37	(Kitaysky et al. 2007)
Black-legged Kittiwake (*Rissa tridactyla*)	Food Availability	Fed vs control baseline CORT level	E	I	32	-0.518	(Kitaysky et al. 2010)
Black-legged Kittiwake (*Rissa tridactyla*)	Food Availability	Beach seine food level	C	I	16	-0.728	(Kitaysky et al. 2010)
Black-legged Kittiwake (*Rissa tridactyla*)	Food Availability	Mid-water trawl to food	C	I	6	-0.98	(Kitaysky et al. 2010)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Fledging success	C	C	5	-0.94	(Kitaysky et al. 2010)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Laying success	C	I	9	-0.75	(Kitaysky et al. 2010)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Clutch size	C	I	9	-0.51	(Kitaysky et al. 2010)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Hatching success	C	I	9	-0.42	(Kitaysky et al. 2010)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Delayed egg-laying	C	I	9	0.87	(Kitaysky et al. 2010)
Black-legged Kittiwake	Condition	Hindered vs control	E	C	53	-0.113	(Leclaire et al. 2011)

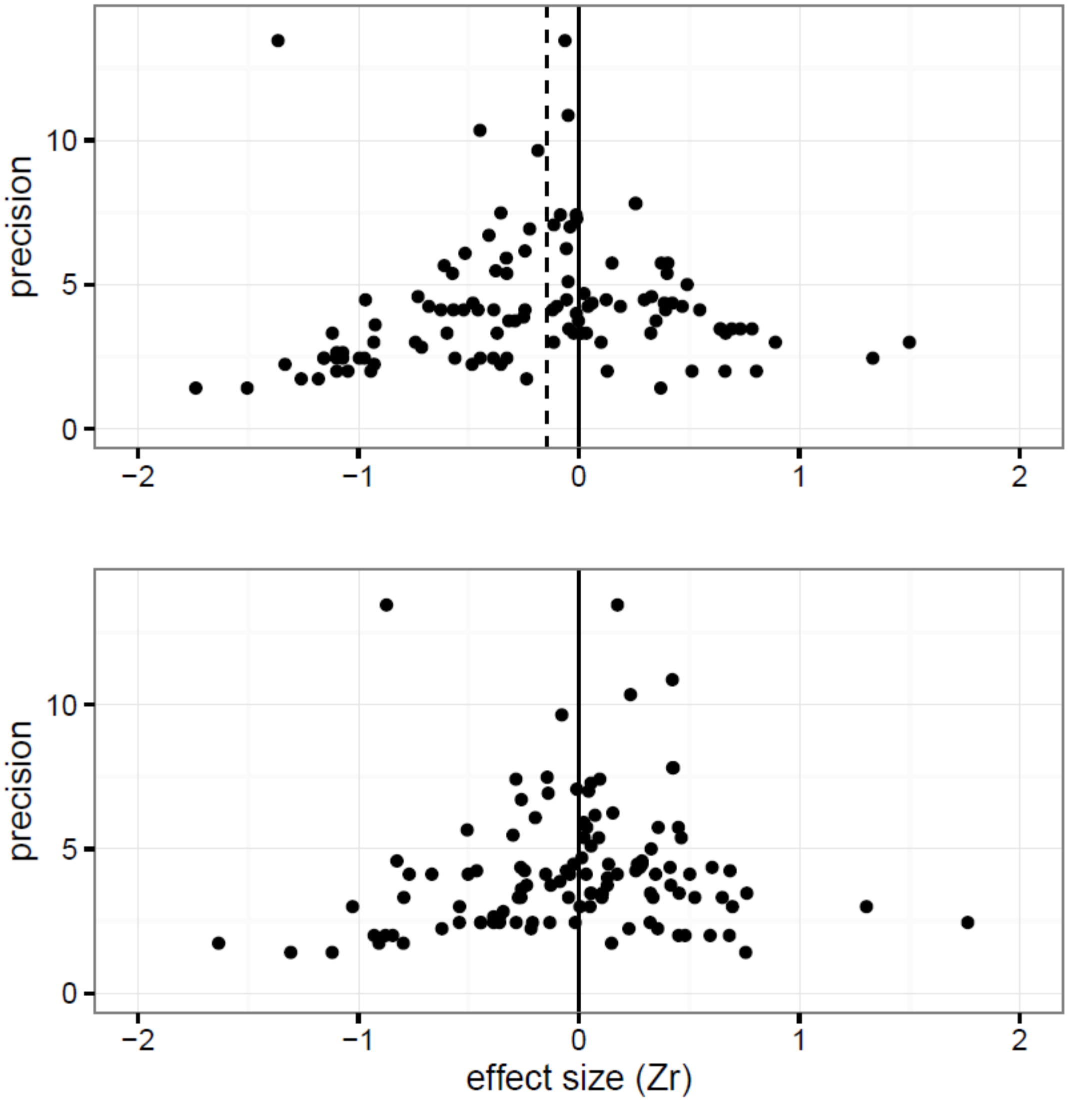
(*Rissa tridactyla*)		birds					
Red-footed Booby (*Sula sula*)	Condition	Body condition - males	C	B	51	-0.22	(Lormée et al. 2003)
Red-footed Booby (*Sula sula*)	Condition	Body condition - females	C	B	52	-0.04	(Lormée et al. 2003)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Experimental CORT increase to fledging success	E	B	38	-0.318	(Nelson et al. 2015)
Wilson's Storm-petrel (*Oceanites oceanicus*)	Reproductive success	Failed vs successful adults	C	C	42	-0.057	(Quillfeldt and Möstl 2003)
Atlantic Puffin (*Fratercula arctica*)	Condition	Body mass	C	B	230	-0.14	(Rector et al. 2012)
Atlantic Puffin (*Fratercula arctica*)	Food Availability	High and low food availability years	C	B	121	-0.049	(Rector et al. 2012)
Common Tern (*Sterna hirundo*)	Reproductive success	Mean hatching success	C	I	7	0.472	(Riechert et al. 2014)
Common Tern (*Sterna hirundo*)	Reproductive success	Mean fledging success	C	I	7	-0.8	(Riechert et al. 2014)
Common Tern (*Sterna hirundo*)	Reproductive success	Mean breeding success	C	I	7	-0.781	(Riechert et al. 2014)
Common Tern (*Sterna hirundo*)	Reproductive success	Fledging success - males in one year	C	I	64	0.253	(Riechert et al. 2014)

Common Tern (*Sterna hirundo*)	Reproductive success	Breeding success - males in one year	C	I	64	0.25	(Riechert et al. 2014)
Black-legged Kittiwake (*Rissa tridactyla*)	Reproductive success	Number of chicks fledged	C	B	32	-0.316	(Satterthwaite et al. 2012)
Adelie Penguin (*Pygoscelis adeliae*)	Condition	Experimental CORT increase to body mass	E	C	14	0.034	(Thierry et al. 2013)
Adelie Penguin (*Pygoscelis adeliae*)	Effort - Foraging	Experimental CORT increase to time spent at sea - male	E	C	14	-0.024	(Thierry et al. 2013)
Adelie Penguin (*Pygoscelis adeliae*)	Effort - Nesting	Experimental CORT increase to nesting bouts - male	E	C	14	0.582	(Thierry et al. 2013)
Adelie Penguin (*Pygoscelis adeliae*)	Reproductive success	Experimental CORT increase to chicks per nest - male	E	C	14	-0.807	(Thierry et al. 2013)
Adelie Penguin (*Pygoscelis adeliae*)	Reproductive success	Experimental CORT increase to brood mass	E	C	14	-0.536	(Thierry et al. 2013)
Adelie Penguin (*Pygoscelis adeliae*)	Reproductive success	Experimental CORT increase to chick mass after 21 days	E	C	14	0.012	(Thierry et al. 2013)
Adelie Penguin (*Pygoscelis adeliae*)	Reproductive success	Experimental CORT increase to brood mass after 39 days	E	C	14	-0.355	(Thierry et al. 2013)
Adelie Penguin	Reproductive	Experimental CORT	E	C	14	0.315	(Thierry et al. 2013)

(*Pygoscelis adeliae*)	success	increase to chick mass after 39 days					
Adelie Penguin (*Pygoscelis adeliae*)	Condition	Experimental CORT increase to body mass at 9 days	E	C	18	-0.246	(Thierry et al. 2014)
Adelie Penguin (*Pygoscelis adeliae*)	Condition	Experimental CORT increase to body mass at 17 days	E	C	12	-0.114	(Thierry et al. 2014)
Adelie Penguin (*Pygoscelis adeliae*)	Effort - Foraging	Experimental CORT increase to time at sea	E	C	20	-0.555	(Thierry et al. 2014)
Adelie Penguin (*Pygoscelis adeliae*)	Effort - Foraging	Experimental CORT increase to trip duration - males	E	C	20	-0.48	(Thierry et al. 2014)
Adelie Penguin (*Pygoscelis adeliae*)	Effort - Nesting	Experimental CORT increase to time on nest	E	C	20	0.499	(Thierry et al. 2014)
Adelie Penguin (*Pygoscelis adeliae*)	Effort - Nesting	Experimental CORT increase to nest duration - males	E	C	20	0.374	(Thierry et al. 2014)
Adelie Penguin (*Pygoscelis adeliae*)	Effort - Nesting	Experimental CORT increase to nest duration - females	E	C	20	-0.428	(Thierry et al. 2014)
Adelie Penguin (*Pygoscelis adeliae*)	Reproductive success	Experimental CORT increase to chicks per	E	C	20	-0.515	(Thierry et al. 2014)

		nest - male					
Adelie Penguin (*Pygoscelis adeliae*)	Reproductive success	Experimental CORT increase to chick mass	E	C	17	-0.282	(Thierry et al. 2014)
Adelie Penguin (*Pygoscelis adeliae*)	Reproductive success	Experimental CORT increase to brood mass	E	C	17	-0.002	(Thierry et al. 2014)
Adelie Penguin (*Pygoscelis adeliae*)	Reproductive success	Experimental CORT increase to chick mass at 17 days	E	C	20	-0.368	(Thierry et al. 2014)
Adelie Penguin (*Pygoscelis adeliae*)	Reproductive success	Experimental CORT increase to brood mass at 17 days	E	C	20	-0.24	(Thierry et al. 2014)
Tufted Puffin (*Fratercula cirrhata*)	Condition	Body condition index	C	B	96	-0.184	(Williams et al. 2008)
Thick-billed Murre (*Uria lomvia*)	Condition	Body condition (St Paul)	C	C	33	-0.36	(Young 2014)
Thick-billed Murre (*Uria lomvia*)	Condition	Body condition (St George)	C	C	36	0.357	(Young 2014)
Thick-billed Murre (*Uria lomvia*)	Condition	Body condition (Bogoslov)	C	C	20	-0.119	(Young 2014)

Appendix 4 - Funnel plot (effect size plotted against precision) of the original data points used in the meta-analysis (top) along with the meta-analytic mean (dashed line), and the model residuals from M3 (the model with the lowest DIC; bottom). Plots show no apparent asymmetry around the mean values and therefore do not indicate systemic publication bias.



Appendix 5 - Parameter estimates for fixed effects, 95% confidence intervals, and p-values of each meta-analytic Bayesian Mixed Model (M1-M8 - see main document, Table 2). Response variables are Fisher's *Zr* for the relationship between corticosterone and fitness-related trait. Reference level for Trait is [Body Condition], for Method is [Correlational], and for Stage is [Both].

Model	Fixed Effect	Estimate	Low CI	Upper CI	pMCMC
M1	Intercept	-0.145	-0.311	0.036	0.105
M2	Intercept	-0.133	-0.405	0.140	0.293
M3	Intercept	-0.059	-0.273	0.170	0.591
	Trait [Effort – Foraging]	0.318	-0.030	0.673	0.073
	Trait [Effort – Nesting]	0.201	-0.138	0.549	0.252
	Trait [Food Availability]	-0.497	-0.942	-0.066	0.025
	Trait [Reproductive Success]	-0.251	-0.500	-0.005	0.045
M4	Intercept	-0.046	-0.339	0.266	0.737
	Trait [Effort – Foraging]	0.309	-0.043	0.662	0.085
	Trait [Effort – Nesting]	0.210	-0.134	0.552	0.223
	Trait [Food Availability]	-0.486	-0.932	-0.051	0.031
	Trait [Reproductive Success]	-0.254	-0.499	-0.003	0.044
M5	Intercept	-0.095	-0.319	0.142	0.417
	Trait [Effort – Foraging]	0.241	-0.130	0.607	0.201
	Trait [Effort – Nesting]	0.156	-0.172	0.527	0.378
	Trait [Food Availability]	-0.505	-0.957	-0.078	0.026
	Trait [Reproductive Success]	-0.264	-0.503	-0.002	0.040
	Method [Experimental]	0.181	-0.095	0.460	0.196
M6	Intercept	-0.079	-0.380	0.239	0.577
	Trait [Effort – Foraging]	0.234	-0.122	0.608	0.203
	Trait [Effort – Nesting]	0.164	-0.183	0.519	0.346
	Trait [Food Availability]	-0.489	-0.941	-0.053	0.029
	Trait [Reproductive Success]	-0.268	-0.525	-0.031	0.033

	Method [Experimental]	0.197	-0.092	0.503	0.184
M7	Intercept	-0.033	-0.276	0.229	0.789
	Trait [Effort – Foraging]	0.222	-0.146	0.593	0.233
	Trait [Effort – Nesting]	0.188	-0.171	0.543	0.306
	Trait [Food Availability]	-0.512	-0.950	-0.050	0.028
	Trait [Reproductive Success]	-0.251	-0.498	0.010	0.058
	Method [Experimental]	0.225	-0.070	0.510	0.125
	Stage [Chick-Rearing]	-0.157	-0.434	0.136	0.280
	Stage [Incubation]	-0.117	-0.448	0.201	0.477
M8	Intercept	-0.032	-0.367	0.290	0.845
	Trait [Effort – Foraging]	0.216	-0.162	0.585	0.259
	Trait [Effort – Nesting]	0.193	-0.175	0.551	0.290
	Trait [Food Availability]	-0.500	-0.958	-0.038	0.032
	Trait [Reproductive Success]	-0.254	-0.519	0.000	0.057
	Method [Experimental]	0.235	-0.065	0.561	0.133
	Stage [Chick-Rearing]	-0.141	-0.444	0.154	0.339
	Stage [Incubation]	-0.114	-0.446	0.220	0.496

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