**Introduction**

Within a given species, or group of species, survival typically declines with increasing latitude (salmon: Koenings et al., 1993; thrushes: Ricklefs, 1997; songbirds: Ghaliambor and Martin, 2001). The usual explanation for high survival (low “pace of life”) in the tropics is that abiotic factors are more common at high latitudes than in the benign and stable climate of the tropics. Similarly, in the classical free radical theory of aging, the higher metabolic costs of sustaining a constant internal temperature in the face of harsh Arctic environments are predicted to increase the production of free radicals and oxidative stress, leading to higher rates of mortality among high-latitude individuals.

Despite the prediction that survival should decrease at higher latitudes, many of the longest-lived warm-blooded animals live in the polar regions. For example, the longest-lived wild birds (albatrosses, Ricklefs, 2008) and mammals (bowheads/arviq, George et al., 2011) live at high latitudes. Similarly, the longest-lived animal, the quahog clam *Arctica islandica*, is found in Arctic waters (Strahl et al., 2007). These animals, like the phoenix, keep the fire of life alive for decades or centuries, returning each spring from the ashes of an Arctic winter. How they do so is the focus of my doctoral dissertation, entitled “How can Arctic birds work hard and live long?”

Both physiological and behavioural mechanisms likely underlie the ability of Arctic birds to live extraordinarily long in pulsed-resource systems. Physiological traits linked to body size explain some of the variation: animals tend to be larger near the poles because a low surface area to volume ratio reduces heat loss (Bergmann’s rule), and larger animals live longer (Ricklefs, 2008). In addition, some Arctic birds have high levels of oxidative defense. For example, when foraging conditions deteriorate, some species (e.g., penguins) show no oxidative damage presumably because of greater oxidative defense (Beaulieu et al., 2011). Both albatrosses and terns show no detectable physiological senescence with advancing age (Lecomte et al., 2010; Nisbet, 2001). Can Arctic birds such as arctic terns (*imiqqutaitlat*), which migrate up to 80,000 km annually, or thick-billed murres (*akpâta*), which have the highest flight costs of any bird, sustain high levels of metabolism without any cost to survival?

Recent work on albatrosses suggests a role for behavioural mechanisms (Catry et al., 2006; Lecomte et al., 2010). Reduced foraging performance is presumably linked to reduced muscle efficiency, but changes in muscle physiology with age have never been examined in Arctic animals. Reduced muscle performance might mean no change in large-scale activity budgets, but reductions in short-scale behaviours (predator avoidance, prey capture). The invention of miniature accelerometers permits examination of muscle physiology and behaviour by permitting the measurement of wingbeat kinematics.

Related to changes in foraging performance are changes in contaminant burdens. As with other long-lived marine wildlife in the Arctic, seabirds experience “the calamity of so long life” (Rowe, 2008:623). They live in areas with high contamination (Arctic), live long (high bioaccumulation), and feed high in the food web (high biomagnification). To understand the effect of longevity on contaminant burdens, it is important to know whether contamination continues to increase with age, or whether contamination burdens stabilize at equilibrium beyond a certain age.

Of particular interest is the possibility that older birds may acclimate or adjust to contaminant burdens. For example, a recent review based on comparisons between adults and nestlings (Cescht et al., 2010) suggested that the effect of PCBs and PBDEs on thyroid hormones is reduced in old birds. The difference between young and old birds may represent adjustments in the role of the thyroid axis during development. Thyroid hormones in the adult bird are related to metabolism, and old birds may be able to adjust receptivity to hormones so that a constant net effect is achieved. In contrast, thyroid hormones in young birds are associated with growth and may help regulate specific timing of different growth stages. Thus, it may be more difficult to make those adjustments rapidly.

I will be investigating these ideas in two species of long-lived seabirds, thick-billed murres (*Uria lomvia*) and black-legged kittiwakes (*taaeraaqsi, Rissa tridactyla*). I will study murres at Coats Island, Nunavut, the location of the longest-running thick-billed murre study in the world, and the only place in the world where I can study senescence in banded murres of known age (Fig. 1). My study site for kittiwakes is the long-term banding site at Middleton Island in Alaska, where nesting on a radar tower facilitates observation.

I am studying aging in the thick-billed murre, a seabird whose eggs are still harvested annually in many communities where stone cairns, used by local people for centuries, dot the landscape around the colonies. Murre meat has
long been a staple diet of Northerners in Canada. Hunting has decimated murre colonies elsewhere because hunters selected the oldest, most successful individuals. By understanding the effect of age on demography, I will be providing information necessary to manage murre harvests, thereby helping to ensure that the Arctic phoenix continues to live long and return to its Arctic home each summer.

I predict two general outcomes: (1) Long-lived birds will show behavioural senescence. Specifically, old birds will cope with increased physiological deterioration by increasing effort; they will use more wing beats, or a slower flight speed, or both, to move a given distance in space. (2) Contaminant levels (mercury, PBDEs and PCBs) will increase with age in long-lived birds up to an asymptote. Thyroid hormone levels will decrease with PCB-153 and BDE-47 in young birds, but not in old birds.

**METHODS**

I propose to attach GPS loggers and accelerometers to 144 murres and kittiwakes (72 chick-rearing pairs, 36 of each species), including 24 young (5–10 years old), 24 middle-aged (11–20 years old), and 24 old (20+ years old) birds of each species. Continuous 24-hour feeding watches for all three age groups will take place simultaneously, and birds will be weighed before and after deployment of the instruments (see Elliott et al., 2008 for details). For these deployments, the GPS loggers (CATTRAQ, Berlin, Germany) and G6A triaxial accelerometers (CEFAS, Cambridge, UK) will be combined into a single package that includes the attachment gear. In previous studies, I have deployed more than 600 loggers (including 150 accelerometers and GPS loggers) on murres at my study site with a success rate at retrieving the devices of over 99%.

Eight 24-hour deployments will be made for each sex, each including three young, three middle-aged, and three old birds. Parameters will be analyzed using a general linear model with deployment period as a covariate, controlling for environmental conditions. I will combine these parameters to determine wing beats needed to move a given distance in space (horizontal distance flown or vertical depth swum), and decline in wing beat frequency or amplitude with distance (exhaustion), along with energy delivery rates to offspring at the colony, to determine two parameters: wing beats per distance flown and wing beats per depth swum. I will examine whether these parameters influence mass gain per trip or energy delivered to offspring, and whether that relationship is influenced by age. Judging by the effect sizes in albatrosses (Lecomte et al., 2010), I should have a 92% chance of detecting the effect sizes in murres and kittiwakes given my sample size (24 birds per age group per sex).

As in previous studies, I will obtain blood samples from each bird for mercury, PBDE, and PCB analyses (Fig. 2) and use the same samples for studies of hormone levels and oxidative stress.

**FIG. 1. Josiah Nakoolak, Kerry Woo, Kyle Elliott, and the pilot (from left to right) unloading a Twin Otter at the Coats Island landing strip to begin the 2009 field season.**

**FIG. 2. Obtaining a blood sample from a murre along the Coats Island cliffs in June 2009. Visible from left to right are Kyle Elliott, Josiah Nakoolak, and Kerry Woo (boots). Photo by Birgit Braune.**
TABLE 1. Statistical tests for ten parameters in murres collected from 2007 to 2010 show that behaviour over long time scales does not change with age. In each case, an ordinary least-squares quadratic polynomial was fit with behaviour as the dependent variable and age as the independent variable. The coefficient of determination and \( p \)-values (ANOVA) are shown.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>( R^2 )</th>
<th>( p )</th>
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<tbody>
<tr>
<td>Nest attendance</td>
<td>0.00</td>
<td>0.84</td>
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<tr>
<td>Time allopreening</td>
<td>0.04</td>
<td>0.24</td>
</tr>
<tr>
<td>Time flying</td>
<td>0.01</td>
<td>0.79</td>
</tr>
<tr>
<td>Time diving</td>
<td>0.02</td>
<td>0.52</td>
</tr>
<tr>
<td>Ratio of surface pause to dive depth</td>
<td>0.00</td>
<td>0.86</td>
</tr>
<tr>
<td>Return flight time</td>
<td>0.00</td>
<td>0.98</td>
</tr>
<tr>
<td>Trophic level</td>
<td>0.01</td>
<td>0.85</td>
</tr>
<tr>
<td>Energy delivery rate</td>
<td>0.03</td>
<td>0.33</td>
</tr>
<tr>
<td>Energy efficiency</td>
<td>0.01</td>
<td>0.92</td>
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<tr>
<td>Mass gain</td>
<td>0.01</td>
<td>0.87</td>
</tr>
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</table>

PRELIMINARY RESULTS

In contrast to the studies examining senescence in albatrosses, the present study of murres and kitiwakes has shown physiological aging in birds, but not behavioural aging. Age had no significant effect for either species on any of the behavioural parameters I examined (See Table 1 for test results on murres). However, metabolism and corticosterone levels changed with age for both species. As metabolism decreased with age, I propose that long-lived charadriiform birds, with their high levels of oxygen expenditure, altered their energy consumption to reduce oxidative (or other) damage.

The GPS loggers attached to murres have shown that birds forage primarily to the west of the colony, with no effect of age. Since murre foraging hotspots often are also hotspots for other wildlife (seals, whales, fish), my research will identify key habitats for protection. Indeed, if Evans Strait becomes a location for a promised future Foxe Basin Marine Conservation Area, such regions may play an important role. Additional studies are planned in 2012 to test my two main predictions using the deployment schedule outlined in the Methods section.

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REFERENCES


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