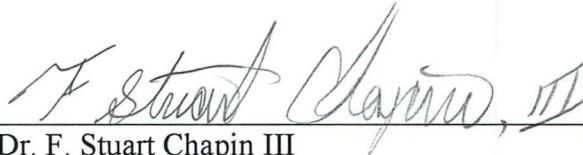


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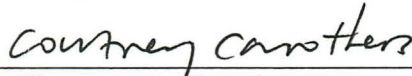
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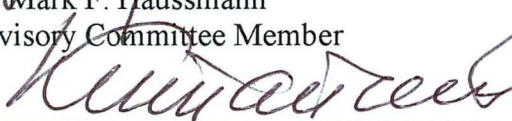
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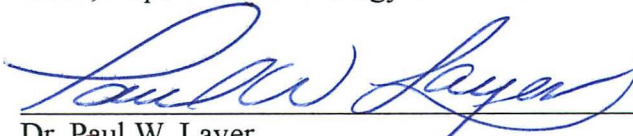


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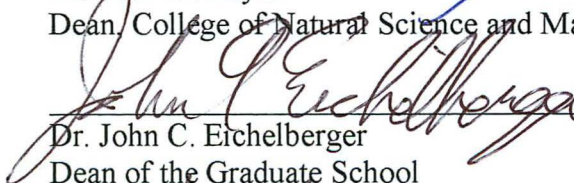


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BEHAVIOR, PHYSIOLOGY, BIOLOGICAL AGE, AND CULTURAL ROLE OF
LONG-LIVED BERING SEA SEABIRDS

A
DISSERTATION

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By

Rebecca C. Young, B.S.

Fairbanks, Alaska

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Abstract

This dissertation focuses on the intersection of behavior, physiology, and biological age. Biological age is a measure of an organism's progress through life, and it incorporates chronological age as well as the actions of environment and innate quality at the individual level. We estimate biological age using telomere length as a biomarker. Telomere degradation in relation to oxidative stress links it directly to purported proximate mechanisms of aging under the free radical theory of aging. Short telomeres, or telomere loss, have been related to ecological indicators of lowered fitness. Our work focuses on aging in the thick-billed murre (*Uria lomvia*), a long-lived seabird breeding in the Bering Sea. Seabirds exemplify the "slow-lived" paradigm; they have long lifespans, low reproductive rates, and high adult survival. First we address the relationship between chronological age and telomere length in the thick-billed murre. We found longer telomeres in chicks than in adults, and longer telomeres in adult females than in adult males. Then we examine biological age, telomere length, in relation to physiology and behavior of murre equipped with a recording device to monitor foraging behavior. Chapter two describes the physiological and reproductive investment of these murre in relation to their biological age, while chapter three addresses the habitat and prey choices made by these birds in relation to sex, biological age, and environment. Behaviorally murre remain healthy into their old ages, with physiological diving capacity similar or improved in old birds. Stress patterns demonstrate that when conditions are good, older birds are more stressed, but experience buffers their stress levels under poor conditions. The fourth chapter of this thesis deals with seabirds as part of the larger socio-ecological

system that includes the indigenous people living on the Pribilof Islands. The Priblovians value seabirds, but are members of periphery communities troubled by a poor economy and disconnected from a past that was tightly coupled to the natural world. Development requires active management by local stakeholders to reconnect with cultural and economic resources (like seabirds) and to make the communities more sustainable and resilient.

Dedication

I dedicate this dissertation to Warren and Mary Young and George and Mary Weinland.

My four grandparents have been role models, inspirations, and loving support always.

Table of Contents

	Page
Signature Page	i
Title Page	iii
Abstract	v
Dedication	vii
Table of Contents	ix
List of Figures	xv
List of Tables	xvii
List of Appendices	xix
Acknowledgements	xxi
Introduction	1
Literature Cited	6
Chapter 1 Age, sex, and telomere dynamics in a long-lived seabird with male-biased parental care	11
1.1 Abstract	11
1.2 Introduction	12
1.3 Methods	15
1.3.1 Ethics Statement	15

	Page
1.3.2 Techniques and sample collection.....	15
1.3.3 Statistics	18
1.4 Results.....	19
1.4.1 Relationships between different measures of telomere length.....	19
1.4.2 Chronological age and telomeres	19
1.4.3 Longitudinal sampling	20
1.5 Discussion.....	21
1.5.1 Comparison of telomere length technique	21
1.5.2 Sex differences in TL in the thick-billed murre	22
1.5.3 Longitudinal analysis of TRF indicates signature of local ecological conditions?.....	25
1.6 Figures	28
1.7 Tables.....	30
1.8 Literature Cited.....	32
1.9 Acknowledgements.....	38
Chapter 2: Pros and cons of old age: Biological age and sex predict behavior of a long- lived bird breeding under varying conditions	39
2.1 Abstract.....	39

	Page
2.2 Introduction.....	40
2.3 Methods	44
2.3.1 Study sites and sampling	44
2.3.2 Lab techniques.....	46
2.3.2.1 Corticosterone assay	46
2.3.2.2 Telomere restriction fragment assay	47
2.3.2.3 Stable isotope analysis	48
2.3.2.4 Diving parameters.....	48
2.3.3 Statistics	48
2.3.3.1 Body condition calculation	49
2.4 Results.....	49
2.4.1 Physiological state (Tables 2.3 and 2.5).....	49
2.4.2 Reproductive investment (Tables 2.4 and 2.5).....	51
2.5 Discussion.....	52
2.5.1 CORT and biological age.....	52
2.5.2 Colony as driver of physiology and behavior	56
2.5.3 Conclusion.....	59

	Page
2.6 Figures	60
2.7 Tables.....	65
2.8 Literature Cited	70
2.9 Appendix.....	81
2.10 Acknowledgments	86
Chapter 3 Biological age is a major driver of foraging behavior in a long-lived vertebrate.....	87
3.1 Abstract.....	87
3.2 Introduction.....	88
3.3 Methods	92
3.3.1 Study sites and sampling.....	92
3.3.2 Diving parameters and variables of interest.....	94
3.3.3 Lab techniques.....	96
3.3.3.1 Telomere restriction fragment assay.....	96
3.3.3.2 Stable isotope analysis	97
3.3.3.3 Genetic sexing.....	97
3.3.4 Statistical analyses.....	98
3.4 Results.....	99

	Page
3.4.1 Spatial variables	99
3.4.2 Temporal variables	101
3.4.3 Prey selection variables	101
3.5 Discussion	102
3.5.1 Biological aging, senescence, and experience	103
3.5.2 Conclusion	106
3.6 Figures	108
3.7 Tables	114
3.8 Literature Cited	115
3.9 Appendices	127
3.10 Acknowledgements	133
Chapter 4 Making the periphery enticing: Increased ecotourism as an option for increasing resilience of remote Alaskan communities	135
4.1 Abstract	135
4.2 Introduction	136
4.3 Methods	140
4.4 Results	141
4.4.1 Demographic results	141

	Page
4.4.2 Seabird importance (Table 4.2)	141
4.4.3 Current seabird use (Table 4.3)	143
4.4.4 Seabird knowledge (Table 4.4)	144
4.4.5 Economic outlook (Table 4.5).....	146
4.5 Discussion.....	147
4.5.1 Conclusion.....	152
4.6 Figures	153
4.7 Tables.....	154
4.8 Literature Cited	159
4.9 Acknowledgements.....	163
Conclusion	165
Major Findings.....	165
Future Research Directions.....	171
Literature Cited	175

List of Figures

	Page
Figure 1.1 Telomere loss with age and sex in thick-billed murres.	28
Figure 1.2 Longitudinal (inter-annual) percent change in telomere length of breeding thick-billed murres depends on colony, but not sex.	29
Figure 2.1: Baseline corticosterone (CORT) levels predicted by telomere length and colony. ...	60
Figure 2.2: Scaled body condition by colony and sex.	61
Figure 2.3: Trip rate by colony.	62
Figure 2.4: Colony attendance by colony and sex.	63
Figure 2.5: Experience and senescence model.	64
Figure 2.A-1: Corticosterone (CORT, log-transformed) predicted by colony and year.	83
Figure 2.A-2: Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope signatures for St. Paul (SP), St. George (SG), and Bogoslof (Bog) in 2008 and 2009.	84
Figure 3.1 The Bering Sea.	108
Figure 3.2 Diving depths.	109
Figure 3.3 Diving in darkness and daylight.	110
Figure 3.4 Time spent underwater.	111
Figure 3.5 Stable isotope signatures of breeding thick-billed murres on three colonies.	112
Figure 3.6 Nitrogen signatures by biological age.	113
Figure 4.1 Importance of seabirds by age of respondent.	153

List of Tables

	Page
Table 1.1: Sample sizes of cross-sectionally sampled birds.....	30
Table 1.2: Sample sizes and colony of origin for longitudinally sampled birds.	31
Table 2.1: Hypotheses and predictions.....	65
Table 2.2: Sample sizes and dates of logger deployment and recaptures of adult thick-billed murre breeding on three colonies in two years.	66
Table 2.3: Physiological state summary.	67
Table 2.4: Reproductive investment summary.	68
Table 2.5: Effect sizes for best models.....	69
Table 3.1 AICc weights for each response parameter and explanatory variable.....	114
Table 3.A-1 Variables and Model Building.	127
Table 3.A-2 Model output for foraging variables.....	128
Table 4.1 Demographic parameters.....	154
Table 4.2 Survey responses to questions about the importance of seabirds.	155
Table 4.3 Survey responses to statements assessing current seabird use and preferences. ...	156
Table 4.4 Survey responses to statements assessing knowledge of seabird biology and harvest regulations.	157
Tables 4.5 Survey responses to statements assessing tourism attitudes and economic outlook.	158

List of Appendices

	Page
Appendix 2.A Stress levels and stable isotopes of murres breeding on St. Paul, St. George, and Bogoslof Islands in 2008 and 2009.	81
Appendix 3.A Variables and Model Selection.	127
Appendix 3.B Discussion of TBMU Foraging behavior in relation to habitat quality (colony) and sex.....	129

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Introduction

This work focuses on the intersection of behavior, physiology, and biological age. Biological age is a concept developed most in biomedical literature. For work outside human systems, and specifically in ecology, it has been defined as, “the current position of the individual in its journey through life” (Monaghan and Haussmann 2006).

Biological age has informative power as an aging metric which incorporates chronological aging processes as well as the actions of both quality and environment at the individual level (Nakagawa et al. 2004, Dunshea et al. 2011). As variation in maximum lifespan within a species is not due solely to extrinsic mortality, it follows that the aging process varies between individuals. This variation may be due to early-life conditions, individual quality (at the geno- or phenotypic levels), prior breeding experience, and various cohort effects. Biological age incorporates these effects into a single theoretical quantity (Aviv 2002). In this thesis, I estimate biological age using telomere length as a biomarker. Telomeres are non-coding DNA repeats that cap eukaryotic chromosomes (Blackburn 1991). They degrade with cellular divisions and metabolic stressors (Haussmann and Marchetto 2010, Monaghan 2010). Their degradation in relation to oxidative stress links them directly to purported proximate mechanisms of aging under the free radical theory of aging (von Zglinicki 2002, Brandl et al. 2011). In addition, they can be elongated by the reverse transcriptase telomerase (Blackburn 2005) or via the Alternative Lengthening of Telomeres method (Grach 2011).

The use of telomeres as a physiological tool in behavioral, physiological, and ecological studies has increased dramatically in the past decade. Many of these studies

deal with telomere dynamics in non-model systems and how these patterns may be used to age individuals (Benetos et al. 2011, Kim et al. 2011, Pauli et al. 2011) or what they may imply about aging processes in species with very different life histories or growth patterns (Scott et al. 2006, Ujvari and Madsen 2009, Xu et al. 2009). Avian systems have particularly lent themselves to telomere research as birds live much longer than comparably sized mammals, despite higher metabolic rates (Holmes and Austad 1995). Birds are also a good system for telomere research because males are the homogametic sex (i.e. they have two similar sex chromosomes, instead of two different as in humans), separating some genetic and evolutionary effects on aging from other gender-specific differences (Horn et al. 2011). Avian telomeres have been found to decline with age in most species studied (Haussmann et al. 2003), but to maintain length in others, especially many long-lived seabirds, notably Leach's storm-petrel (Hall et al. 2004, Haussmann and Mauck 2008). Short telomeres or telomere loss have been related to lowered survival (Barrett et al. 2013), poor early life conditions (Geiger et al. 2012), and poor quality habitat (Angelier et al. 2013).

With their diverse life histories and aging patterns, birds make good systems for aging research and pelagic seabirds especially so. Seabirds exemplify the "slow-lived" paradigm; they have long lifespans, low reproductive rates, and high adult survival with low predation risk. Aging research on species so far removed from a fast-living life history, typical of model species, is especially relevant to wider understanding of drivers of aging mechanisms and evolutionary patterns (Holmes and Austad 1995). In this thesis, aging work has focused on the thick-billed murre (*Uria lomvia*), a long-lived

seabird breeding in the Bering Sea. Thick-billed murres (hereafter, murres) are a 1 kg alcid with high breeding densities, high wing-loading, and an obligate clutch size of one egg per year (Gaston and Jones 1998). These abundant top-predators breed under a variety of conditions in Arctic and sub-Arctic waters, allowing for inter-colony comparisons. In addition, murres have an unusual chick-rearing strategy: the chick fledges after only two weeks in the nest, when it is about one third of the adult's size. These semi-precocial chicks are accompanied to sea by the male parent who provides many additional weeks of protection and care to the flightless young. As sex differences in telomere length and loss are expected to be driven by patterns of reproductive investment, as well as genetics, size, and hormonal differences (Kyo et al. 1999, Barrett and Richardson 2011, Horn et al. 2011), this unbalance in murre offspring investment is of particular interest.

In order to use telomere length as a biological aging tool its change with age must be established. The first chapter of this thesis deals with the relationship between chronological age and telomere length in the thick-billed murre (Young et al. 2013). Telomeres were measured using three methods, two derived from Southern blotting methods and one using quantitative PCR. We found longer telomeres in chicks than in adults, and longer telomeres in adult females than in adult males.

The second and third chapters of this thesis deal with telomere length in relation to physiology and behavior of murres equipped with a recording device to monitor foraging behavior. These chapters are based on five colony-years of logged birds from three colonies which vary in their environmental conditions. St. Paul has poor population

trends and high nutritional stress. Bogoslof has escalating seabird populations and low nutritional stress. St. George is intermediate. Chapter two describes the physiological and reproductive investment of these murres in relation to their biological age, while chapter three addresses the habitat and prey choices made by these birds in relation to sex, biological age, and environment. Behaviorally murres remain healthy into their old ages, with physiological diving capacity similar or improved in old birds. Stress patterns demonstrate that when conditions are good, older birds are more stressed than young birds, likely due to the effort of maintaining behavioral output with degraded systems. However when conditions are poor, older birds are not more stressed than young birds, indicating that, when conditions call for it, experience helps balance the stress of old age.

Murres, like the other seabirds that share the cliffs, are excellent systems for studies of life history, effects of a changing environment on top predators, and behavior and physiology of long-lived species. In addition, these birds are part of the larger social-ecological system that includes the people living on Bering Sea islands. The Pribilof Island system, located in the center of the Bering Sea, is marine-dependent, with the livelihoods of both people and birds depending on the sea for weather, nutrition, and support. The fourth chapter of this thesis is the report of a survey and interviews done with members of the Pribilof Island communities, St. George and St. Paul. This survey addressed use of seabirds, importance of seabirds, and the potential of improving the local economy via seabird ecotourism. The Pribilof communities are periphery communities troubled by a poor economy, disconnected from a past that was tightly coupled to the natural world, and located distantly from centers of power and decision-

making (Young 1987, Huntington et al. 2009). Development is slow and requires active management by local stakeholders to reconnect with cultural and economic resources (e.g. seabirds) and to make the communities more sustainable and resilient (Sherwonit 1994).

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with male-biased parental care. PLoS ONE 8(9):e74931.

Chapter 1 Age, sex, and telomere dynamics in a long-lived seabird with male-biased parental care¹

1.1 Abstract

The examination of telomere dynamics is a recent technique in ecology for assessing physiological state and age-related traits from individuals of unknown age. Telomeres shorten with age in most species and are expected to reflect physiological state, reproductive investment, and chronological age. Loss of telomere length is used as an indicator of biological aging, as this detrimental deterioration is associated with lowered survival. Lifespan dimorphism and more rapid senescence in the larger, shorter-lived sex are predicted in species with sexual size dimorphism, however, little is known about the effects of behavioral dimorphism on senescence and life history traits in species with sexual monomorphism. Here we compare telomere dynamics of thick-billed murres (*Uria lomvia*), a species with male-biased parental care, in two ways: 1) cross-sectionally in birds of known-age (0-28 years) from one colony and 2) longitudinally in birds from four colonies. Telomere dynamics are compared using three measures: the telomere restriction fragment (TRF), a lower window of TRF (TOE), and qPCR. All showed age-related shortening of telomeres, but the TRF measure also indicated that adult female murres have shorter telomere length than adult males, consistent with sex-specific patterns of ageing. Adult males had longer telomeres than adult females on all colonies examined, but chick telomere length did not differ by sex. Additionally, inter-annual

¹ R. C. Young, A. S. Kitaysky, M. F. Haussmann, S. Descamps, R. A. Orben, K. H. Elliott, and A. J. Gaston. *PLoS ONE*. 8(9):e73941. 2013.

telomere changes may be related to environmental conditions; birds from a potentially low quality colony lost telomeres, while those at more hospitable colonies maintained telomere length. We conclude that sex-specific patterns of telomere loss exist in the sexually monomorphic thick-billed murre but are likely to occur between fledging and recruitment. Longer telomeres in males may be related to their homogamous sex chromosomes (ZZ) or to selection for longer life in the care-giving sex. Environmental conditions appeared to be the primary drivers of annual changes in adult birds.

1.2 Introduction

Individuals vary in their rate of senescence, measured by declines in physiological and reproductive performance [1]. Sex, with its suite of genetic, physiological, and behavioral effects, is an obvious source of this variation. Sex-specific life histories may be driven by many factors: long life in either gender can be driven by differential parental investment [2]; low growth rates [3]; and sex-specific genetic causes, including estrogen or homogamy (in mammals, females are XX and may inactivate a chromosome, this is reversed in birds: males are ZZ while females are ZW) [4]. Mammalian females usually live longer than males despite providing most offspring care. However, females also possess life-extending traits: slower growth rates, smaller adult sizes, higher estrogen, and homogamy [4], which may counterbalance the costs of high parental investment. Avian systems may help disentangle these mechanisms because the homogametic sex is the male, separating effects of parental investment from some genetic and endocrine causes (e.g. [5]). This study addresses telomere decay rates in a structurally

monomorphic seabird where parental care is provided by both sexes for the first two to four weeks and exclusively by males for one to two months post-fledging [6].

Senescence effects on survival rates or reproductive output are often catastrophic, with rapid onset shortly before death [7]. However, individual-specific deterioration of body reserves may not be well predicted by chronological age [8]. We refer to chronology-decoupled aging as biological aging and measure it with telomere length (TL). TL may reflect aging on a physiological and cellular level, as well as incorporating chronological age, and usually shows steady rates of decline instead of catastrophic loss, making it an excellent candidate for a biomarker of individual biological age [8]. TL is measured in a variety of ways in the ecological literature. The most common methods are the Southern blot-derived telomere restriction fragment (TRF) assay [9-11], smaller windows of the TRF smear [12], and quantitative PCR [8,13-14]. Here we compare the effects of age, sex, and colony on telomere length as estimated by each of those methods.

Sex-specific TL is documented in many taxa [15-16], but often in species with female-biased parental care and large sexual dimorphism in body size. When neonates do not differ in TL, such differences may be related to level of parental investment or developmental rates [3]. However, it is possible that telomeres would be more protected in the homogametic gender, which can select between two germ-line sex chromosomes [5,17], or the gender which receives more parental investment in the nest [18]. Little work has focused on systems with morphologically uniform sexes but behavioral differences in parental care.

The thick-billed murre (*Uria lomvia*) is a long-lived seabird in the Alcidae family. Like other alcids, it has slow maturation, low annual fecundity (obligate clutch of one), and high adult survival [6]. Thick-billed murres are monogamous birds which share incubation and nestling care (2-4 weeks) equally [6], and the sexes are essentially monomorphic. Nonetheless, strong behavioral dimorphism manifests in male care; males provide several months of post-fledging care to the chick, which leaves the colony at only 1/3 of adult size. Females are not associated with offspring after fledging [6]. Here we examine the relationship between chronological age and telomere length in thick-billed murres both cross-sectionally and longitudinally. Cross-sectional sampling allows for an assessment of chronological age effects on TL, but does not eliminate the effects of selective disappearance or cohort differences on the emerging patterns. However, longitudinal sampling, even in birds of unknown age, addresses the mechanisms of aging – potentially eliminating selective disappearance or cohort effects as drivers of the patterns seen in cross-sectional studies [19]. Telomere dynamics are expected to differ by gender when the sexes are very differently sized (not applicable to murres), reproductive investment differs strongly, or due to genetic and evolutionary differences in protective mechanisms. These latter two effects could drive differences in telomere losses between male and female murres. We predict that males will show faster rates of biological aging (determined by telomere attrition) due to heavier reproductive investment. This would result in adult males having lower TL than females, and a more negative slope in the cross-sectional sampling. Longitudinally, they should show higher rates of annual TL loss. Our alternative prediction is that males will have slower

telomere attrition due to the benefits of homogamy, resulting in higher TL than in females, shallower cross-sectional slope, and slower rates of loss. Lastly, since conditions affecting telomere attrition or ability of murres to regulate telomere changes may differ by colony, and murres are highly faithful to their breeding sites, we included colony as an explanatory factor in the longitudinal analysis.

1.3 Methods

1.3.1 Ethics Statement

This study was approved by the University of Alaska Fairbanks IACUC (156937-3 to A. S. Kitaysky), Canadian Wildlife Service NWRC & Ontario Region Animal Care Committee (0800AG01 to A. J. Gaston), and the Canadian Wildlife Service (NUN-SCI-08-55 to A. J. Gaston and NUN-SCI-6-01 to M. Mallory). All sampling was done under approved guidelines of these agencies. All field work was carried out under appropriate regional and federal permits. Collection at St. Paul Island (57°08'N, 170°18'W), St. George Island (56°36'N, 169°39'W), and Bogoslof Island (53°56'N, 168°02'W) was authorized by the US Fish and Wildlife Service and the Alaska Maritime National Wildlife Refuge. Collection at Coats Island (62°57'N, 82°00'W) was authorized by the Kivalliq Inuit Association, and collection at Diabasodden (78°21'N, 16°8'E) was authorized by the Governor of Svalbard (program number 361).

1.3.2 Techniques and sample collection

Currently, several methods are used to measure telomeres in the fields of ecology and evolution [20]. Thus, to model the relationship between telomeres and chronological

age, we used two assay techniques, yielding three measures of telomere length or quantity. The first technique, from which two measurements are derived, was the telomere restriction fragment assay, a modified Southern blot visualizing terminal telomere repeat densities at all molecular weights, measuring all cells, all chromosomes, and all telomere lengths. The first measure (which we call TRF) is the average telomere length in the entire smear. The second measure, derived from the same TRF smear, was the telomere optimal estimate (TOE), which measures only the lower molecular weight region of the TRF smear: our upper cut-off was 5 kb for TOE; the lower cut-off was the same as for TRF and followed Salomons et al. [10]. This measure may be more sensitive to telomere shortening, as it focuses on the shortest telomeres in the distribution [12].

TRF and TOE were calculated according to Salomons et al. [10] and Haussmann and Mauck [12]. Briefly, whole blood, stored frozen in a glycerol buffer, was extracted into agarose plugs using a kit (Chef Genomic DNA Plug Kit, Bio-Rad) and digested with a mixture of 3 U HinfI, 15 U HaeIII, and 40 U RsaI (Roche Applied Science). Plugs were separated using pulsed field gel electrophoresis (Bio-Rad ChefMapper) on a 0.8% agarose gel. Run parameters were 21 hours at 3 V/cm and 0.5-7s switch times. The buffer (0.5X TBE) was circulated and kept at 14 °C. Gels were hybridized at 37 °C with 3,000,000 cpm of the telomere-specific radio-labeled oligo (CCCTAA)₄. After hybridization, rinsing and visualization followed Haussmann and Mauck [12]. Samples were analyzed in random order on four gels, and control samples were run twice in each gel to determine inter- (12.8% - TRF; 3.2% - TOE) and intra-assay variability (< 5% per gel).

The second technique, and third measure, quantitative PCR (qPCR) produced a ratio of the quantity of telomeric DNA to a reference gene (T/S ratio), but did not provide lengths. This technique unavoidably includes interstitial repeats (those internal to the chromosome and unaffected by aging). Protocols were adapted from Cawthon [21], reference gene primers were from Criscuolo et al. [14], and telomere primers were from Foote [22]. Samples were run on one plate for telomere primers and another for the reference gene primers, and in each plate samples were in triplicate. Samples where the coefficient of variation was $> 10\%$ were excluded from analysis. Efficiencies of amplification were 100% and 108% for the reference gene and for telomeres, respectively.

Known-age individuals (Table 1.1) were sampled on Coats Island, Nunavut, Canada. Adults were not sampled longitudinally on this colony. Chicks (< 14 days old) were sampled from several colonies: Coats Island; Diabasodden on Svalbard; Bogoslof Island, in the Aleutian Chain; and St. Paul Island in the central Bering Sea. Sample sizes between analysis methods differ; we prioritized the TRF assay, of which TOE is a derived value, which did not always leave sufficient sample for a concentrated high-quality DNA extract for qPCR. Longitudinal murre sampling (Table 1.2) was carried out on Diabasodden, Bogoslof Island, St. Paul Island, and St. George Island (also central Bering Sea). Birds were captured during the breeding season: late July and early August. Recaptures were done in the following breeding season. Most birds ($n = 67$) were recaptured after one year. Two individuals were recaptured after two years, and their change in telomere length was divided in half to reflect changes in a “per year” format.

Blood (0.2 – 1 mL) was collected from the brachial vein. Sampling was not lethal and handling time minimized. Longitudinal sampling was analyzed using TRF and TOE and the changes to these measures (Δ TRF and Δ TOE); there were not enough red blood cells remaining to conduct qPCR analysis. Birds were genetically sexed following Griffiths et al. [23].

1.3.3 Statistics

All statistics were done in the Program R [24, vs. 2.12.2]. Results are presented as mean and 95% confidence intervals. Where necessary, variables were transformed to meet parametric assumptions. The contribution of chronological age and sex to each of three TL measures (TRF, TOE, and qPCR) was modeled with ANCOVA, which included age, sex, and the age x sex interaction term. Despite the appearance of more variability in male telomere lengths (Figure 1.1), variability by gender was not significantly different (TRF: Bartlett's $K^2 = 0.0077$, $p = 0.93$; TOE: Bartlett's $K^2 = 0.64$, $p = 0.43$; and qPCR: Bartlett's $K^2 = 0.36$, $p = 0.54$). Most telomeres are lost during periods of rapid growth, in seabirds between hatching and recruitment [25], therefore the predicted shape of the relationship with age is non-linear. To allow linear modeling, age was transformed as $\log(\text{age}+1)$. This transformation allowed for inclusion of chicks, which otherwise would be excluded as $\log(0)$. For longitudinal sampling, which was only available for adults, simple two-way ANOVAs were used to assess the effect of sex and colony on TRF, TOE, and the percent change in TRF and TOE between 2 years in the same individual. When comparing telomere lengths for longitudinally sampled birds, multiple samples

exist; to control for repeated sampling, a mixed model was used with sex and colony as fixed effects and bird identity as a random effect.

1.4 Results

1.4.1 Relationships between different measures of telomere length

Quantitative PCR correlations with TRF and TOE approached significance (TRF and qPCR: Pearson's $r = 0.29$, $t = 1.88$, $p = 0.068$; TOE and qPCR, Pearson's $r = 0.25$, $t = 1.60$, $p = 0.12$). TRF and TOE were significantly correlated (Pearson's $r = 0.30$, $t = 2.36$, $p = 0.022$).

1.4.2 Chronological age and telomeres

Chicks came from different colonies, but colony never affected chick TL, so we have pooled them (TRF: $F_{3,9} = 1.92$, $p = 0.20$; TOE: $F_{3,9} = 2.86$, $p = 0.097$; qPCR: $F_{2,3} = 2.10$, $p = 0.27$). The model for average terminal TL for all cells (TRF) showed significant effects of age ($\beta = -765 \text{ bp} \cdot \text{year}^{-1}$, $F_{1,56} = 5.16$, $p = 0.027$) and sex ($\beta_{\text{males}} = 8632 \text{ bp}$, $\beta_{\text{females}} = 8183 \text{ bp}$, $F_{1,56} = 5.50$, $p = 0.023$), but no interaction ($F_{1,56} = 0.212$, $p = 0.65$). TL decreased with chronological age in both sexes, but males had longer TL (Figure 1.1A). This sex effect was driven by the large difference in adults; chicks did not differ in their TL by sex ($t = -0.208$, $df = 11$, $p = 0.76$), but adult males had higher TRF ($t = -2.62$, $df = 45$, $p = 0.012$) than females. Results for the lower, age-sensitive window (TOE, Figure 1.1B) were less complex; age had a significant effect ($\beta = -202 \text{ bp} \cdot \text{year}^{-1}$, $F_{1,56} = 5.92$, $p = 0.018$), but sex and the age x sex interaction did not (both $p > 0.5$). The qPCR model

also showed a significant age effect (Figure 1.1C, $\beta = -78.6 \text{ T/S} \cdot \text{year}^{-1}$, $F_{1,37} = 5.63$, $p = 0.023$), a lack of the effect of sex, and no interaction (both $p > 0.2$).

1.4.3 Longitudinal sampling

For the four colonies sampled longitudinally, colony ($F_{3,61} = 4.41$, $p = 0.0071$) and sex ($F_{1,61} = 5.34$, $p = 0.024$) both affected TRF, but there was no interaction ($F_{3,61} = 1.58$, $p = 0.20$). Bogoslof had the longest TL, and the other colonies were shorter (Bogoslof: 7805 [CI: 7555-8055] bp; St. George: 7268 [6865-7672] bp; St. Paul: 7044 [6765-7322] bp; Diabasodden: 6865 [6590-7140] bp). Males again had significantly longer TRF than females (males: 7417 [7168-7666] bp; females: 6925 [6752-7098] bp), providing further support to the pattern of higher TRF in males which was also found in the cross-sectional sampling (above). TOE showed a weak effect of colony ($F_{3,61} = 2.87$, $p = 0.044$), an effect of sex ($F_{1,61} = 5.04$, $p = 0.028$), and a trend for an interaction between the two ($F_{3,61} = 2.56$, $p = 0.064$). Interestingly, females had slightly longer TOE than males (males: 3520 [3468-3571] bp, females: 3609 [3567-3652]), but the difference is likely not biologically significant. When comparing the change in TL from the first year of sampling to the second (ΔTRF), there was a strong effect of colony on ΔTRF (Figure 1.2; $F_{3,61} = 4.82$, $p = 0.0044$), but no sex effect or interaction (both $p > 0.35$). Birds on Diabasodden lost telomeres, while other birds maintained or slightly elongated theirs (Figure 1.2). This pattern was driven by the loss of telomeres in male Diabasodden birds (Figure 1.2): Tukey's post-hoc comparisons showed that most losses or gains did not differ, however, males on Diabasodden had a significantly lower change than males on St. George ($p = 0.047$) and nearly significantly lower than St. Paul ($p = 0.075$). ΔTOE

showed no effect of sex ($F_{1,61} = 2.17$, $p = 0.14$), colony ($F_{3,61} = 0.722$, $p = 0.54$), or the interaction ($F_{3,61} = 1.09$, $p = 0.36$).

1.5 Discussion

1.5.1 Comparison of telomere length technique

This study compared three measures of telomere length or quantity: TRF, TOE, and qPCR. Each parameter quantifies a different subset of telomeric DNA. TRF measures all terminal telomeres; TOE measures all terminal telomeres in a lower window of the smear, and qPCR yields a measure of all terminal and interstitial telomeric DNA relative to a single-copy reference gene. As such, they provide slightly different information on changes in telomere quantities in relation to age and sex of individuals. Each technique showed a significant effect of chronological age on the length of telomeres. However, TRF also showed an effect of sex (Figure 1.1A). The sexes do not differ when examining only the shorter telomeres (TOE) or when including interstitial repeats (qPCR). Thus, it appears that differences between the sexes may be stronger for long telomeres, which are excluded in the TOE analysis and overwhelmed by the sexually similar interstitial signal in qPCR. TOE is valued for its sensitivity to aging, but in our analysis results were comparable, and including the upper portion of the smear may allow analysis of important factors (e.g. sex) to which TOE did not respond in our analysis.

Reassuringly, qPCR yielded similar results to the TRF and TOE measures of telomere length. Its output was correlated with both TRF and TOE, but its detection of

sex effects in conjunction with age may have been diluted by the presence of interstitial repeats [26]. This may also be responsible for the lower correlation between the Southern blot-derived measures, which do not measure interstitial repeats, and qPCR, which does, than have been reported elsewhere [e.g. 14]. It is not uncommon for TRF protocols to denature the DNA before blotting to membrane, which does not occur in our protocol, as we hybridize in the gel itself. Denaturing the DNA allows probing of interstitial repeats as well as terminal repeats, and will increase the correlation between qPCR and TRF measurements. Differences in qPCR output could also be attributable to lower power, due to our smaller qPCR sample size.

1.5.2 Sex differences in TL in the thick-billed murre

This study presents evidence for sex-specific dynamics of biological aging in a species with male-biased parental care. All measures showed a significant decline in telomeres with chronological age (Figure 1.1), and the measure of all terminal telomeres (TRF) also was sensitive to an effect of sex, both in the cross-sectional and in the longitudinal sample. Most telomere length is lost from chick to age four (the youngest known-age adult in our sample), and adult telomere length is not strongly driven by chronological age (when chicks are excluded from the analysis, there is no effect of age on telomere length). Lower TL for adult females, found in both the cross-sectional and longitudinal analyses, coupled with no differences in telomere rates of change, implies a larger loss before recruitment in this sex. Good candidates for explaining the variation in TL which remains after accounting for chronological age and sex include hatch-year

conditions, physiological stress, and reproductive history [27-28]; such effects on aging would further support the concept of chronologically-independent biological age.

The shorter TL of female murres may have several explanations. The first of these non-mutually exclusive explanations is that inflexible female investment results in a “faster-living” life history, according to the theory of disposable soma. This would result in faster biological aging of females, despite the costly male investment in post-fledging care of young. Females bear high pre-fledging costs, consisting of egg production and post-fledging nest defense [6,29-30]. In addition the metabolic and physiological stress associated with these activities produces oxidative stress, which is known to negatively affect TL [31-32]. The female’s investment is primarily early in the reproductive bout, while male reproductive costs peak post-fledging. If reproduction fails prior to fledging, the female has invested more than the male. Since murre laying and hatching success are relatively high and constant from year to year [33], a female’s reproductive investment is then insensitive to environmental changes; it is constant as long as the egg hatches, but regardless of fledging success. Male investment would then be highest when it has the most payoff and lowest in poor years when conditions do not allow successful reproduction. Common murres (*Uria aalge*), sister species to the thick-billed murre, show more rapid female senescence and male-biased parental care patterns; this work predicts faster female senescence as the price of high reproductive investment and is consistent with the disposable soma theory [34-35]. The less environmentally sensitive (“risk-prone”) female strategy may reduce survival and result in higher mortality. Lowered survival prospects would select females for a “faster-track” life history

involving less somatic investment, including telomere maintenance. If telomere length reflects the evolutionary cost of cumulative reproductive investments [36], then this could explain why females' telomeres are shorter than those of males, despite occurring primarily before first reproduction.

Other potential explanations for shorter adult female TL is that males with short TL are selectively removed from the population before breeding, however there is no empirical evidence of differential selective forces acting on juvenile murre. Another explanation for short female TL is that murre parents invest more highly in their male offspring. Seabird parents are often willing to invest more energy into male offspring, because the difference between high and low quality males in terms of future reproductive value is much greater than that between high and low quality female offspring [37]. In the common murre, parents provisioning male chicks bring back more food and lose more mass than those raising female chicks [18]. Access to fewer resources in early life could increase female physiological stress levels, resulting in increased loss of telomere lengths in this sex, despite the similar lengths at the chick stage.

For thick-billed murre the sex which provides more long-term parental care is the one with slower telomere loss. This is also true in most mammalian taxa, where females provide most of the offspring care and also have longer lifespans. Males senesce quickly when there is large sexual dimorphism or high intra-sexual competition for mates [38], and long female post-reproductive lifespans have been attributed to kin selection and lower intra-sexual competition [39]. Neither of these explanations fit the monomorphic

monogamous murre. In addition, female mammals have the benefits of life-extending estrogen [40] and smaller female body size effects, and again neither of these factors can explain the evidence for faster biological aging in female murres. In both mammals and murres, direct parental care by the homogametic gender (females in mammals and males in birds) is associated with slower aging [4]. However, in southern giant petrels, females invest more than males in reproduction, but still senesce more slowly [41], lending support for the idea that parental care also plays a role in driving longevity. Selection for longevity in primary care-givers could result in mechanisms maintaining male TL which are not present in females. Among the Alcidae seabird family the pattern of extended paternal care is found only in thick-billed murres and their close relatives, other bird taxa show varying male investment strategies, including complete sex-role reversal (some shorebirds) and heavy male investment (e.g. some penguins). Furthermore, sex-specific telomere loss rates have not been found in other monomorphic avian species with equal or female-biased parental care [15,27]. A phylogenetically-controlled inter-species comparison is needed to determine if the care-giving gender is longer-lived than the other and whether this trait is adaptive. Further work should attempt to link potential mechanisms to this phenomenon.

1.5.3 Longitudinal analysis of TRF indicates signature of local ecological conditions?

Longitudinal change in TRF showed a strong colony effect. On Diabasodden, a colony with strong negative population trends [42], we see an average loss of telomeres in males (Figure 1.2). The other colonies did not statistically gain or lose, but trended towards slight increases in telomere length, although variability is large. Bogoslof, a

colony with evidence for high food availability and increasing seabird populations [43-44], showed the most evidence for telomere length increases, and also the longest telomere lengths. St. Paul and St. George are colonies where populations are relatively stable yet nutritional stress is often high [33]; on these colonies birds maintained, but did not significantly gain or lose, TL. Based on these findings, longitudinal changes in telomeres appear to be related to colony conditions: conditions leading to low stress and positive population trends may also allow birds to elongate telomeres over a one year timeframe, but certainly do not appear to result in losses; poor conditions result in telomere deterioration, and moderate conditions lead to maintenance. Foraging conditions are linked to population trends in the Bering Sea system [45], and presumably those in the Atlantic as well, providing a demographic link between biological aging and foraging conditions. It has been previously demonstrated that early-life conditions can strongly affect telomere loss rate [25] and lifespan [46], and current habitat conditions can also affect telomere loss rates and survival in adults [47]. Telomere elongation is a more unusual finding [but see 36,48]. Maintenance of telomere length over long time periods has been demonstrated in Leach's storm-petrel [19], likely due to the actions of the telomere-lengthening enzyme telomerase [19,49], which is the likely mechanism here as well.

In conclusion, the three methods of telomere measurement all demonstrated a significant loss with age. However, TRF also indicated a sex effect: that as adults, male thick-billed murre have longer telomere lengths than females. Chicks do not differ in their lengths by sex, but as expected, have longer telomeres than adults. Thus, sex-

specific patterns of telomere loss most-likely occur in the thick-billed murre between fledging and recruitment. Unlike mammals, in murre males have longer telomeres than females, and also provide the majority of parental care. Their longer telomeres may be related to their homogamous sex chromosomes or to selection for long life in the caregiving sex. Lastly, longitudinal sampling of adults on four colonies indicates that annual changes in telomere length may be related to conditions at the colony, implying that telomere change could act as a signal of physiological changes effected by ecological conditions.

1.6 Figures

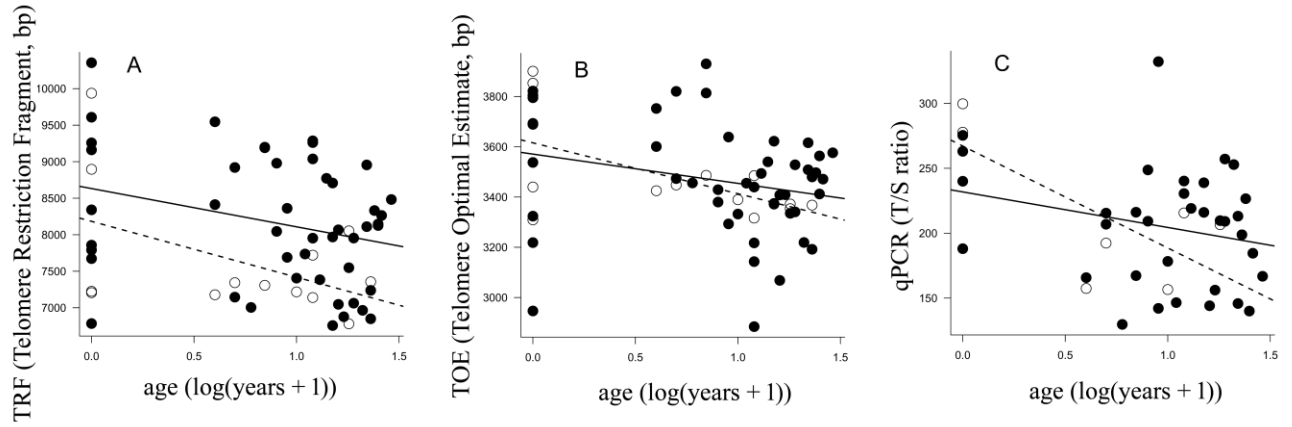


Figure 1.1: Telomere loss with age and sex in thick-billed murres. Telomere length is measured as TRF (A), TOE (B), and qPCR (C). Males are closed circles and solid lines. Females are open circles and dashed lines.

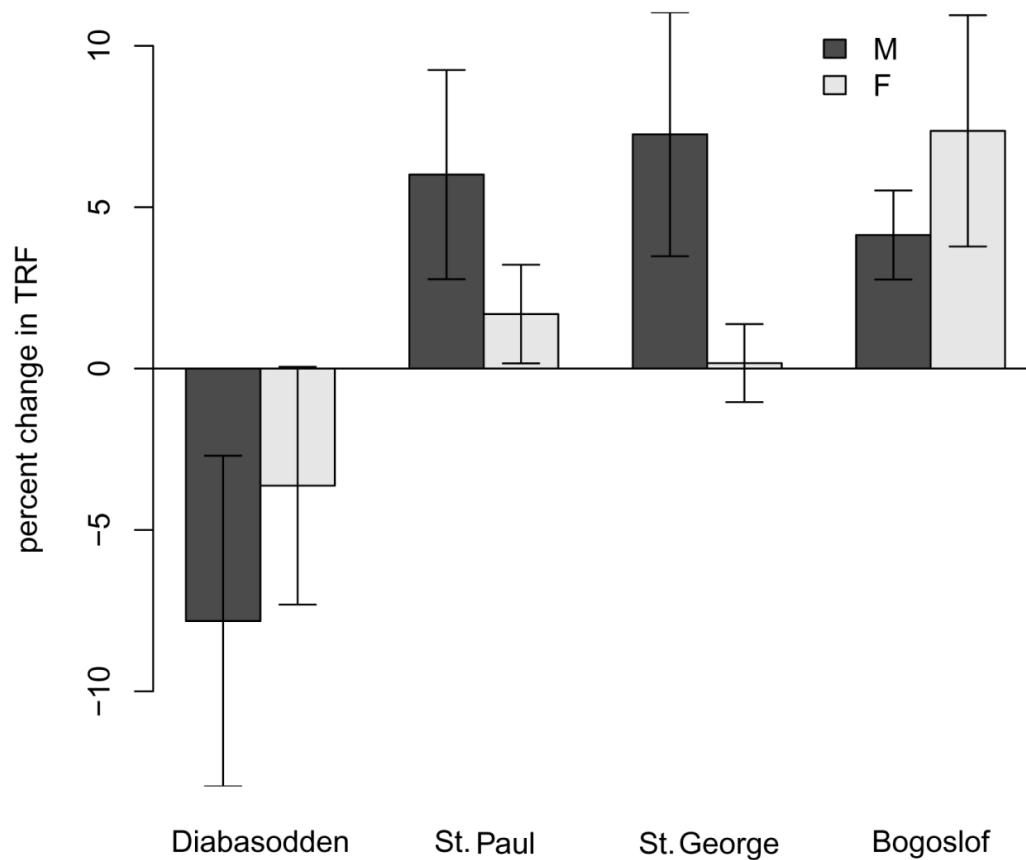


Figure 1.2: Longitudinal (inter-annual) percent change in telomere length of breeding thick-billed murres depends on colony, but not sex. Diabasodden males lost telomere length, compared to St. Paul or St. George males; all other colonies did not show changes statistically different from zero. At no colony were the differences between the sexes significant. Diabasodden has the poorest conditions and negative population trends and is the only colony where loss occurred. Changes are over one year, and are presented as mean \pm 95% confidence interval.

1.7 Tables

Table 1.1: Sample sizes of cross-sectionally sampled birds. All adults were sampled on Coats Is. while chicks came from four colonies (see Methods for details).

Technique		TRF & TOE	qPCR
Adults	Males	38	30
	Females	9	5
Chicks	Males	9	4
	Females	4	2
All Ages	Both Sexes	60	41

Table 1.2: Sample sizes and colony of origin for longitudinally sampled birds. All

birds were breeding adults of unknown chronological ages.

Colony	Bogoslof	St. George	St. Paul	Diabasodden	All Colonies
Males	8	9	10	10	37
Females	6	4	11	11	32
Total	14	13	21	21	69

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Chapter 2: Pros and cons of old age: Biological age and sex predict behavior of a long-lived bird breeding under varying conditions¹

2.1 Abstract

Life history theory's terminal investment hypothesis predicts that in long-lived species older individuals should invest more in current reproduction than young ones. However empirical evidence is conflicting; the senescence concept predicts that reproductive output will decline with age. The concept of biological age incorporates inter-individual variation to assign individuals as "older" or "younger" based on their rate of systems deterioration, rather than time since birth or until death. In this study, we evaluated the senescence and terminal investment hypotheses by addressing the effects of biological age, proxied by telomere length, on the physiology and parental investment of chick-rearing thick-billed murres (*Uria lomvia*) breeding on three Bering Sea colonies in two years. Physiological condition was assessed with nutritional stress levels and scaled body condition, while parental investment was colony attendance and the rate of chick provisioning. Older birds showed higher stress than young birds (evidence for senescence) on a good-quality colony, while they showed comparable or lower stress than young birds on a poor-quality colony, indicating potential terminal investment. Evidence in support of both hypotheses, in conjunction with the gradient of colony conditions, led to our "senescence and experience conceptual model." Biological aging patterns may be environmentally linked, and can manifest themselves unexpectedly (e.g.

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experience providing benefits most noticeably under the worst conditions). Under the challenging conditions engendered by a changing climate, experience may be necessary to buffer colonies from immediate costs while transitioning to new foraging conditions.

2.2 Introduction

Life history theory's terminal investment hypothesis predicts that in long-lived species older individuals should invest more in current reproduction than young ones (Curio 1983, Wingfield and Sapolsky 2003, Velando et al. 2006). However, empirical evidence is conflicting, confounded by individual quality, variable environments, and other factors (Hirshfield and Tinkle 1975, Clutton-Brock 1984). Residual lifespan is a promising measurement, as terminal investment is likely more dependent on time until death rather than time since birth (Reed et al. 2008). Yet residual lifespan is difficult to measure, requiring long datasets that follow marked individuals until death from a known cause. Biomarkers predicting residual lifespan or biological age may be more informative, especially in age-unknown populations (Holmes and Martin 2009). The concept of biological age incorporates inter-individual variation to assign individuals as "older" or "younger" based on their rate of systems deterioration, rather than time since birth or until death (Alviggi et al. 2009).

In this study, we addressed the effects of biological age, proxied by telomere length, on the physiology and parental investment of chick-rearing thick-billed murres (*Uria lomvia*, Linnaeus, hereafter murres) breeding on three Bering Sea colonies in two years. Telomeres are non-coding DNA caps on eukaryotic chromosomes which degrade

with cellular division (the end replication problem) and cellular stress (Haussmann and Marchetto 2010, Monaghan 2010). The predictable loss of telomeres with cellular division and their further deterioration from oxidative damage has resulted in their utility as a biological age indicator (von Zglinicki 2002, Richter and von Zglinicki 2007). Telomere length is beneficial when longer, reflects replicative history, stress, and damage when it is shortened, and acts as a link between physiological aging (accumulated damage to tissues) and organism health (Monaghan 2010, Barrett et al. 2013). Telomere length has been shown to have a negative relationship with chronological age, or conversely a positive relationship with physiological condition, in mammals (Cherif et al. 2003, Pauli et al. 2011), reptiles (Bronikowski 2008, Olsson et al. 2010), fish (Hatakeyama et al. 2008, Anchelin et al. 2011), and birds (Haussmann et al. 2003, Kim et al. 2011); in our focal species chronological age explains ~30% of variability in telomere length (Young et al. 2013). We use telomeres as a biological age marker, where the age of an “older” bird is a combination of chronological years and the cumulative effects of stress. Previous work has also indicated that males and females may differ in their biological aging processes, so we include sex as a factor in our analyses (Reed et al. 2008, Young et al. 2013).

Murre physiological condition was assessed with baseline corticosterone (CORT) levels and scaled body condition. CORT is the primary avian glucocorticoid, and in seabirds, is associated with variations in food availability (Kitaysky et al. 2007, Kitaysky et al. 2010). As they are a response to limited resources, elevated CORT secretion promotes mobilization of endogenous energy reserves (potential decrease in body

condition), food-seeking behaviors, and in chronic cases, decreased reproductive investment or even reproductive abandonment in favor of self-preservation (Kitaysky et al. 2001, Wingfield and Sapolsky 2003, Angelier et al. 2007a, Davies et al. 2013). This relationship in a long-lived bird makes it ideal for life history studies. Parental investment was measured by proportion of time spent attending the colony and the rate of chick provisioning (number of foraging trips per day). Murres carry only a single fish in the bill at once and seldom return from a foraging trip without a prey item for the chick (Gaston and Jones 1998). The nest site is a cliff edge with no nest platform or cup built, so parental attendance is crucial in preventing chick loss through exposure, predation, or accidental death. Attendance and provisioning rate trade off against each other (a parent who returns to feed the chick more is likely to attend the nest less), and increasing both must come at the expense of self-maintenance and resting activities in the time budget (Harding et al. 2007).

Biological aging incorporates innate geno- and phenotypic changes in somatic function, but also the effect of the environment. In long-lived seabirds, reproductive success can be strongly affected by habitat, including relative latitude (Laidre et al. 2008), proximity to productive oceanic resources (Paredes et al. 2012), regional climate indices (Smith and Gaston 2012), and food web composition (Karnovsky et al. 2011, Dorresteijn et al. 2012). The predicted age-related changes in investment and physiology predict that biologically older birds may differ from younger birds, but also that aging patterns may be dependent on environmental conditions at the breeding colonies and surrounding foraging areas.

To capture variation in environmental conditions, we sampled birds from three colonies: St. Paul Island and St. George Island (the two major islands of the Pribilofs), and Bogoslof Island in the eastern Aleutian Archipelago. These islands differ in dominant physical processes governing population size and trajectories (Hunt and Byrd 1999, Byrd et al. 2008) and the composition and structure of food webs (Jahncke et al. 2008, Dorresteijn et al. 2012, Harding et al. 2013). Physical processes and food web composition in this system affect food availability to the birds at the colony (Dorresteijn et al. 2012), which in turn affects population trends (Kitaysky et al. 2007, Kitaysky et al. 2010).

Biological age may affect physiology and investment in two non-exclusive manners. If senescence impairs older birds' foraging ability, their stress levels may increase and body condition decrease (Lecompte et al. 2010; Table 2.1, first hypothesis). However, older birds also have more foraging experience and may be able to mitigate poor conditions through more efficient foraging (Rutz et al. 2006; Table 2.1, second hypothesis). In addition, decreased residual lifespan would predict that older birds will invest more heavily in their current offspring than younger birds, consistent with the terminal investment hypothesis (Angelier et al. 2007b, Heidinger et al. 2010). The first hypothesis ("detrimental") is analogous to senescence (Peron et al. 2010), while the second comprises the predictions of both constraint and restraint (Curio 1983, Wiebe and Martin 1998, Limmer and Becker 2009), without attempt to differentiate.

2.3 Methods

2.3.1 Study sites and sampling

Chick-rearing adult thick-billed murres were sampled on three colonies in two years, for a total of five colony-years. The islands fall on a rough north-to-south gradient. The Pribilof Islands: St. Paul Island (57°08'N, 170°18'W) and St. George Island (56°36'N, 169°39'W), are located in the central Bering Sea along the shelf-edge, and were sampled in 2008 and 2009 (Table 2.2). They are separated by about 88 km, with St. George Island located to the south and closer to the productive shelf edge. Bogoslof Island (53°56'N, 168°02'W) is located in oceanic waters in the eastern Aleutian Archipelago. The waters of the Bering Sea shelf-break and the mixing water masses of the North Pacific and Bering Sea are highly productive oceanic environments (Harding et al. 2013). CORT and stable isotope values were collected in both years on all islands, but on Bogoslof effects of age and sex on focal parameters (via TDR deployments) were measured only in 2009 (Table 2.2). These islands work to compare different environmental conditions; both St. Paul and St. George saw dramatic population crashes during a region-wide regime change in the 1970's (Hare and Mantua 2000), and St. Paul continues to decline, although St. George is seeing moderate recovery (Byrd et al. 2008). Current thick-billed murre populations are about 57,000 on St. Paul, 1,500,000 on St. George, and 33,000 on Bogoslof – differences ranging across almost two orders of magnitude (Renner and Williams 2005, Byrd et al. 2008, Dragoo et al. 2012, Harding et al. 2013). Productivity is similar between the colonies (Dragoo et al. 2012, Harding et al. 2013), so the observed changes in populations must be influenced by emigration,

dispersal, survival, and recruitment rates (Schmutz and Byrd 2004), likely driven by dominant environmental conditions. The post-1970's patterns of resource distribution and population trends indicate that these islands experience consistent environmental quality variation and can therefore be characterized as follows: Bogoslof is a high-quality colony in the consistently productive oceanic waters near Aleutian passes and the Pribilofs benefit from being near the extremely productive Bering Sea Green Belt, associated with the shelf break which marks a change from relatively shallow continental shelf waters to deeper oceanic ones, but this effect is more pronounced at St. George, which is closer to the shelf break (Harding et al. 2013). Furthermore, both in long-term studies (Hare and Mantua 2000) and in birds sampled in our study years (Appendix 2.A), measures of stress and body condition confirm poor conditions on St. Paul (relatively far from the shelf break), good conditions on Bogoslof (highly productive oceanic waters close to the island), and intermediate conditions on St. George (nearer the shelf break than St. Paul) during our study period. Good conditions were represented by lower nutritional stress (CORT) and higher body condition. A comparison of the stress and stable isotopes of this larger sample indicates different food webs and prey sources for each colony and supports a stress gradient from St. Paul (highest), to St. George (middling values), to Bogoslof (low stress).

Chick-rearing murres were captured at their nests using noose poles. Birds were targeted when their chicks were approximately 7-10 days old (large enough to be left alone during logger deployment, and small enough that they would not fledge before retrieval); dates of capture are found in Table 2.2. At first capture, birds were weighed to

the nearest 5 g and banded for individual identification. Blood sampling was completed within three minutes of capture for hormone analysis, stable isotope measurements, and genetic sexing. Blood was drawn from the brachial vein, separated, and plasma (for hormone analysis) and red blood cells (for gender determination and stable isotopes) were frozen and stored separately. Since murrelets are monomorphic, sexing was done molecularly using primers and protocols described in Griffiths et al. (1998). Blood for telomere analysis was preserved in a 2% EDTA buffer, transferred to a glycerol storage buffer, and frozen for shipment to the laboratory. Temperature-depth recorders (TDRs, Cefas G5, Cefas Technologies) were attached to the keel feathers with Tesa tape (Tesa, Charlotte, NC, Ito et al. 2010). Weight of deployment package was ~1.5 g, less than one percent of bird body mass. TDRs recorded time, pressure, and temperature every two seconds. The majority of birds were recaptured after three days: deployment length = 73.1 ± 3.7 h (22 – 220 h), to retrieve TDRs. Skeletal measurements for body condition (lengths of head and bill, tarsus, and wing) were also taken at second capture.

2.3.2 Lab techniques

2.3.2.1 Corticosterone assay

Total corticosterone (free and bound fractions) was measured according to established protocols (Benowitz-Fredericks et al. 2008) at the University of Alaska Fairbanks. Briefly, for each sample, 20 μ l of plasma was equilibrated with 2000 cpm of tritiated corticosterone and then extracted with 4 ml of re-distilled dichloromethane. After extraction, recoveries (percent tritiated hormone recovered from each individual sample) were used to correct final values. Samples were reconstituted in PBSG buffer and

combined with antibody and radiolabel in a radioimmunoassay (Wingfield and Farner 1975, Wingfield et al. 1991). Dextran-coated charcoal was used to separate antibody-bound hormone from unbound hormone. Inter- and intra-assay CV's were less than 4% and 2%, respectively.

2.3.2.2 Telomere restriction fragment assay

Telomeres were measured using the telomere restriction fragment (TRF) assay, according to Haussmann and Mauck (2007). Briefly, whole blood, stored frozen in a glycerol buffer, was extracted into agarose plugs using the Chef Genomic DNA Plug Kit (Bio-Rad, Hercules, CA) and digested with a mixture of 3 U HinfI, 15 U HaeIII, and 40 U RsaI (Roche Applied Science, Indianapolis, IN). DNA was separated using pulsed field gel electrophoresis (PFGE) on a 0.8% agarose gel. Run parameters were 21 hours at 3 V/cm and 0.5-7 s switch times. Buffer (0.5X TBE) was circulated and kept at 14 °C. Hybridization was at 37 °C with 3,000,000 cpm of the telomere-specific radio-labeled oligo (CCCTAA)₄. After hybridization, rinsing and visualization followed Haussmann and Mauck (2007). Samples were analyzed in random order on four gels with two control samples per gel to determine inter- (10.9%) and intra-assay variability (1.42%).

Telomere length values were calculated from gel images following Salomons et al. (2009). The shortest telomeres in a cell are the drivers of cellular senescence (Hemann et al. 2001, Zou et al. 2004), and it is believed they are more sensitive to aging in whole organisms as well (Haussmann and Mauck 2007, Smith et al. 2011). Following Haussmann and Mauck's (2007) identification of the optimal analysis window, we have analyzed the TRF smear from 5 kb to the bottom of the gel.

2.3.2.3 Stable isotope analysis

Sub-samples of red blood cells were freeze-dried and analyzed with continuous flow isotope ratio mass spectrometry (CF-IRMS) using a Costech Elemental Analyzer (Model ECS 4010, Valencia, CA), a Thermo Finnigan MAT ConFlo III interface (San Jose, CA), and a Delta Plus IRMS (Asheville, NC) at the Alaska Stable Isotope Facilities at the University of Alaska Fairbanks (Williams et al. 2007). Isotope results are presented in δ notation according to:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}} - 1)] \text{‰}$$

where X is ^{13}C or ^{15}N and R is the ratio of heavy to light isotope ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). The standard for carbon was PDB belemnite; and for nitrogen, atmospheric N_2 . Measurement precision (SD) was $\pm 0.13\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.16\text{‰}$ for $\delta^{15}\text{N}$.

2.3.2.4 Diving parameters

TDR data were extracted following Ito et al. (2010). Attendance was calculated as the proportion of total deployment time which the bird spent at the colony. Trip rate was the number of trips per day, calculated as the number of complete foraging trips performed during deployment divided by the total deployment time in days.

2.3.3 Statistics

Statistical analyses were performed using the program R (R Development Core Team 2011, v. 2.12.2). Model selection for each analysis was done using AIC_c for small sample sizes. Statistics are reported for the best model and as mean \pm standard error,

unless otherwise noted. Parameter weights were calculated by summing the model weights of the all models that included the parameter.

2.3.3.1 Body condition calculation

Body size was calculated using a principal components analysis, performed on measures of head and bill length, tarsus, and wing length. The first principal component explained 41.9% of the variance. Next we performed a linear regression where body mass depended upon first principal component. The residuals of this equation can be seen as a measure of body condition, as positive residuals indicate larger than expected size and vice versa. A scaled body condition was calculated as the residuals divided by the fitted values, standardizing the response (e.g. 5% larger than expected).

2.4 Results

Physiological and reproductive investment variables were modeled with linear mixed models using the nlme package in R (Pinheiro et al. 2011). Telomere length, sex, colony, and Julian date (of deployment) were fixed effects, and year was a random effect. CORT titers and trip rate were log-transformed to meet parametric assumptions.

2.4.1 Physiological state (Tables 2.3 and 2.5)

Physiological condition was assessed with baseline CORT levels and body condition at deployment. CORT results on a colony-wide sampling indicate that the colonies vary in their nutritional stress exposure (Appendix 2.A). Colony-wide patterns were the same as those found in our smaller analysis of birds which had data loggers attached for this study; where deployment CORT was best predicted by the interaction of

telomere length (TL) and colony (Fig. 2.1, $F_{2,93} = 6.02$, $p = 0.0035$). Older birds (those with shorter TL) had higher CORT on Bogoslof, lower CORT on St. Paul, and there was no relationship with age on St. George (Fig. 2.1). Although sex and Julian date also appeared in models with $\Delta AIC_c < 2$, neither was significant ($p > 0.26$). The parameters of TL, colony, and their interaction each had a model weight greater than 0.90, indicating strong explanatory power.

Body condition was best explained by colony ($F_{2,89} = 8.14$, $p < 0.001$) and the interaction of sex and Julian date ($F_{1,89} = 5.74$, $p = 0.019$). Body condition was significantly higher on St. Paul compared to St. George and Bogoslof (Fig. 2.2; Tukey post-hoc comparisons: St. Paul-St. George: $p = 0.0084$, St. Paul – Bogoslof: $p = 0.0025$, St. George-Bogoslof: $p = 0.71$). This pattern is partially elaborated in the colony:sex interaction trend, which appeared in the model with the second lowest AIC_c (Body Condition Model 2; $F_{2,87} = 2.90$, $p = 0.060$). This indicates that the high body condition on St. Paul is driven by high male condition; St. Paul males have higher condition than St. Paul females ($F_{1,33} = 8.50$, $p = 0.0063$) and higher than St. George and Bogoslof males (Tukey post-hoc comparisons: $p < 0.01$). Females do not differ between islands (Tukey post-hoc comparison, all $p > 0.27$), and the sexes do not differ on St. George and Bogoslof (both $p > 0.59$). The top body condition model also included the interaction of sex and Julian date, which showed that females sampled later in the season were in lower condition ($F_{1,49} = 11.03$, $p = 0.0017$), while there was no such relationship for males ($F_{1,43} = 0.77$, $p = 0.38$).

In addition, body condition was related to deployment CORT values in a colony-specific manner (colony:cort interaction: $F_{2,88} = 4.19$, $p = 0.018$). On St. Paul, there was a negative relationship with deployment CORT ($t = -2.15$, $df = 33$, $p = 0.039$), while on St. George the relationship was positive ($t = 2.23$, $df = 36$, $p = 0.032$). Bogoslof had no relationship ($t = -0.508$, $df = 20$, $p = 0.62$).

2.4.2 Reproductive investment (Tables 2.4 and 2.5)

Reproductive investment was measured as trip rate, indicating maximum potential provisioning rate, and the percent of deployment time that birds spent attending the colony versus on foraging trips. Trip rate was best explained by a model including only colony and Julian date. Despite large variation, the trip rate differed significantly between colonies (Fig. 2.3; $F_{2,95} = 3.28$, $p = 0.042$). St. Paul birds made significantly more trips than St. George birds, and Bogoslof was not different from either (Fig. 2.3; planned contrasts: St. Paul-St. George: $p = 0.037$; St. Paul-Bogoslof: $p = 0.73$, St. George-Bogoslof: $p = 0.30$). Julian date was also retained in the best model, and although it was not significant in the best model ($F_{1,95} = 2.47$, $p = 0.12$), it was highly weighted (Table 2.4) and was significant or trending in other high-performing models (Trip Rate Model 3: $F_{1,97} = 3.67$, $p = 0.058$; Trip Rate Model 4: $F_{1,96} = 4.73$, $p = 0.032$; Trip Rate Model 5: $F_{1,94} = 3.01$, $p = 0.086$). This relationship shows a higher trip rate later in the season.

Attendance was explained by significant interactions of colony with sex ($F_{2,90} = 6.72$, $p = 0.0019$) and colony with Julian date ($F_{2,90} = 4.34$, $p = 0.016$). Males attended the colony a significantly higher percentage of the time than females on Bogoslof and St.

George (Fig. 2.4, $p < 0.01$). Males did not differ from females on St. Paul and females were similar across all islands (Tukey post-hoc comparisons: all $p > 0.11$). Colonies also differed in attendance patterns over the season. On Bogoslof and St. Paul there was no relationship between attendance and Julian date ($p > 0.12$, Bogoslof attendance: $54.2 \pm 2.9\%$, St. Paul attendance: $49.6 \pm 2.2\%$). However, St. George birds sampled at later dates had lower attendance than those sampled earlier ($F_{1,37} = 4.93$, $p = 0.033$; St. George attendance: $49.0 \pm 2.6\%$). Model weights indicate that colony, sex, Julian date, and the colony-sex interaction are the best predictors.

On both St. Paul and Bogoslof, there was no relationship between trip rate and attendance (both $p > 0.15$). Only on St. George was there a trend in the trip rate and attendance relationship ($t = -1.76$, $p = 0.088$). This relationship did go in the expected direction (negative) indicating that, on St. George only, a higher trip rate means less time for attending the chick.

2.5 Discussion

2.5.1 CORT and biological age

This study tested the effect of biological age on physiology and reproductive behaviors of thick-billed murres breeding under a wide range of environmental conditions. Results have been presented for patterns of stress levels, body condition, attendance at the colony, and foraging trip rate. Hereafter, we will focus on how these patterns are related to biological aging. Levels of the stress hormone CORT support the prediction that the three colonies tested fall in a range from poor (St. Paul), to moderate

(St. George), to good (Bogoslof) conditions (Appendix 2.A, Figure 2.1). These differences are likely driven by differences in food resources, as indicated by stable isotopes (Appendix 2.A, Harding et al. 2013). Predictions 1 and 2 dealt with stress patterns in older animals (Table 2.1). The first prediction, that older birds would be more stressed, was supported on Bogoslof, a food-rich colony. The second prediction, that older birds would show lower stress levels, was supported on St. Paul, the island with overall poor foraging conditions. Under the best foraging conditions (Bogoslof) older birds were more stressed; under poor conditions (St. Paul) they were less stressed than young birds, and at intermediate conditions (St. George) there was no age-related pattern (Fig. 2.1). The support of both these predictions, in conjunction with the gradient of colony conditions, led to our “senescence and experience conceptual model” (Fig. 2.5). When conditions were good, experience had no apparent benefit – i.e. when food was readily available, the skills and experience of age did not provide an added edge. Older birds in those conditions show the effects of senescence: they do not perform more trips or attend the colony more, yet their stress levels are higher (Figs 2.1a and 2.5a). However, when food was limiting (and overall stress levels were elevated), then experience appears to have offset senescence. Reproductive investment parameters are not driven by biological age, yet during poor conditions, older birds had similar, or lower, stress levels than young birds (Figs 2.1b, 1c, and 5b).

Moderate nutritional stress may motivate adults to increase foraging effort, as on Bogoslof, which might benefit the chick. However, even moderate CORT elevation may come at the cost of parental survival probability (Satterthwaite et al. 2012). This strategy

would not be prudent for a young bird, but may be for an older bird with decreased residual lifespan. Where conditions were worse (St. Paul and St. George), adults of all ages had increased stress levels, presumably an unavoidable consequence of lower food availability. However, on these colonies older birds were no longer more stressed than young birds, a possible adaptation allowing them to continue reproduction. When conditions worsen, young birds become more stressed, but older birds do not become any more stressed than they already were. Very high stress levels can result in abandonment of reproduction, which may benefit a young bird that can try again in future years but is maladaptive for old birds with few reproductive attempts remaining. In some species, older birds have lower CORT due to loss of adrenal function (adrenal senescence), which is thought to be adaptive – allowing persistence of breeding in the face of heightened stressors (Angelier et al. 2006, Heidinger et al. 2010). Stress-induced CORT levels decline with chronological age in the common tern (Heidinger et al. 2010), but baseline samples increased (Riechert et al. 2012). Decreases of baseline CORT with age are also seen in wandering albatrosses (Angelier et al. 2006). Our study is unable to differentiate with certainty between a CORT ceiling caused by adrenal senescence in older birds or lowered CORT response as a result of fewer inputs elevating CORT. However, it is likely that the reduced CORT in older birds on St. Paul is due to experience rather than adrenal senescence, because birds of comparable biological ages on St. George or Bogoslof are able to elevate CORT above the St. Paul levels.

For these CORT patterns in older birds to be an adaptive strategy, rather than evidence of physiological senescence, parental investment must be similar or higher in

old birds. We did not find biological age effects on the investment parameters of trip rate and colony attendance at any colony, indicating consistent investment across the lifespan. Studies on thick-billed murres (Kitaysky et al. 2000) and their sister species (common murre, *U. aalge*; Burger and Piatt 1990) found that parents providing constant age-independent levels of parental effort under all but the most extreme environmental conditions. Instead of measurably more effort in older parents, we are seeing maintenance of the effort that younger birds can provide, made possible through higher stress levels and increased foraging experience. These consistent reproductive investment patterns are managed by behavioral flexibility, indicating that age may play a role in selection of prey, choice of foraging habitat, and/or diving behaviors. These relationships need to be addressed in future studies.

Our results demonstrate support for both detrimental aging (increased stress in older birds at Bogoslof, a food-rich colony) and beneficial aging (comparable stress levels of old and young birds breeding on poorer colonies). These two mechanisms are by no means mutually exclusive, but their dual presentation here is somewhat unexpected. It would be logical to expect beneficial aging to be apparent under all conditions – with older birds demonstrating their experience via behavioral parameters. In this scenario, we would expect that the costs of aging (detrimental aging) would only be realized when conditions were challenging, with older animals demonstrating higher stress levels. Instead we found just the opposite. Detrimental aging is apparent under good foraging conditions, but behavior is unchanged under all conditions. However, beneficial aging is only apparent under poor conditions, when the experience of age

allows older birds to maintain foraging behaviors as well as younger birds and to not further increase their stress levels. Environmental conditions interact strongly with age to determine whether experience will pay off. This indicates that in populations of long-lived organisms, the older, more experienced, individuals are likely to play a large role in adapting to shifting climate conditions. For example, elephants show an analogous system, where the memories and experiences of older females help the herd react appropriately to environmental risks (McComb et al. 2011). If colonial organisms, like seabirds, can cue on each other to locate appropriate foraging areas (Silverman et al. 2004, Weimerskirch et al. 2010), the presence of experienced individuals benefits not only that year's productivity, but also builds future capacity by providing an example for younger individuals.

2.5.2 Colony as driver of physiology and behavior

In contrast to the evidence for effects of biological age and environmental conditions on stress levels, body condition was highest in St. Paul males (Fig. 2.2), contrary to the lower condition predicted for a poor quality colony. Traditionally, body condition has been seen as an index of individual quality and food availability: higher body condition is always better. This is the case on St. Paul, food is unpredictable and nutritional stress is likely, resulting in a colony where birds spend energy conservatively, attempt to maintain high condition, and only lose it when food is unavailable: there is a negative relationship between body condition and CORT levels on St. Paul. However, when foraging conditions are favorable, as they were on Bogoslof and to a lesser extent on St. George, murres may reduce wing loading by shedding extra fat stores and

maximizing flight efficiency. This may be especially important for the male, since he needs to accompany the chick to sea after fledging and spends several months with restricted foraging opportunities as both he and the chick are flightless (Bridge 2004). Adaptive mass loss has been seen in murres (Croll et al. 1991) and other seabirds (Schultner et al. 2013), functioning during chick-rearing to lower the cost of chick provisioning. Under these good conditions, we would only see stressed birds putting on weight, and on St. George this is the case: there is a positive relationship between body condition and deployment CORT. This provides an adaptive explanation of the dual results of lower CORT and lower body condition on St. George and Bogoslof. It should be noted that had we only analyzed the Bogoslof colony, we would have found increases in stress hormones with aging. However, analysis of three colonies allowed a more complete understanding of the CORT dynamics of our species: namely that under poor conditions, even young birds can be more stressed than our old Bogoslof birds, and that the pattern of an increase in CORT secretion with age is not universal. As found with albatross molt patterns (Catry et al. 2013), the story at one colony may not generalize to the species.

Colony condition gradients are driven by their proximity to productive oceanic resources; trip rate was driven largely by colony (Fig. 2.3). St. George is located relatively near the productive shelf-break feature in the Bering Sea, and the low number of trips indicates that adults are likely making the long journey to the shelf-break to take advantage of predictable prey (Harding et al. 2013). Long flights to the shelf-break result in lower trip rates, but predictable high-quality prey likely contributed to St. George's

lower stress levels (Appendix 2.A). St. Paul is so far from the shelf-break that murre foraging trips to the shelf are not energetically lucrative (Harding et al. 2013). Instead, St. Paul birds foraged in nearby waters, where productivity was lower and less predictable (Hunt et al. 2008, Harding et al. 2013); nearby sources of poor prey resulted in higher provisioning rates, but also higher physiological stress incurred by murres breeding at this colony. Finally, it should be noted that the null model performed well for trip rate, although not within two ΔAIC_c (Table 2.4), which implies that trip rate may be driven by factors other than those we measure here, perhaps chick condition or perceptions of mate contribution.

Mate contributions may differ by sex, and previous work has indicated that in murres males and females have different patterns of biological aging (Young et al. 2013). It is not surprising, then, that differences in attendance were primarily driven by sex and colony interactions. On St. George and Bogoslof, males spent about 60% of their time at the nest, while females were closer to 40-45% (Fig. 2.4). These differences were significant, while on St. Paul the sexes spent an equal amount of time attending the chick. Although we did not track both parents in any pair, it is notable that the sums of male and female attendance patterns on each island equaled or exceeded 100%, indicating that the murre parental priority to not leave the chick unattended is met by different divisions of labor at different colonies. Unattended chicks are more at risk for death by predation, conspecific attack, or accident. The differing patterns between the islands may indicate colony-specific foraging strategies where parental duties are partitioned by sex.

2.5.3 Conclusion

This study addresses physiological and reproductive investment patterns in thick-billed murres by colony, sex, and biological age. Telomeres proxied biological age, and the evidence was consistent with findings in studies where the chronological age of long-lived animals was known. Biological age provides a measurement of the aging process in populations where chronological age is unknown, allowing access to colonies and systems that have not been studied for aging patterns previously. In this species, behavioral investment was independent of age, implying that classic trade-offs are expressed physiologically rather than behaviorally, and that maintenance of consistent levels of parental care is prioritized. Aging murres balance both the deleterious effects of aging (detrimental aging) and its benefits in terms of increased experience (beneficial aging). The patterns we found in murres demonstrate that physiological aging patterns may be environmentally linked, and can manifest themselves unexpectedly (e.g. experience providing benefits most noticeably under the worst conditions). Under the challenging conditions engendered by a changing climate, experience may be necessary to buffer colonies from immediate costs while transitioning to new foraging conditions.

2.6 Figures

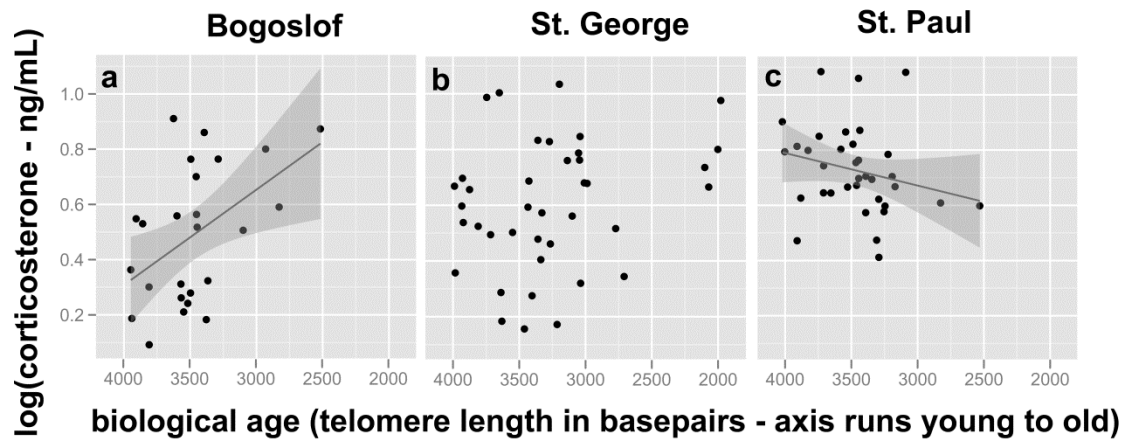


Figure 2.1: Baseline corticosterone (CORT) levels predicted by telomere length and colony. Panels are a) Bogoslof, b) St. George, and c) St. Paul

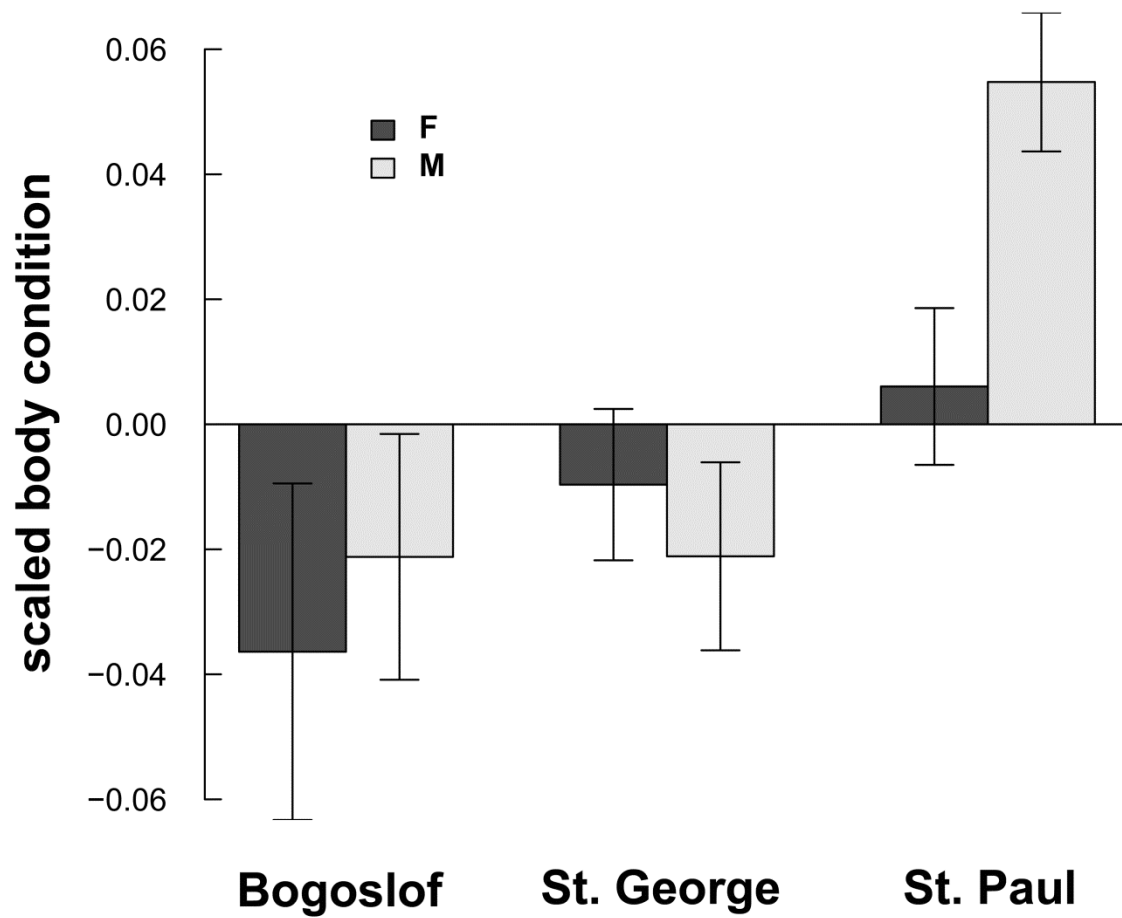


Figure 2.2: Scaled body condition by colony and sex. St. Paul has a significantly higher body condition than St. George and Bogoslof. This is driven by the high body condition in males.

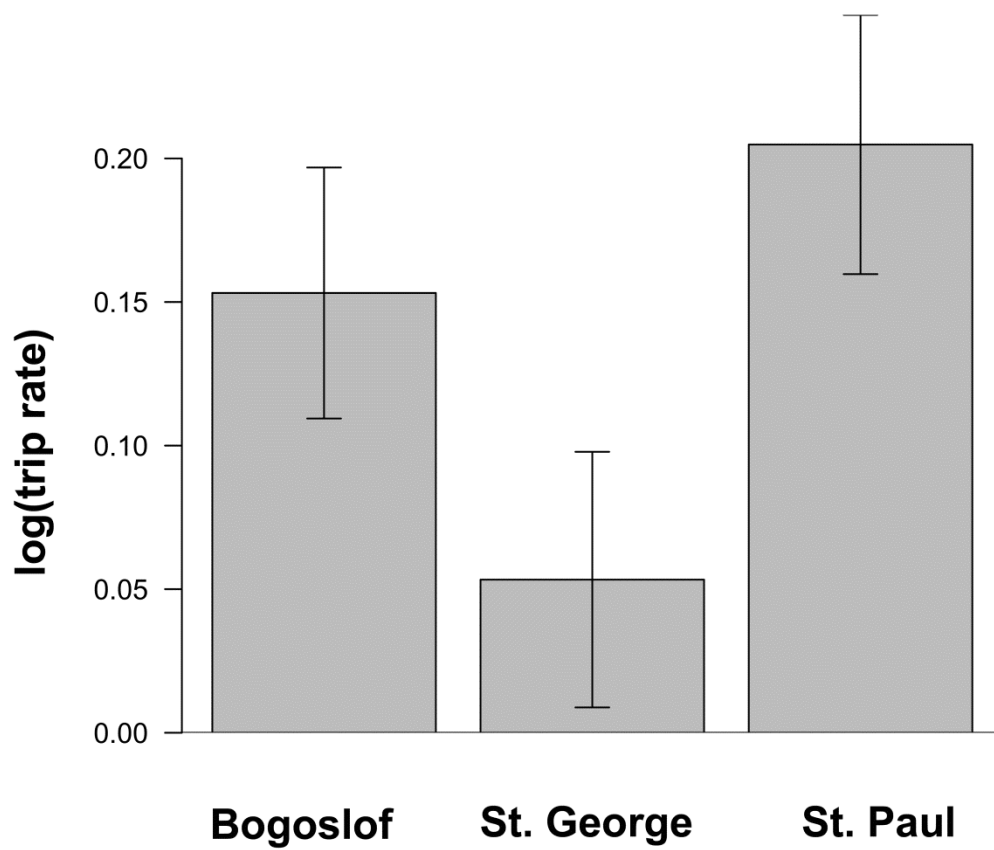


Figure 2.3: Trip rate by colony. St. Paul birds perform significantly more trips per day than St. George birds. Bogoslof presents intermediately.

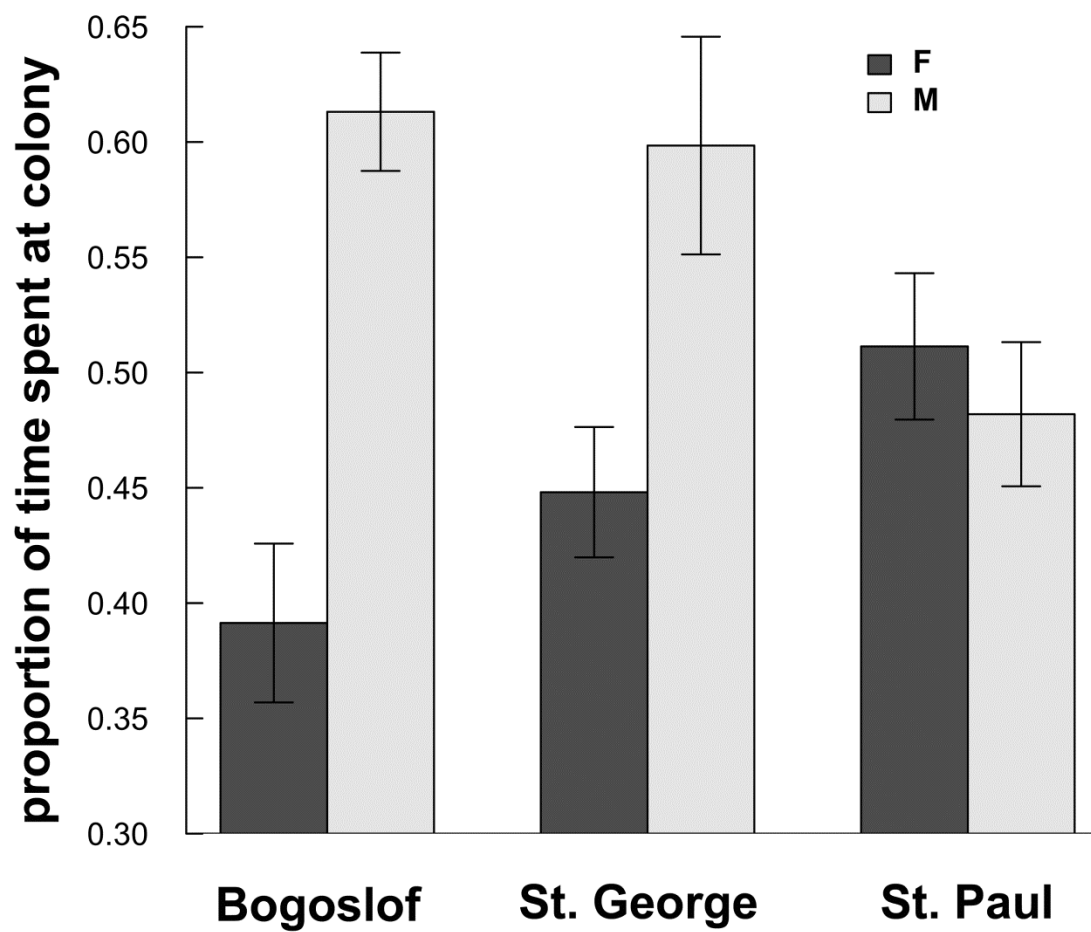


Figure 2.4: Colony attendance by colony and sex. Males on Bogoslof and St. George have higher attendance than other birds.

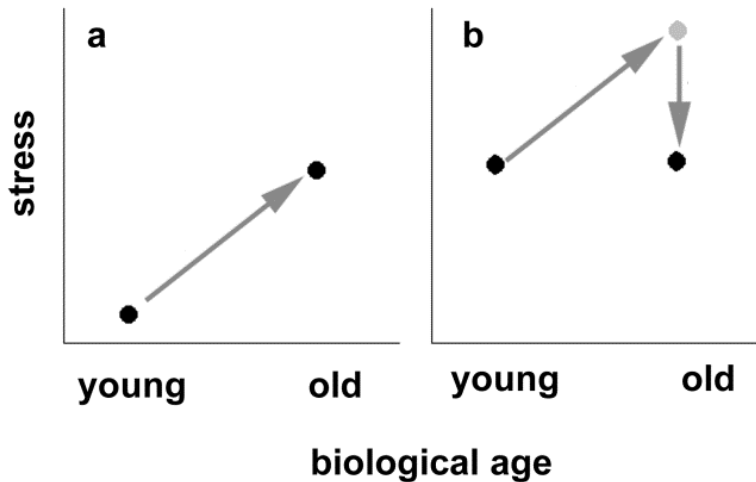


Figure 2.5: Experience and senescence model. Under good foraging conditions (A, e.g. Bogoslof) younger birds have low stress compared to older birds are more stressed; senescence results in a need to work harder to maintain their level of parental investment and overcome physiological and somatic degradation. Under poor foraging conditions (B, e.g. the Pribilofs, esp. St. Paul) all birds (young and old) experience high levels of physiological stress, and old individuals are expected to be affected more strongly due to their senescent phenotype. However older birds might offset the costs of the poor conditions by using their years of experience foraging in variable conditions, thus effectively avoiding additional stress.

2.7 Tables

Table 2.1: Hypotheses and predictions.

Hypotheses – Is it good to be older?			Relevant Predictions
1.	Detrimental Aging: Older birds are senescing and paying higher physiological costs of reproduction compared to young birds.		1 & 3
2.	Beneficial Aging: Older birds are more experienced, which brings benefits to fitness and allows maintenance of physiological condition.		2, 4, & 5
Predictions			Relevant Variables
1.	Older birds are more stressed and/or are in worse condition because they are poorer foragers.		CORT and body condition
2.	The experience of previous reproductive attempts makes older birds more efficient foragers. Their stress levels and body condition are comparable or better than those of younger birds.		CORT and body condition
3.	Older birds need to take long foraging trips to maintain their condition: they cannot attend the nest often and may not return to feed the chick as often as younger birds.		Trip rate and attendance
4.	Older birds have more time to attend the nest because they are efficient foragers.		Attendance
5.	Older birds know where food is located and can make several trips per day to provision the chick.		Trip rate

Table 2.2: Sample sizes and dates of logger deployment and recaptures of adult thick-billed murre breeding on three colonies in two years.

Year	Colony	Males	Females	Deployment Dates (Julian Dates)	Recapture Dates (Julian Dates)
2008	St. Paul Island	6	5	28 July – 11 August (210 – 224)	31 July – 14 August (213 – 227)
	St. George Island	7	12	26 July – 16 August (208 – 229)	29 July – 18 August (211 – 231)
2009	St. Paul Island	13	12	1 August – 16 August (213 – 228)	4 August – 20 August (216 – 232)
	St. George Island	4	16	30 July – 17 August (211 – 229)	1 August – 22 August (213 – 234)
	Bogoslof Island	18	8	25 July – 16 August (206 – 228)	27 July – 18 August (208 – 230)

Table 2.3: Physiological state summary. Models presented are all $\Delta AIC_c < 2$ and the null model (for comparative purposes). Terms in the model are indicated by a “*”. TL is telomere length, and ΔAIC_c is the difference between the model and the lowest AIC_c . AIC weights are presented as “w.” The summed weight for models including the term is indicated below its column in the “Term Weight” rows. Effect sizes for best models are in Table 2.5.

Deployment CORT												
Model	Int	TL	Col- ony	sex	J. date	TL: colony			df	AIC_c	ΔAIC_c	w
Best Model	*	*	*			*			8	-24.10	0	0.37
Model_2	*	*	*		*	*			9	-22.70	1.40	0.18
Model_3	*	*	*	*		*			9	-22.29	1.81	0.15
Null Model	*								3	-5.188	18.9	0.00
Term Weight:	-	97.6	99.98	42.5	35.0	93.8						
Deployment Body Condition												
Model	Int	TL	Col- ony	sex	J. date	colony :sex	TL :sex	sex: Jdate	df	AIC_c	ΔAIC_c	w
Best Model	*		*	*	*			*	8	-262.1	0	0.12
Model_2	*		*	*	*	*		*	10	-261.6	0.491	0.09
Model_3	*	*	*	*	*		*	*	10	-260.9	1.18	0.064
Model_4	*	*	*	*	*			*	9	-260.7	1.43	0.056
Null Model	*								3	-245.3	16.8	0.00
Term Weight:	-	64.1	99.9	94.8	98.5	38.9	30.0	64.9				

Table 2.4: Reproductive investment summary. Models presented are all $\Delta AIC_c < 2$ and the null model (for comparative purposes). Terms in the model are indicated by a “*”. TL is telomere length, and ΔAIC_c is the difference between the model and the lowest AIC_c . AIC weights are presented as “w.” The summed weight for models including the term is indicated below its column in the “Term Weight” rows. Effect sizes for best models are in Table 2.5.

Trip Rate											
Model	Int	TL	colony	sex	Jdate			df	AIC_c	ΔAIC_c	w
Best Model	*		*		*			6	22.57	0	0.12
Model_2	*		*					5	22.94	0.372	0.10
Model_3	*				*			4	23.60	1.02	0.075
Model_4	*	*			*			5	23.95	1.38	0.063
Model_5	*	*	*		*			7	24.03	1.46	0.060
Null Model	*							3	25.19	2.62	0.034
Term Weight:	-	48.6	65.2	-	67.3						
Percent Attendance											
Model	Int	TL	colony	sex	Jdate	colony: sex	colony: Jdate	df	AIC_c	ΔAIC_c	w
Best Model	*		*	*	*	*	*	11	-110.3	0	0.30
Null Model	*							3	-91.72	18.6	0.00
Term Weight:	-	-	97.9	99.9	90.4	97.3	80.2				

Table 2.5: Effect sizes for best models. For each dependent variable analysis the terms of the best model are provided, along with factor-level effect sizes and std. errors. The “Change” column indicates the change of the factor level (if appropriate) or a 1% change in the continuous variable. One percent of Julian date was 2.2 days and one percent of telomere length was 33.8 basepairs.

Dependent Variable	Term	Factor Levels	Estimate	Std. Error	Change
Deployment CORT	Intercept	-	1.69	0.42	-
	TL	-	-0.000345	0.00012	0.69%
	Colony	George	-0.748	0.46	44%
		Paul	-1.46	0.51	86%
	TL:colony	George	0.000241	0.00013	0.48%
		Paul	0.000487	0.00014	0.97%
Deployment Body Condition	Intercept	-	0.947	0.29	-
	Colony	George	0.0201	0.016	2.1%
		Paul	0.0627	0.016	6.6%
	Sex	M	-0.973	0.41	100%
	J. Date	-	-0.00453	0.0013	1.0%
	sex:J.Date	M	0.00455	0.0019	1.0%
Trip Rate	Intercept	-	-1.29	0.92	-
	Colony	George	-0.103	0.067	8.0%
		Paul	0.0302	0.069	2.3%
	J. Date	-	0.00665	0.0042	1.1%
Percent Attendance	Intercept	-	1.30	0.98	-
	Colony	George	0.756	1.2	58%
		Paul	-2.46	1.3	190%
	Sex	M	0.219	0.056	17%
	J. Date	-	-0.0042	0.0045	0.71%
	Colony:sex	George:M	-0.0751	0.072	5.8%
		Paul:M	-0.268	0.071	21%
	Colony:J.Date	George	-0.00321	0.0054	0.54%
		Paul	0.0118	0.0062	2.0%

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2.9 Appendix

Appendix 2.A Stress levels and stable isotopes of murres breeding on St. Paul, St. George, and Bogoslof Islands in 2008 and 2009

Our study uses three murre colonies as a natural laboratory of different environmental conditions. For murres in 2008 and 2009, an ANOVA of CORT levels supported the long-term assessment of colony conditions in the Bering Sea, under the current climate regime (Fig. A2.1.1). These measures came from murres sampled during our study years and include the individuals in the focal study as well as other breeding adults. Although colony interacted with year to predict CORT (colony-year interaction: $F_{2,23} = 4.45$, $p = 0.023$), St. Paul always had the highest CORT levels, followed by St. George, while Bogoslof birds were least stressed in both years (St. Paul 2008: 9.24 ± 0.64 ng/mL; St. Paul 2009: 7.37 ± 0.57 ng/mL; St. George 2008: 5.08 ± 0.37 ng/mL; St. George 2009: 6.93 ± 0.57 ng/mL; Bogoslof 2008: 2.76 ± 0.40 ng/mL; Bogoslof 2009: 4.45 ± 0.29 ng/mL). ANOVA of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicate that each island draws from a unique food web of carbon and nitrogen sources (Fig. A2.1.2). Although we do not dwell on specific dietary interpretations of stable isotope signatures here, heuristically higher nitrogen signatures indicate a higher trophic position and higher carbon signatures indicate a more on-shore food source. Significant differences in signatures indicate different sources of food, differing either in trophic levels of foraging (e.g. fish vs. invertebrates), different species (shelf vs. oceanic zooplankton), or location and water masses of foraging (Dorresteijn, Kitaysky et al. 2012). Nitrogen ($\delta^{15}\text{N}$) interacts with colony and year (colony-year interaction: $F_{2,159} = 5.83$, $p = 0.0036$). It generally

increased from south to north (Bogoslof < St. George < St. Paul) and from 2008 to 2009, except for Bogoslof, which had similar signatures between 2008 and 2009. Carbon ($\delta^{13}\text{C}$) was also predicted by colony ($F_{2,159} = 9.8$, $p < 0.001$) and year ($F_{1,159} = 24.0$, $p < 0.0001$), but not by their interaction. Carbon also increased from south to north, but Bogoslof and St. George were similar (Bogoslof = St. George < St. Paul). Carbon increased as well from 2008 to 2009, but most strongly on Bogoslof and St. Paul. Bogoslof in 2008 is the least enriched in both isotopes and the least stressed of any colony-year. Strong colony effects on stable isotopes (Fig. A2.1.2) and stress levels indicate that colonies are nutritionally and physiologically independent, good measures of variation in conditions, and support our prediction that conditions fall in a gradient, with Bogoslof showing the least nutritional stress and St. Paul, the most.

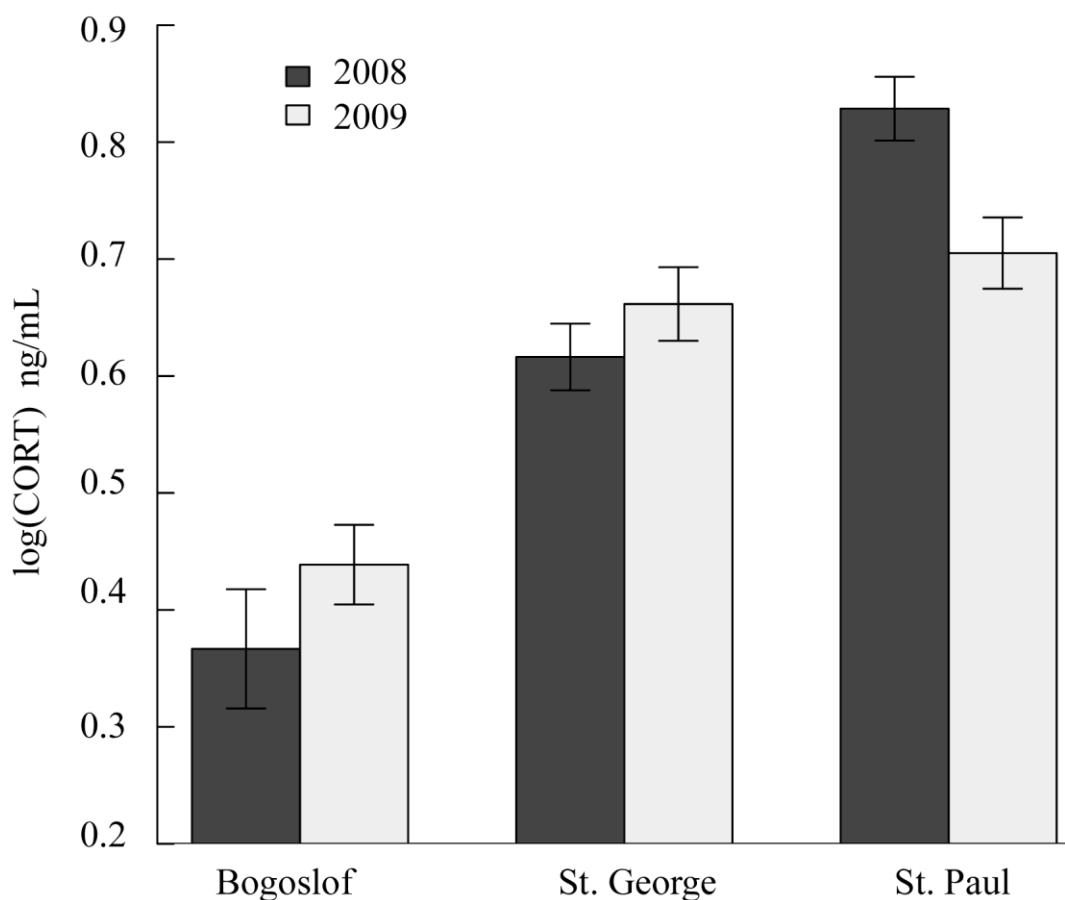


Figure 2.A-1: Corticosterone (CORT, log-transformed) predicted by colony and year.

CORT is highest on St. Paul, a declining colony that is furthest from oceanic resources, and lowest on Bogoslof, which has an increasing population and access to oceanic systems. The trends from 2008 to 2009 were for a decrease in CORT in the basin (St. Paul), an increase in oceanic waters (Bogoslof) and no difference on St. George, a relatively stable colony, which is situated at the shelf break and has relatively easy access to both systems.

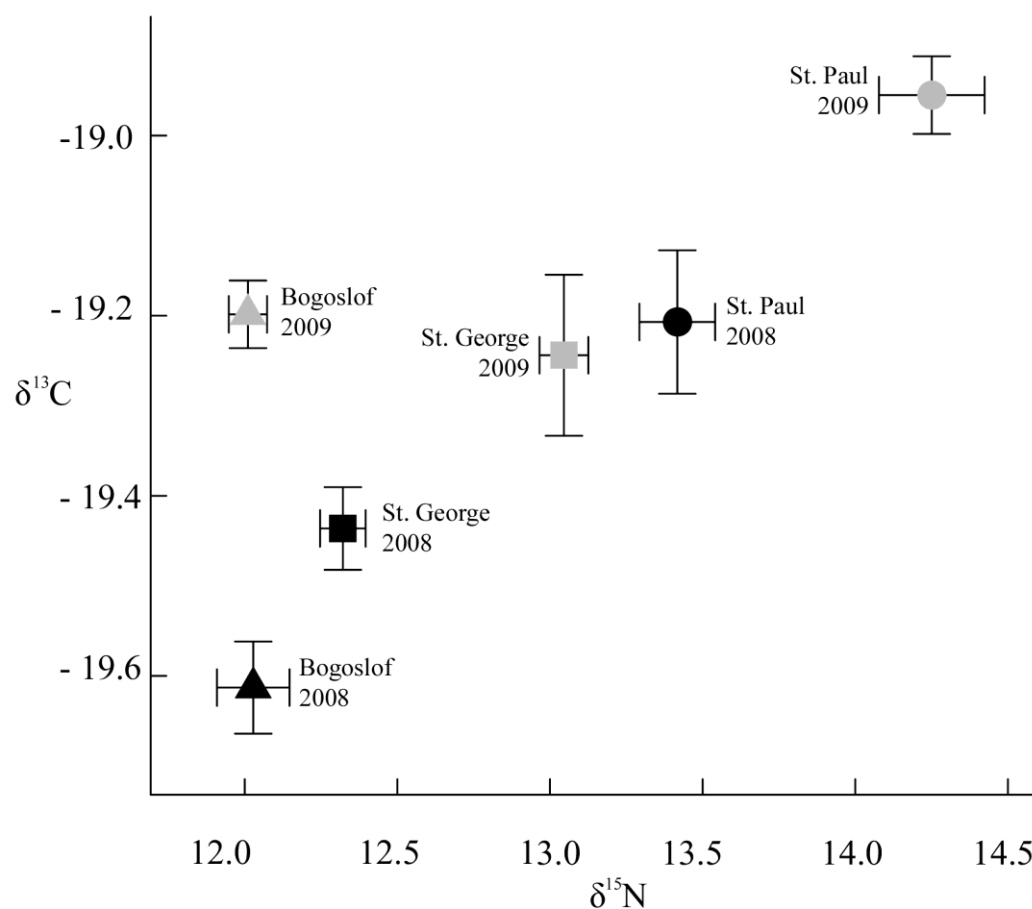


Figure 2.A-2: Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope signatures for St. Paul (SP), St. George (SG), and Bogoslof (Bog) in 2008 and 2009. Both isotopes increase from Bogoslof (oceanic system, furthest south) to St. George (shelf break, middle latitude) and to St. Paul (basin system, furthest north). Carbon also increases from 2008 to 2009, and nitrogen does so on St. Paul and St. George, but not on Bogoslof.

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2.10 Acknowledgments

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Chapter 3 Biological age is a major driver of foraging behavior in a long-lived vertebrate¹

3.1 Abstract

Biological aging may result in physiological deterioration (senescence) but also in improved performance due to previous experience. Whether the force of senescence or experience dominates behaviorally and physiologically will depend on environmental quality, life history, and sex roles within the species. Here we examine the effects of biological age (assessed by telomere length), sex, and habitat (colony), based on a three-colony comparison of breeding thick-billed murres (*Uria lomvia*) in the Bering Sea. We defined foraging behavior along three axes of habitat and prey selection, determined using bird-borne data loggers. Foraging habitat was defined by spatial habitat choice (foraging radius, sea-surface temperature, and foraging depths), temporal use (day/night preference and foraging time budget), and prey selection (stable isotope signatures of carbon and nitrogen). As expected, sex and habitat contributed strongly to explaining foraging behavior. Biological age also played a large explanatory role: it was weighted highly in most analyses, demonstrating comparable explanatory power to sex or habitat. Prey selection was related to colony; changes in murre trophic level depended on age, but their direction also depended on habitat quality. We found support for increased ability of older birds, indicating experience, and limited evidence for senescence, mostly in prey selection. Mechanisms consistent with senescence and experience appear to be working

¹ R. C. Young, A. S. Kitaysky, C. P. Barger, I. Dorresteijn, M. Ito and Y. Watanuki. *Ecology* in preparation

simultaneously, allowing organisms to modify behavior depending on environmental conditions as they age. Experience associated with longevity is an important factor that might enhance resilience of long-lived seabirds and ameliorate the effects of climate change on their populations. We conclude that age-dependent patterns of foraging behavior are context-dependent, as the effects of aging largely depend on the habitat in which they are expressed.

3.2 Introduction

Senescence is an important factor determining behavior of long-lived vertebrates. Senescence has now been widely documented in free-living animals (Bonduriansky and Brassil 2002, Williams et al. 2006, Nussey et al. 2008), and variations in maternal investment and hormonal responses demonstrably change with age (Beamonte-Barrientos et al. 2010, Riechert et al. 2012). However, evidence for behavioral senescence is inconsistent across studies – chronological age has an effect, but is often confounded by issues of quality and experience (Aubry et al. 2011, Mauck et al. 2012); and the effects of aging on behavior might depend on environmental context (Pärt 2001, Reid et al. 2010, Pardo et al. 2013). Patterns of steep declines before death, catastrophic senescence, also complicate the measurement of age-related changes (Reed et al. 2008, Mauck et al. 2012). The emerging concept of biological age provides a connection between physiology and chronology. Biological age is a theoretical concept that modifies chronological age at an individual level. It may provide insight into incremental changes in behavior during an individual's lifespan by incorporating intrinsic and extrinsic drivers

of inter-individual variability (Alviggi et al. 2009, Tuljapurkar et al. 2009). Here, we investigate whether biological age of individuals (proxied by telomere length) is an important factor predicting foraging behavior of long-lived seabirds breeding under varying environmental conditions.

Although relatively new to ecological studies, biological age is a common term in human studies (Klemera and Doubal 2006, but see this review - Monaghan 2010). Unfortunately, it is often undefined, as noted by Klemera and Doubal (2006), or defined solely as the biomarker used in the study to indicate it, without further theoretical discussion (Bae et al. 2013, Holly et al. 2013, Wijsman et al. 2013), or is reported and contrasted to chronological age, but not defined (Suhr et al. 2009, Steptoe et al. 2011, Sutton et al. 2013). We would like to clearly separate the theoretical concept of biological age from the biomarkers which merely indicate it. Biological aging has been compared to a “weathering” process (Geronimus et al. 2010) through which the soma becomes more degraded due to environmental factors or genetic predispositions to accelerated rates of decay (Tsuji et al. 2002, Aviv 2006, Alviggi et al. 2009). In these definitions biological age is “variation in physiological state or condition” (Barrett et al. 2013), a measure of declining vigor (Park et al. 2009), residual lifespan (Monaghan 2010), or as the capacity of the body to resist damage (Wilson 1988, Gunn et al. 2008). In this paper, we define biological age as a theoretical value reflecting the “current position of the individual in its journey through life” (Monaghan and Haussmann 2006), as driven by processes of somatic decay and disease and which ought to have predictive value for performance and fitness.

While residual lifespan can be informative, it requires following all study subjects until they die of natural causes. Biological age measures may be thought of as predictive of residual lifespan since they quantify decline from a hypothetical 100% (birth or early development) to 0% (death) without regard to chronological age. Biological age is responsive to the drivers of lifespan variation, including genotype differences, epigenetic differences, maternal effects, cohort effects, early-life conditions (e.g. chronic nutritional stress during development, weather and predation effects, sibling competition) (Kitaysky et al. 2006, Needham et al. 2012), and responds throughout life to the behaviors and events that may accelerate or reduce aging, e.g. reproductive effort (Bouwhuis et al. 2010), inter- and intraspecific competition, disease status, social status, predation pressure, and adverse or favorable environmental conditions. Any event which accelerates somatic deterioration (e.g. increased metabolic rate, disease, or elevated immune activity) will result in faster biological aging. Biological age includes both measures of innate quality or “fixed heterogeneity” (Tuljapurkar et al. 2009) but also of extrinsic forces to which organisms respond, therefore it more closely predicts senescence and residual lifespan than chronological aging (Gunn et al. 2008, Bize et al. 2009). To be a useful biological age marker, a measure should be a strong explanatory variable for the residual variation in performance of organisms (Nakagawa et al. 2004, Bae et al. 2008, Dunshea et al. 2011). Common biomarkers of biological age include inflammation, oxidative stress (Valdes et al. 2005), expression rates of aging-related genes (Holly et al. 2013), and, most commonly, telomere length (Benetos et al. 2001, Monaghan 2010, Barrett et al. 2013). Telomere length has strong potential as a

biological age marker, because loss of telomeric sequence reflects the combined actions of a wide variety of mechanisms and drivers (e.g. rapid growth, inflammation pathways), thus accounting, as biological age ought, for the “multifactorial and highly variable” character of aging (Benetos et al. 2001).

This study examines biological age, as reflected in individual telomere lengths, in relation to foraging patterns in a typical long-lived seabird breeding under varying environmental conditions. Chronological age can affect foraging behavior (Desrochers 1992, Rutz et al. 2006, Le Vaillant et al. 2012), but has only been examined in a few species. In addition, breeding experience often positively affects both annual fitness and foraging behavior (Desrochers 1992, Rutz et al. 2006, Limmer and Becker 2009). Breeding experience increases with chronological age (although not necessarily linearly) but also increases exposure to drivers of biological aging: metabolic rate is elevated (Thomson et al. 1998), stress hormones increase (Crossin et al. 2013), oxidative and immune systems are unbalanced (Alonso-Alvarez et al. 2004, Harshman and Zera 2007, Stier et al. 2012), and parasite loads increase (Christe et al. 2012). Since increases in experience directly increase rates of biological aging, we would also expect biological age to outperform chronological age in correlation with experience as well as senescence, at least in those healthy enough to breed. In this study, we examine telomere length (TL) as a proxy for biological age and its effect on foraging behavior in chick-rearing thick-billed murres (*Uria lomvia*, hereafter murres) on three Bering Sea colonies.

Biological aging is predicted to be affected by external environmental drivers (Kawasaki et al. 2008), with poor conditions expected to result in more rapid aging (Hall

et al. 2004). To address this context-dependence of biological aging, we studied three colonies of varying habitat quality, as determined by previous studies on population trends and other parameters. Since biological age captures somatic decay, we predict that biologically older birds will show more evidence of decreasing performance. But biological age also captures reproductive experience, so aspects of foraging performance related to foraging efficiency and high-quality diet may improve with increased biological age. We also predict that habitat quality will mediate the effects of age. Previous findings in the thick-billed murre indicate that under good foraging conditions biologically older birds have higher corticosterone than younger ones, but under poor foraging conditions, the difference vanishes, while overall corticosterone levels are higher (Young et al. in preparation). This indicates that senescence affects physiological performance regardless of food conditions, but that when conditions are poor, experience is able to offset the effects of senescence in older birds.

3.3 Methods

3.3.1 Study sites and sampling

Adult thick-billed murres were sampled on three colonies in two years, for a total of five colony-years. The three colonies form a north to south gradient in the Bering Sea (Fig. 3.1). The two northernmost colonies, St. Paul Island (57°08'N, 170°18'W) and St. George Island (56°36'N, 169°39'W), are part of the Pribilof Island archipelago and lay near the productive Bering Sea shelf edge. St. Paul lies farther north and is located farther from the shelf edge than St. George Island, 88 km to the southeast. Bogoslof

Island (53°56'N, 168°02'W) is located in oceanic waters in the eastern Aleutian Archipelago. The Pribilof Islands were sampled in 2008 and 2009, while Bogoslof was only sampled in 2009. This study takes advantage of a gradient of colony-specific environmental conditions and habitat qualities to effect a “natural experiment” (Byrd et al. 2008, Harding et al. 2013, Young et al. in preparation). Colonies differ from each other due to recognized differences in latitude, oceanic environment, and prevailing food conditions. Previous work has characterized the study system during our study years (2008 and 2009) as a “food-rich colony,” Bogoslof; a “food-poor colony,” St. Paul; and one which presents intermediately, St. George; hereafter “good,” “poor,” and “middling” (Harding et al. 2013, Young et al. in preparation). St. Paul is a colony with relatively poor conditions: it has not recovered from a population crash in the 1970's, and many seabird species exhibit higher stress levels here than elsewhere. St. George, on the other hand, has partially recovered its population since the crash and has mid-levels of stress hormones. Lastly, Bogoslof has a positive population trend and low stress levels. Despite its positive trends, Bogoslof is geographically the smallest colony, the newest, and also has the lowest absolute population levels. Current estimates for thick-billed murre numbers are 57,000 on St. Paul; 1,500,000 on St. George; and 33,000 on Bogoslof – differences ranging across almost two orders of magnitude (Renner and Williams 2005, Byrd et al. 2008, Dragoo et al. 2012). Productivity is similar between the colonies (Dragoo et al. 2012, Harding et al. 2013), so changes in populations are likely driven by emigration, dispersal, recruitment, or adult survival (Schmutz and Byrd 2004).

Chick-rearing murres were captured at their nests using noose poles, and were targeted when the chick was old enough to be left unattended while loggers were deployed and young enough not to fledge during the days of logger recording. Blood was sampled from the brachial vein for telomere quantity determination and genetic sexing, with some red blood cells set aside for stable isotope analysis. Blood for telomere analysis was preserved in a 2% EDTA buffer, transferred to a glycerol storage buffer, and frozen for shipment to the laboratory. Temperature-depth recorders (TDRs, Cefas G5, Cefas Technologies) were attached to the keel feathers with Tesa tape (Tesa, Charlotte, NC, Ito et al. 2010). Weight of deployment package was ~1.5g. This mass is less than one percent of bird body mass, well below masses demonstrated to affect behaviour (Vandenabeele et al. 2012). TDRs recorded time, pressure, and temperature every two seconds. The majority of birds were recaptured after three days: deployment length = 73.1 ± 3.7 h (22 – 220 h), and skeletal measurements for body condition were taken.

3.3.2 Diving parameters and variables of interest

Foraging behavior was assessed using bird-borne data loggers. TDR data were analyzed following Ito et al. (2010) using IGOR Pro (WaveMetrics 2008). The macros and extraction software identify dives, and generate maximum dive depth and sea-surface temperature data from raw records. Presence at the colony, in the air, or on the sea were determined by temperature changes via visual examination of temperature and depth (pressure) records. These TDR data were used in conjunction with stable isotope analysis to generate foraging parameters along three axes: spatial use of habitat, temporal use of habitat and prey selection. Variable names are given in parentheses. Spatially, we

recorded how far birds foraged from the colony, using return flight times as recorded by loggers (flight); the type of waters chosen for foraging, described by sea-surface temperature (SST); depth of foraging (foraging depth); and the maximum foraging depth for each bird (max depth). Temporally, dives were recorded as being in daylight or at night (dark). We also used the time spent underwater (descending, foraging, and ascending) as an index of foraging effort and time budgeting (underwater). Lastly, prey selection was determined by stable isotope signatures of murre red blood cells, we measured both $\delta^{13}\text{C}$, as an indicator of pelagic vs. on-shore food webs, and $\delta^{15}\text{N}$, as an indicator of trophic level.

Where possible, return flight time (flight) was calculated as the time of return to the colony minus the time of leaving the sea from the last bout of a trip, assuming birds return directly to the colony when foraging concludes. Foraging depth (foraging depth) described the foraging depth for all dives recorded to a bird. Maximum depth (max depth) was the deepest dive depth recorded for each bird. Sea-surface temperature (SST), indicating water mass selection, was defined by a stable post-diving temperature at the sea surface after a diving bout. Light status of a dive (i.e. whether each dive was during daylight or darkness) was determined by colony specific sunrise and sunset times, and then averaged for each trip, so that each trip's light status is read as the proportion occurring in the night (dark). Diving efficiency was the time spent subsurface, including descent, bottom time, and ascent, measured in hours per day (underwater).

3.3.3 Lab techniques

3.3.3.1 Telomere restriction fragment assay

Telomeres were measured using the telomere restriction fragment (TRF) assay, according to Young et al. (2013) and Haussmann and Mauck (2007). Briefly, whole blood, stored frozen in a glycerol buffer, was extracted into agarose plugs using the Chef Genomic DNA Plug Kit (Bio-Rad, Hercules, CA) and digested with a mixture of 3 U HinfI, 15 U HaeIII, and 40 U RsaI (Roche Applied Science, Indianapolis, IN). DNA was separated using pulsed field gel electrophoresis (PFGE) on a 0.8% agarose gel. Run parameters were 21 hours at 3 V/cm and 0.5-7s switch times. Buffer (0.5X TBE) was circulated and kept at 14 °C. Hybridization was at 37 °C with 3,000,000 cpm of the telomere-specific radio-labeled oligo (CCCTAA)₄. After hybridization, rinsing and visualization followed Haussmann and Mauck (2007). Samples were analyzed in random order on four gels with two control samples per gel to determine inter- (10.9%) and intra-assay variability (1.42%). TRF values were calculated from gel images following Salomons et al. (2009) and using ImageJ (Schneider et al. 2012). The shortest telomeres in a cell are the drivers of cellular senescence (Hemann et al. 2001, Zou et al. 2004), and it is believed they are more sensitive to aging in whole organisms as well (Haussmann and Mauck 2007, Smith et al. 2011). Following Haussmann and Mauck's (2007) identification of the optimal analysis window, we have analyzed the TRF smear from 5 kb to the bottom of the gel.

3.3.3.2 Stable isotope analysis

Sub-samples of red blood cells were freeze-dried and analyzed with continuous flow isotope ratio mass spectrometry (CF-IRMS) using a Costech Elemental Analyzer (Model ECS 4010, Valencia, CA), a Thermo Finnigan MAT ConFlo III interface (San Jose, CA), and a Delta Plus IRMS (Asheville, NC) at the Alaska Stable Isotope Facilities of the University of Alaska Fairbanks (Williams et al. 2007). Isotope results are presented in δ notation according to:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}} - 1)] \text{‰}$$

where X is ^{13}C or ^{15}N and R is the ratio of heavy to light isotope ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). The standard for carbon was PDB belemnite; and for nitrogen, atmospheric N_2 . Measurement precision (SD) was $\pm 0.13\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.16\text{‰}$ for $\delta^{15}\text{N}$.

3.3.3.3 Genetic sexing

Sex is a common driver of foraging patterns in many taxa (Marquiss and Newton 1982, Aho et al. 1997, Coddling et al. 2011) including seabirds (e.g. Weimerskirch et al. 1997, Welcker et al. 2009). In murres, diving patterns differ by sex (Jones et al. 2002), and in the common murre (*Uria aalge*, sister species to the thick-billed murre), females provide more food to the chick, perhaps because males invest in themselves during the nestling phase, saving chick investment for the extended post-fledging care period (Thaxter et al. 2009). Sexing was done using PCR amplification of two CHD genes, following Griffiths et al. (1998).

3.3.4 Statistical analyses

Analyses were performed in the program R (R Development Core Team 2011, vs. 2.12.2), using package nlme. Response parameters, used to characterize habitat selection, were the eight variables nested within three foraging axes: spatial variables (flight, SST, foraging depth, and max depth), temporal variables (dark and underwater), and prey selection variables ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). In addition to biological age (telomere length), explanatory variables included sex, colony of origin, and in some analyses (see Appendix 3.A) whether the dive was in daylight or darkness. Our “dark” variable was highly correlated with some of the other response variables, e.g. depth (Dias et al. 2012), and is expected to drive some foraging patterns, so it was included in relevant analyses (Appendix 3.A). Each parameter was analyzed with generalized least squares and mixed models. The GLS approach was used to control heterogeneity in the dataset, and the random term in the mixed model controlled for repeated sampling. For example, in some cases variables were analyzed at the level of the dive, diving bout, or trip, thus birds were represented by more than one observation (Appendix 3.A). Each response variable, except flight, was detrended for correlation with Julian date at the colony*year level. For most variables, the full model for each response was telomere length, colony of origin, sex, and all interactions. For SST, foraging depth, and max depth, the full model additionally included the “dark” variable and interactions (indicated by joining variables with a colon), except terms which included colony and dark. Model selection was carried out using AIC_c for small sample sizes. Statistics are reported for the best model (defined as that with the lowest AIC_c) and as mean \pm standard error, unless otherwise noted.

Variable weights are derived from the entire family of models. More information can be found in Appendix 3.A.

3.4 Results

3.4.1 Spatial variables

Return flight time indicated how distantly birds foraged from the home colony. The best model for flight included colony and sex, both of which also had model weights > 0.9 (Table 3.1). Females foraged farther from the colony than males (females: 37.5 ± 4.0 min; males: 20.4 ± 1.7 min), and foraging distances were higher in the Pribilofs than on Bogoslof (St. Paul: 29.4 ± 2.5 m; St. George: 44.2 ± 6.1 m; Bogoslof: 18.5 ± 1.8 m). Biological age did not strongly affect foraging distance, and was weighted at 0.49 (Table 3.1).

Water mass selection was indicated by the SST associated with a dive bout. The best model for SST included biological age, colony, sex, dark, biological age:sex, and sex:dark. Warmer waters were preferred by the two colonies with access to oceanic water masses, Bogoslof and St. George, as compared to St. Paul in the north (St. Paul: 7.88 ± 0.034 C; St. George: 8.58 ± 0.030 C; Bogoslof: 8.36 ± 0.031). Older males preferred warmer waters, while females had no preference with age, and although all birds foraged in slightly warmer waters during darkness, this was more accentuated in males.

Foraging depth indicated prey depth or ocean depth, if murres were foraging benthically. Results were similar to those of SST, the best model included biological age,

colony, sex, dark, biological age:dark, and sex:dark. Dives in the Pribilofs were deeper than dives on Bogoslof, where birds usually foraged over shallow near-shore features (St. Paul: 20.2 ± 0.17 m; St. George: 20.3 ± 0.15 m; Bogoslof: 18.4 ± 0.20 m). It was not retained in the top model, but the highly weighted interaction between sex, dark, and biological age (Table 3.1) indicated that dives were deeper during daylight, as expected, but also that depth increased with age, indicating that with age, birds did not lose their ability to reach deep depths (Fig. 3.2A). In addition, males dove more deeply than females (males: 21.8 ± 0.17 m; females: 18.5 ± 0.12 m). Although male murrelets in this sample were heavier than females (body mass: males: 1104 ± 14 g, females: 1050 ± 10 g, mass difference: $t = 3.14$, $df = 89.9$, $p = 0.0023$), mass did not drive diving depths ($t = 0.661$, $df = 99$, $p = 0.51$). The difference between male and female dive depths was greater at night than in the daylight, and the rate of depth increase with age was greatest in daylight and lowest in males at night. (Fig. 3.2A)

Maximum depth represents a combination of the maximum depth available for foraging and the physiological capacity of the birds themselves. The model selection told a comparable story to average depth. The best model included biological age, colony, and dark. As with average depth, older birds dove deeper, but although Bogoslof had birds with deeper maximum depth records than those on St. Paul, in contrast to foraging depth results (Fig. 3.2B). Despite nighttime diving being on average shallower, birds that dove more at night, were also more likely to have deeper maximum depth records.

3.4.2 Temporal variables

Diving occurred at night on each colony. Major drivers of dive timing (dark) were colony and sex (Table 3.1). Predictably, more night diving occurred on colonies at lower latitude, where there are more hours of darkness during the midsummer breeding season, and on all colonies, females spent more time than males diving in darkness (Fig. 3.3).

The best model for foraging efficiency (underwater) included the terms biological age, colony, sex, and the interaction of colony and sex. Older birds spent less time underwater (Fig. 3.4A), indicating higher efficiency ($t = 2.087$, $p = 0.040$). Male efficiency did not vary by colony, but female efficiency was negatively associated with colony quality, i.e. female murrelets spent less time underwater (indicating higher efficiency) on poor colonies (Fig. 3.4B).

3.4.3 Prey selection variables

Prey choice was described by two stable isotope signatures, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. In our study system, carbon signatures indicated whether prey were sourced through on-shore food webs or off-shore marine systems: lower carbon signatures were indicative of a more pelagic food web, while higher ones indicated on-shore food sources. Trophic level of prey was indicated with nitrogen signature; enrichment indicated foraging on prey of a higher trophic level. However, carbon and nitrogen signatures were correlated (correlation = 0.56, $t = 6.39$, $df = 91$, $p < 0.0001$), and are known to be mechanistically related, making it difficult to determine drivers of changes that affect both these measures. In our analysis, carbon signature was strongly driven by colony and biological

age, although sex was also highly weighted (Table 3.1). Carbon signatures enriched (became more on-shore) in older birds. As predicted, carbon signatures were highest on St. Paul, the most on-shore colony. Other carbon signatures were similar, with the lowest carbon signatures in St. George males, who foraged more oceanically than Bogoslof murres or St. George females (Fig. 3.5).

The best model of nitrogen signature included colony, and sex, although biological age also performed highly in the model weighting (Table 3.1). Nitrogen signature decreased with age on Bogoslof, had no relationship on St. George, and increased with age on St. Paul (Fig. 3.6). Nitrogen signature was also negatively related to habitat quality – increasing from Bogoslof to St. Paul. The interaction of colony and sex, which was retained in the top model, meant that the sex which foraged at a higher trophic level differs by colony: males were more enriched on Bogoslof, while females were more enriched on St. Paul.

3.5 Discussion

We used telomere length as a marker of biological age in the thick-billed murre and found it to have widespread predictive value for determining foraging behavior of individuals. Evidence was found for both senescence and experience, but the effects of experience appear to outweigh those of senescence. Differential foraging by age has not been widely studied, likely due to the paucity of well-monitored known-age colonies. In several bird species, aging affected foraging (Desrochers 1992, Rutz et al. 2006, Lecompte et al. 2010), usually by improving foraging success, indicating a strong role for

experience in these systems. We found that biological age was not as highly weighted as sex and colony, which had large predictive ability for nearly every variable (Appendix 3.B), but biological age performed as well as sex, and nearly as well as colony in many analyses, indicating strong relationships with key drivers of foraging ecology. Biological age was most important in predicting spatial variables, and was very highly weighted in predicting SST and both depth variables (Table 3.1 and Fig. 3.2). High predictive ability for SST and also for carbon signatures indicate that foraging habitat selection differs with age. The variable “underwater,” which indicates foraging efficiency, was also well-predicted by biological age (Fig. 3.4A). The association between foraging efficiency and age supports the prediction that biological aging and experience are correlated: birds become more efficient foragers as they age.

3.5.1 Biological aging, senescence, and experience

Previous work with murres has shown that they may make physiological trade-offs rather than compromise parental and foraging behaviors as they age (Young et al. in preparation, Elliott et al. submitted). In support of this, we did not find age differences in how far from the colony birds foraged or whether they foraged during daylight or nighttime. As in albatrosses (Lecompte et al. 2010), we found that age interacted with sex to determine spatial habitat selection: older males foraged in warmer waters than younger males, but females showed no preference associated with age. In addition, we found that both foraging depth measures increased with age for both sexes, indicating that older birds were not compromised in their ability to dive deeply. The maximum depth to which our birds dove was 125 m, a considerable feat for birds with masses of one

kilogram. This record was set by a bird in the shortest quartile of telomere length, indicating a biologically older bird. The ability to maintain diving depth while aging is evidence against the senescence hypothesis in this species. At the same time, younger birds spent more time underwater than older birds. This is somewhat counterintuitive, considering that older birds consistently dove to greater depths. Shallower dives yet more time underwater together indicated that younger birds were less efficient or experienced divers. Young birds may have poorer foraging abilities, be unable to locate high-quality prey patches, or have a physiological inability to dive to the depths achievable by older birds; despite diving to deeper depths, older birds did not need to stay there long to achieve their goals.

On the other hand, prey selection variables may indicate self-maintenance tactics in older birds, which may result in lowered reproductive output and thus reproductive senescence. Nitrogen signatures enriched with age on St. Paul, decreased with age on Bogoslof, and did not vary with age on St. George. This indicated that older birds increasingly rely on higher trophic sources of prey on St. Paul, our food-poor colony. On Bogoslof, our food-rich colony, older birds switched to lower trophic level prey. Bogoslof's lower signatures may be due to a higher proportion of invertebrates in the diet. Squid and euphausiids are common prey items on Bogoslof, and murrelets choose between them and higher trophic level prey items like pollock (Harding et al. 2013); pollock and other gadids dominate in more northerly waters in the vicinity of the Pribilof Islands. If higher trophic level prey are advantageous, then older birds at St. Paul were able to access it when younger ones were not, but on Bogoslof, older birds chose the

more abundant and less nutritious prey (Benoit-Bird et al. 2011). Searching for high-trophic level prey takes time away from foraging for the chick (St. Paul) while loafing near the colony foraging on easy-access prey (Bogoslof) could also indicate self-maintenance strategies. Nitrogen patterns supported a previous finding that under good conditions, older birds showed evidence of senescence (i.e. choosing low-quality abundant prey), while under poor conditions, when all food was scarce, their experience paid off and they could access higher trophic level prey than younger birds (Young et al. in preparation). Experience has been shown to offset the effects of senescence in ptarmigan as well (Wiebe and Martin 1998). Carbon signatures enriched with age, potentially indicating that birds reduce reliance on pelagic food webs, but the effects were small, so they may be due to trophic level increases, as carbon signatures are positively correlated with nitrogen signatures. It is also possible that the differences in stable isotope signatures indicated that older birds differ from younger birds in their isotopic turnover. Older birds may have slower tissue turnover, potentially explained by their lower metabolic rate (Elliott et al. submitted), or older birds could be making seasonal shifts in diet later or more slowly than younger birds. Diet composition shifts as birds move from incubation to chick-rearing (Williams et al. 2008), and although the process of turnover is not important to this study, it is a potential explanation of the differences in stable isotope signatures.

Unlike previous studies, we did not find evidence of senescence in physiological capabilities, but we did find behavioral changes associated with aging. Previous studies have addressed endocrine and metabolic physiology (Young et al. in preparation, Elliott

et al. submitted), and it is possible that these parameters are changing with age in order to support physiological diving capabilities that result in more effective foraging of older individuals. In addition, subtle changes in diet composition may be a form of behavioral senescence missed by previous studies. A more detailed study of the energy content and qualities of various food sources would be needed to address the full ramifications of these age-related changes in diet. Patterns of behavior and physiology in the thick-billed murre are in accordance with life history theory predictions for long-lived species. Younger birds are unwilling or unable to perform at the same level as adults in some parameters, evidence of “constraint” (Wiebe and Martin 1998) but reproductive output is comparable for the many years of adulthood. Murres appear to be “prudent parents” (Drent and Daan 1980) because they are unwilling to make physiological changes until future reproductive attempts are few.

3.5.2 Conclusion

Biological age, environmental conditions, and sex all play pivotal roles in determining foraging habitat selection. The behavioral evidence indicates that older birds retain their ability to use the environment efficiently, which is consistent with previous findings in this species that older birds remain behaviorally flexible, despite paying physiological costs (Young et al. in preparation, Elliott et al. submitted). Spatial, temporal, and prey selection variables all changed with age. Spatial variables were largely sex-dependent: females and males aged differently in spatial use of the environment. Prey selection was related to colony; changes in murre trophic level depended on age, but their direction also depended on habitat quality. We found much

support for increased ability of older birds, indicating experience, and limited evidence for senescence, mostly in prey selection. Mechanisms consistent with senescence and experience appear to be working simultaneously, allowing organisms to modify behavior depending on environmental conditions as they age. Experience associated with longevity is an important factor that might enhance resilience of long-lived seabirds and ameliorate the effects of climate change on their populations.

3.6 Figures

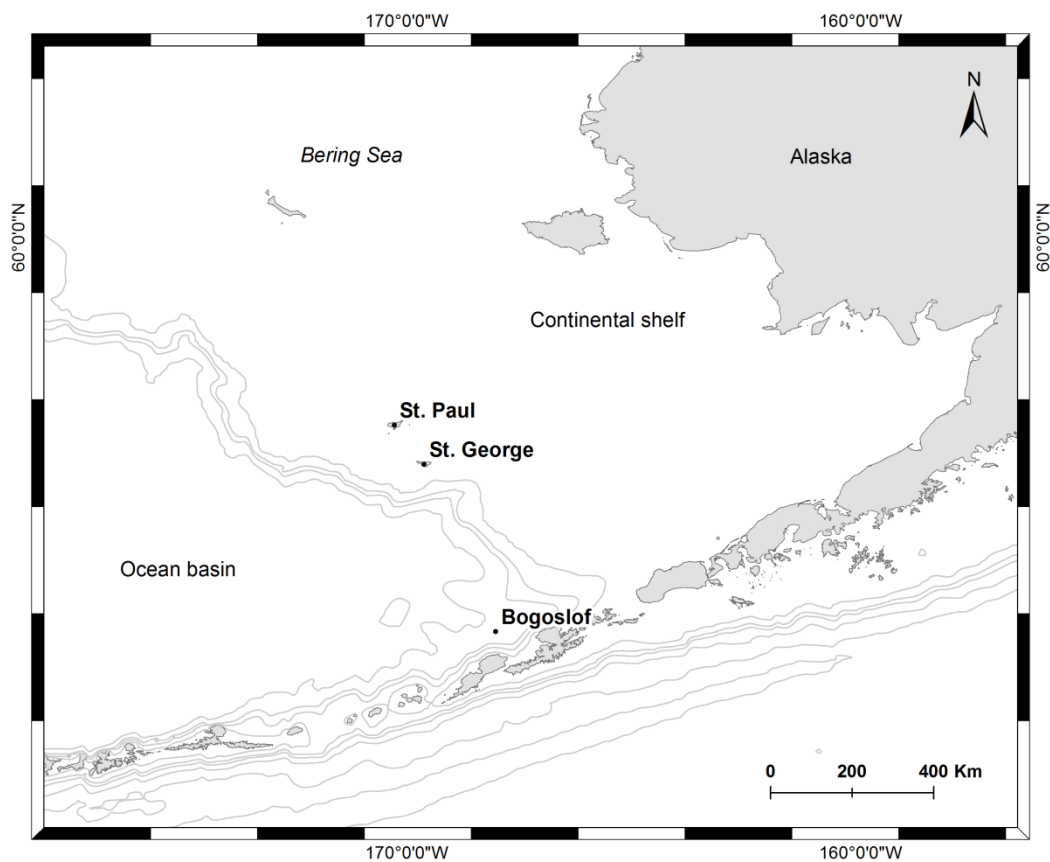


Figure 3.1 The Bering Sea. The three study colonies are indicated and named. The continental shelf and ocean basin are also indicated and topographic lines show the shelf edge, near St. George.

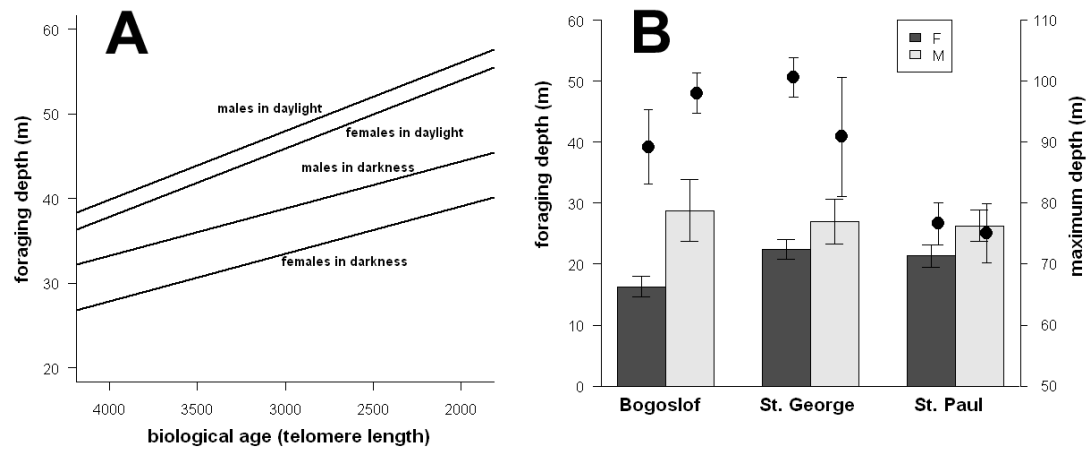


Figure 3.2 Diving depths. A) Foraging depth increases with age. This age-related increase is stronger for day diving than night diving and stronger in females than males. Predicted relationships are derived from the model output of the best model. Note the reversed x-axis: higher telomere length indicates younger biological age, so the axis runs from young to old, as a chronological age axis would. B) Maximum Depth and foraging depth by sex and colony. Dark points and standard errors are maximum depth, and use the right-hand axis; dark and light grey bars are average foraging depth and use the left-hand axis.

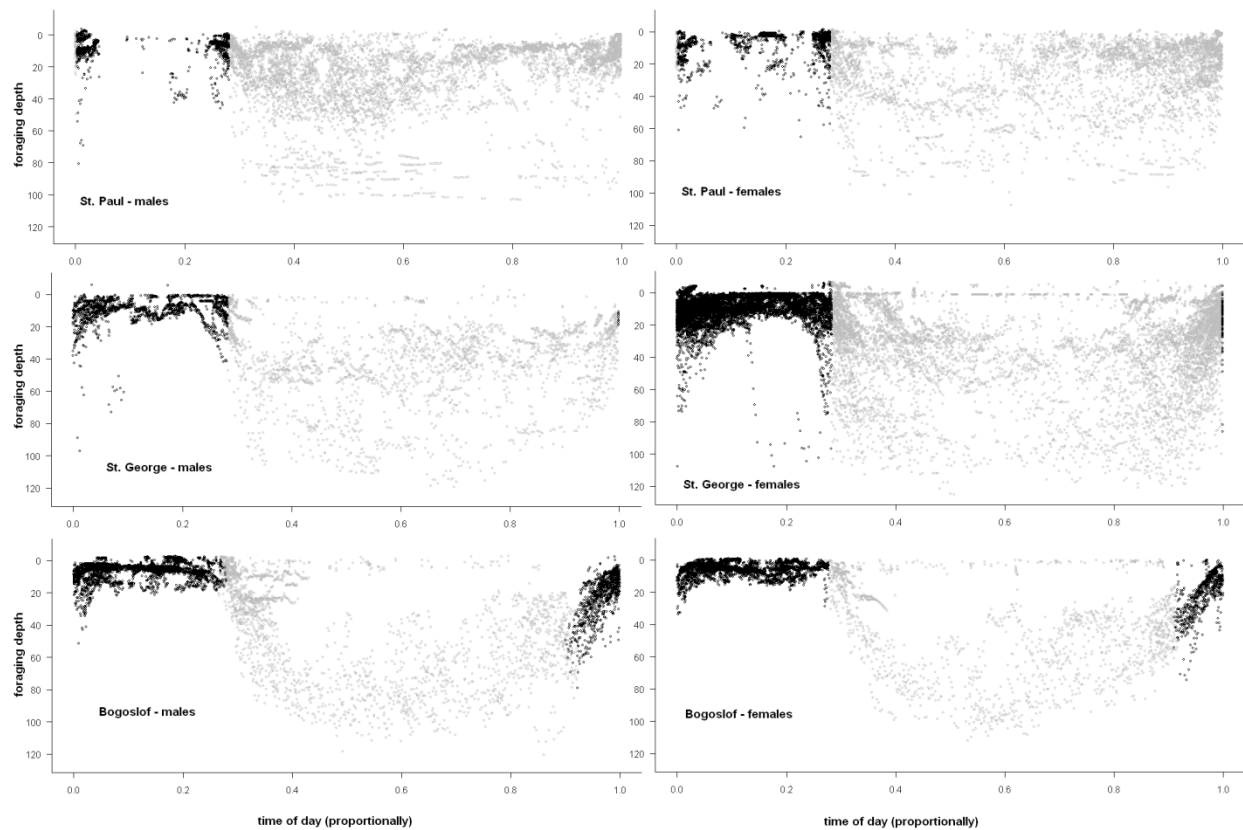


Figure 3.3 Diving in darkness and daylight. Hours of darkness were determined individually for each latitude and day; night length can clearly be seen increasing on the right-hand side of the graphs, with the shortest nights on St. Paul and the longest on Bogoslof. Males are the left column and females the right. It is clear that daylight diving is deeper, and that night diving is shallowest where night is longest. Females have more dives in darkness than males. Benthic diving can be seen on St. Paul where horizontal bars of dives at comparable depths indicate the ocean floor; this pattern is not seen on St. George and Bogoslof.

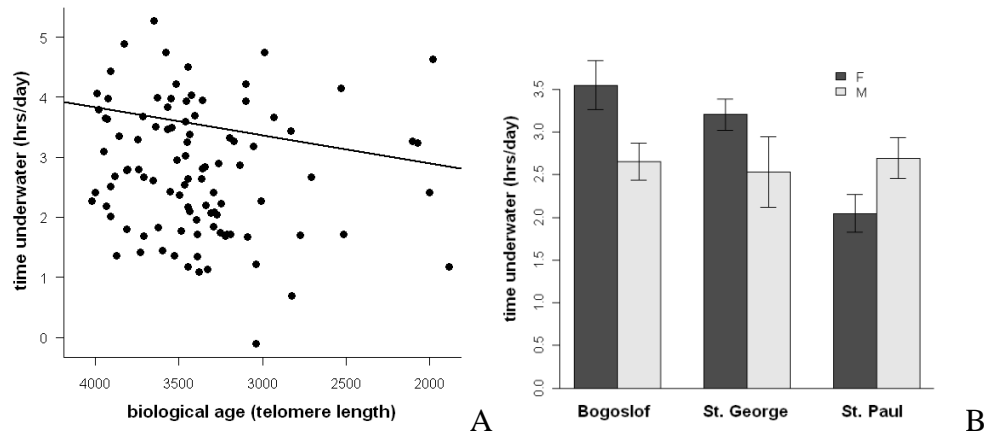


Figure 3.4 Time spent underwater. A) Time spent underwater by biological age. Less time underwater indicates more efficient foraging; thus older birds forage more efficiently than younger birds. Note the reversed x-axis: higher telomere length indicates younger biological age, so the axis runs from young to old, as a chronological age axis would. B) Time underwater by sex and colony. Males consistently spend ~2.5 hrs/day underwater, while females spend less time actively foraging as colony quality decreases, indicating higher efficiency at poor colonies.

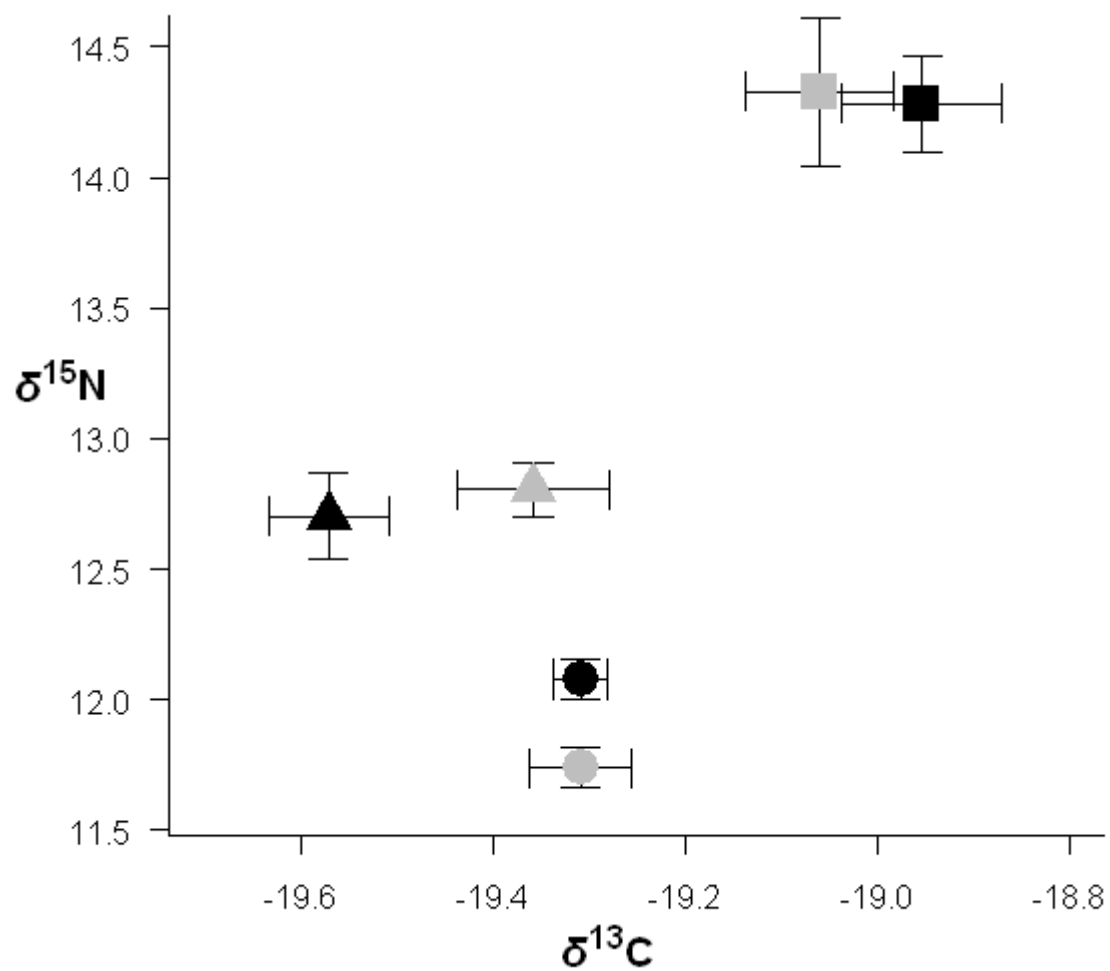


Figure 3.5 Stable isotope signatures of breeding thick-billed murres on three colonies. Males are black symbols; and females, grey. Bogoslof is indicated by circles, St. George by triangles, and St. Paul by squares. Bars indicate standard errors.

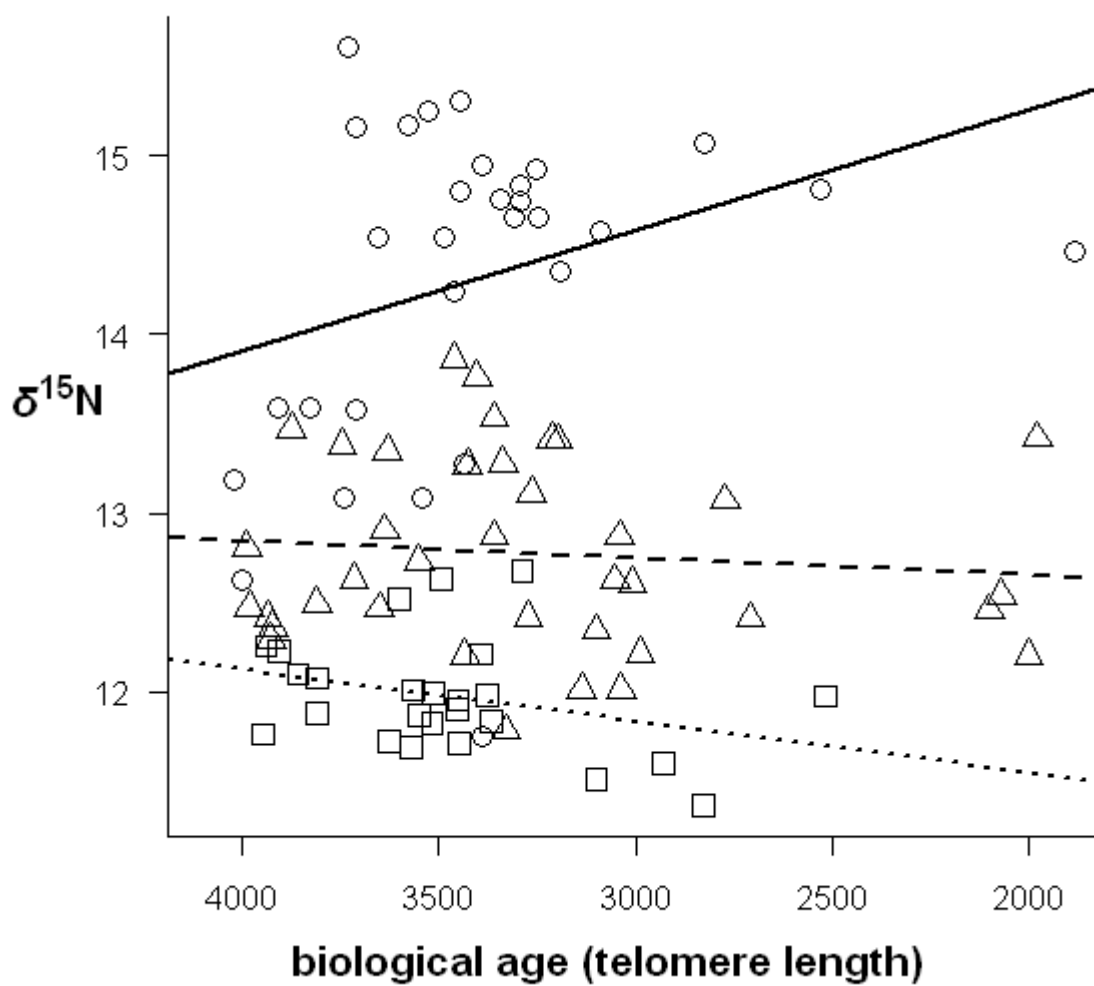


Figure 3.6 Nitrogen signatures by biological age. Trophic changes with age are colony dependent. St. Paul is circles and the solid line; St. George is the triangles and dashed line; Bogoslof is the squares and the dotted line.

3.7 Tables

Table 3.1 AICc weights for each response parameter and explanatory variable. Weights are clustered into: greater than 0.9 (bold); 0.6-0.8 (italics); and lower than 0.5 (plain text). Model weights are based on the entire family of models, not just those with low ΔAIC_c . A “-” indicates that the term was not modeled for that variable. The final column is the difference between the best model’s AIC_c and that of the null model, indicating that each model performed much better than the null at explaining variance in the dataset.

	TL	Colony	Sex	Dark	TL: Colony	TL: Sex	TL: dark	Colony: Sex	Sex: dark	TL:Colony y: Sex	TL:sex :dark	Null ΔAIC_c
Flight	0.490	0.999	0.972	-	0.216	0.143	-	0.130	-	0.023	-	24.32
SST	0.863	0.935	0.945	1.000	0.105	0.593	0.313	0.090	0.472	0.017	0.236	45.27
Foraging Depth	1.000	0.996	1.000	1.000	0.331	0.377	0.650	0.270	0.472	0.095	0.700	2425
Max Depth	0.933	0.992	0.678	0.772	0.219	0.246	0.268	0.275	0.182	0.126	0.134	25.64
Dark	0.362	1.000	0.918	-	0.085	0.091	-	0.102	-	0.009	-	33.70
Under water	0.820	0.993	0.971	-	0.136	0.218	-	0.922	-	0.061	-	10.71
$\delta^{13}C$	0.822	1.000	0.447	-	0.136	0.140	-	0.174	-	0.018	-	25.62
$\delta^{15}N$	0.610	1.000	0.786	-	0.338	0.155	-	0.386	-	0.078	-	86.47

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3.9 Appendices

Appendix 3.A Variables & Model Selection

Table 3.A-1 Variables and Model Building. Each variable is listed with its observation level (i.e. a stable isotope signature for each bird, but a depth for each dive) and the sample sizes. The “observation level” and “nested pattern” columns describes level of analysis, and thus any repeated measures in the data which were addressed in the model. Detrending was done if the data were correlated with Julian date at the colony*year level. The GLS approach was also used to control for heterogeneity in the dataset, and this column indicates the variables that produced heterogeneity. The last column indicates the full model: all interactions were included except for interactions of colony and “dark.” TL is biological age as “telomere length.”

Response	Observation level	N	Nested Pattern	Detrended for Julian Date	Heterogeneity	Full Model
Flight	Trip	186 trips 79 birds	Bird	No	Colony & sex	TL*colony*sex
SST	Bout	3122 bouts 425 trips 93 birds	Bird/ Trip	Colony*year	Colony & sex	TL*colony*sex*dark
Foraging Depth	Dive	51785 dives 3432 bouts 475 trips 101 birds	Bird/ Trip/ Bout	Colony*year	Colony & sex	TL*colony*sex*dark
Max Depth	Bird	99 birds	n/a	Colony*year	Colony & sex	TL*colony*sex*dark
Dark	Trip	475 trips 101 birds	Bird	Colony*year	Colony, sex, toe	TL*colony*sex
Under-water	Bird	99 birds	n/a	Colony*year	None	TL*colony*sex
$\delta^{13}\text{C}$	Bird	93 birds	n/a	Colony*year	Colony, sex, TOE	TL*colony*sex
$\delta^{15}\text{N}$	Bird	93 birds	n/a	Colony*year	Colony	TL*colony*sex

Table 3.A-2 Model output for foraging variables. Each variable is grouped within one of the three foraging axes and described by which niche characteristics it captures. The best model (lowest AIC_c) is listed, along with the number of models with $\Delta AIC_c < 2$, and which variables had model weights > 0.9 . Model weights were based on the entire family of models, not just those with low ΔAIC_c .

TL is biological age as “telomere length.”

Response	Axis	Niche characteristics	Best model	Models: $\Delta AIC_c < 2$	Weighted > 0.9
Flight	Spatial	Distance from colony	Colony+sex	1	Colony, sex
	Spatial	Water mass	TL+colony+sex+dark+ TL:sex+sex:dark	4	Colony, sex
Foraging Depth	Spatial	Water column (vertical)	TL+colony+sex+dark+ TL:sex+sex:dark	8	TL, colony, sex, dark
	Spatial	Physiological capability	TL + colony + dark	4	TL, colony
Max Depth	Temporal	Timing of diving	Colony + sex	1	Colony, sex
Dark	Temporal	Foraging effort	TL+colony + sex + colony:sex	1	Colony, sex, colony:sex
$\delta^{13}C$	Prey selection	Prey selection (on- / off- shore)	TOE + colony	1	Colony
$\delta^{15}N$	Prey selection	Prey selection (trophic level)	colony + sex + colony:sex	8	Colony

Appendix 3.B Discussion of TBMU Foraging behavior in relation to habitat quality (colony) and sex.

Habitat quality (colony) and foraging behavior

All parameters were heavily colony-dependent. Colony-level differences usually reflect the large-scale ways in which habitat differs from colony to colony. For example, days are shorter at lower latitudes in the summer, and here we found birds allocating more of their time to diving after sunset. Night diving takes advantage of the diel migration of zooplankton (Regular et al. 2010). Night diving may also have been higher on colonies where an overnight at sea provided long-term access to productive prey sources. St. George murres overnighted away from the colony on 50% of their trips, compared to 25% and 33% overnight trips on St. Paul and Bogoslof respectively. The high percentage of overnight trips may indicate that St. George murres were spending more time at the shelf edge, which is near the limit of foraging distance and thus more profitable for an overnight trip than a short day trip (Harding et al. 2013).

This is corroborated by the return flight time data. The average return flight time on St. George was nearly twice that on Bogoslof and 1.5x that on St. Paul, indicating long commuting trips to the shelf-edge on St. George. Bogoslof birds could access abundant prey close to their colony, indicated by their short return flight times as well as by their shallow dive depths, indicating near-colony foraging, while their maximum dive records were high, indicating access to oceanic habitat. St. Paul birds had fewer local food resources available, but were too far from the shelf-edge to make traveling there

profitable (Harding et al. 2013). As a result, St. Paul birds stayed close to the colony, and foraged in the cooler waters of the Bering Sea cold pool (Stevenson & Lauth 2012).

Prey selection also differed by colony. Both stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) enriched with latitude – indicating more reliance on shelf sources of carbon in the north, as expected, but also higher trophic levels. Bogoslof murre's nitrogen signatures were almost an entire trophic level lower than St. Paul (Figures 4 and 5, of the main manuscript). Although nitrogen signatures indicated that St. Paul murre's ate the most fish, it is likely quantities were lower or that more energy was required to catch these prey, as their stress levels indicated lower food availability (Harding et al. 2013).

Sex and foraging behavior

Sex differences in behavior may be driven by the differing parental roles in the thick-billed murre: males care for the chick for 4-8 weeks post-fledging, while females pay the up-front costs of reproduction, i.e. egg production (Gaston & Jones 1998). In addition, females linger at the colonies, securing the nesting site for future years (Harris & Wanless 1990), and may feed the chick more while males invest in themselves in anticipation of their heavy post-fledging parental care (Thaxter et al. 2009). Unlike, Thaxter et al. (2009) and Paredes et al. (2008), we found that females foraged farther from the colony and in warmer waters than males. At our colonies these distances likely indicated females searching the distant shelf-edge for high quality prey for the chick (at St. George) or searching farther abroad for fish instead of squid (at Bogoslof). Females' long return flight times indicated long trips, and were associated with more overnights

away from the colony. Indeed, 43% of females' trips included a night away from the colony, while males only were away overnight on 26% of trips. Male murrens attend the colony more at night so as to be available to accompany the chick to sea at fledging, which occurs at dusk. Night diving is usually shallower (Regular et al. 2010, this study), and females dove more shallowly in our study, yet this difference was not driven by body size. Despite their longer commutes and more nights away from the colony, females did not perform fewer trips than males (Young, unpubl. data), so their parental investment is quite high. This corroborates previous findings that female murrens may senesce more quickly than males (Young et al. 2013), which could be due to higher investment. A comparison of energy expenditures between males and females is warranted.

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Chapter 4 Making the periphery enticing: Increased ecotourism as an option for increasing resilience of remote Alaskan communities¹

4.1 Abstract

Small rural communities are particularly prone to social and ecological change. This is especially true in peripheral communities, like islands, remote locations, and extreme environments. In this study, we look at the Pribilof Islands as a vulnerable island socio-ecological system, characterized by strong core-periphery dynamics. We investigate the relationship between the humans and seabirds as a natural resource, representing ties to older ways of life and with potential for future economic opportunities. We conducted a survey and semi-structured interviews of residents of the two Pribilof Island communities in the south-eastern Bering Sea, to assess opinions toward seabirds and harvest levels. Seabirds were generally regarded as important both to individuals and to the wider community. However, current levels of subsistence harvest are low, and few people continue to actively harvest or even go out on the landscape to visit seabird colonies. Respondents expressed a wish to know more about the seabirds and also concern about the poor economy of the islands and about the lack of future development prospects. Despite the poor economic prognosis, the communities retain strong interconnectedness and place value on their environment and on seabirds. Tourism has large potential in this system, and there is interest by community members. Careful management of a developing tourism industry may offer a way forward, with

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leadership and participation at the community level. With input and care, seabirds are a highly sustainable resource, and tourism could be managed to have high economic benefit and low environmental impact.

4.2 Introduction

Dependency on outside economies and decision-making has led to “internal colonialism” for remote small communities in northern regions (Dryzek and Young 1985). Social transformation, especially in recent decades, has led to high levels of unemployment, increased economic dependence on subsidies and outside economic demand, decreased participation in traditional lifestyles, and the deterioration of ecosystems and the services they provide. These changes make rural communities vulnerable to social and ecological change (Chapin III et al. 2009). Island systems, especially in polar regions, are particularly disposed to vulnerability due to climate change and limited economic options (Stewart et al. 2007; Hay 2013). However, these problems can be offset by access to a productive mainland economy, abundant natural resources, and strong local human capital. In this study, we look at the Pribilof Islands as a vulnerable island socio-ecological system, characterized by strong core-periphery dynamics (Young 1987). In particular, we describe the relationship between the humans and seabirds, a natural resource representing ties to older ways of life and the potential for future economic opportunities using this resource.

The Pribilof Island group, located in the center of the eastern Bering Sea, is comprised of four islands, only two of which are large enough to support communities:

St. Paul and St. George. Not long after their mid-eighteenth century discovery by Russian explorers and fur seal hunters, those groups forced Unangan-speaking Aleut people from nearby islands to settle the main Pribilof Islands as slaves of the seal harvest (Jones 1980). Oppressive conditions continued until the twentieth century, setting up a system of economic dependence and lack of self-governance that has hindered the islands through the mid-twentieth century and is still being overcome. Although historically used as a fishing and sealing area, pre-contact Aleuts did not inhabit the Pribilofs, in part because natural resources are scarce compared to the Aleutian Islands. Today the vast majority of islanders are still Aleuts, although there is more diversity on the larger, more heavily populated, and northerly of the two islands, St. Paul (demographic data from the Alaska Department of Commerce, Community, and Economic Development at <http://commerce.alaska.gov/cra/DCRAExternal/community>). Pre-contact, the Aleut people were sea-faring subsistence harvesters relying primarily on marine mammals, fish, and seabirds. Use of terrestrial mammals, salmon, and plant resources was common to Aleut lifestyles. However the forced settlement of the Pribilofs cut people off from these resources, which are not available on the Pribilofs (Veltre and Veltre 1981). Culturally, the people of the Pribilofs remain tied to these norms: fishing is the primary commercial and subsistence activity, but for entirely marine species, as there are no natural salmon runs in the Pribilofs. There is still limited harvest of fur seals and an even more limited harvest of seabirds.

The two communities, St. Paul and St. George, are tight-knit, with a total population of under a thousand residents. Nearly all community members are related by

blood or marriage, sharing a small selection of primarily Russian surnames. Family ties are strong and meals are often shared, generating a strong sense of self and place (this study). Politically the islands harbor wariness towards federal authority, a remnant of the restrictive rules and conditions of the oppressive fur seal companies (Foote et al. 1968). Economic prospects are of primary concern to the locals and will play large role in determining long-term prospects for the communities. Employment is diminishing as fisheries and access to catch processing decline (Kruse 2007), and the overall perception by locals is that of economic decay (Kruse 2007). A recent study by Huntington et al. (2009) captured this disconnect: in their analysis, primary factors driving the uncoupling of the socio-economic system were a) a lack of reliance on the natural environment, b) an economy dependent on outside subsidies and markets (e.g. commercial fishing markets), c) residency decisions based on shared history and identity rather than economic opportunity, and d) a people willing to endure. The expectation for rural native communities had been a tight coupling between the socio-ecological system and local economy, so these findings were surprising. On both islands perceptions of the economic future were grim, although this outlook and the reliance on subsistence for economic reasons, as opposed to cultural reasons, was more pronounced on St. George (this study). This pattern of small organizations (e.g. small communities characterized by families, small fishing enterprises, and other small businesses) and high community connectedness is associated with both high levels of vulnerability and high levels of adaptive capacity (Marshall et al. 2013). The Pribilof system unites low resilience, characterized by a decreased connection to the natural environment and a poor economy, with the adaptive

capacity of a close community with a strong sense of identity, indicated by the choice to endure poor conditions and remain, rather than leave for more opportunities on the Alaskan mainland.

In light of the poor economic outlook and subsistence decline (Fall et al. 2013), the seabirds of these islands appear underutilized. The fur seal industry is dying, with remaining harvests for subsistence meat alone. Fisheries for crab and pollock compete with larger commercial fishers based elsewhere and are driven by external markets. The Pribilofs, as small vulnerable periphery communities, need local economic opportunities (Dryzek and Young 1985). Young (1987) characterized the Pribilofs as a “periphery” area, where the economy is dependent on outside markets, policy decisions are often made far from the communities, and local stakeholders have little influence at national or even regional scales. He suggested a more localized economy, but was aware that opportunities are limited and often depend on stochastic availability of resources (e.g. hydrocarbons or fish). Tourism has been suggested as an economic opportunity (Young 1987), yet there are concerns about the specialized appeal, long-term sustainability, and philosophical differences between community members in the direction tourism should take (Sherwonit 1994). Even with investment, tourism is likely to remain expensive, as the islands can only be reached by air or sea. Ecotourism, for viewing seabird colonies and seal rookeries, is the dominant form of tourism today and could be expanded in the future, especially if cultural exploration were included in tour packages (Sherwonit 1994). Yet little research has focused on the role of seabirds in this system: marine mammal subsistence surveys dominate. In a recent study reporting subsistence usage, St.

Paul was the only one of the five target communities for which seabird subsistence was not reported (Fall et al. 2013). In this study, we describe the use of seabirds as a subsistence and cultural resource on St. Paul and St. George, the knowledge about and interest in seabirds by community members, and economic outlook of Priblovians.

4.3 Methods

We conducted a survey and semi-structured interviews of St. Paul and St. George residents to assess opinions toward seabirds and harvest levels. Our surveys and interviews took place in July and August of 2009. On each island, the lead researcher (RCY on St. George, ID on St. Paul) held a public meeting describing current research projects, inviting the views of community members, gathering recommendations for interviews, and distributing questionnaires. Surveys were targeted at heads of households and were taken door-to-door as well as left in the village store, a place where it is likely to be encountered by almost every community member. Interview targets were those who continued to harvest seabirds, community leaders, elders, and any adult who wanted to contribute ideas or memories.

The survey was a questionnaire with sections on: seabird use and importance, knowledge of seabirds, importance of harvest, demographics, and bird identification and names. Responses were on a 5 point Likert scale with 1 indicating “disagree,” and 5, “agree.” The survey included three pairs of questions intended to assess opposite trends: the first pair was, “Current harvest regulations are appropriate,” and “Current harvest regulations should be changed.” The second was, “I prefer to eat seabird meat to other

forms of protein,” and, “I only eat seabird products when there is nothing else.” The last pair assessed attitudes towards tourism and asked, “There is too much tourism on the Pribilofs,” and, “There is not enough tourism on the Pribilofs.” The demographic section was not on a Likert scale, but was rather comprised of multiple choice options for ethnicity, gender, age, income, and time spent on the island annually.

We conducted about 15 semi-structured interviews, 10 on St. Paul and five on St. George. All interviews were conducted in person as informal discussions. Notes were taken by the interviewers, and were later compiled and compared qualitatively for major opinions, anecdotes, and illustrative quotes. Primary interviewers were RCY and SY on St. George and ID and Thibaut Vergoz on St. Paul.

4.4 Results

4.4.1 Demographic results

Twenty-two surveys were collected on St. George and 31 on St. Paul. The 2010 census information lists St. George as having 41 households and St. Paul as having 162 households. Response rates were thus 53% and 19% respectively. Demographic response parameters (Table 4.1) did not differ qualitatively from those in the ADFG 1994 census.

4.4.2 Seabird importance (Table 4.2)

Nearly all survey respondents agreed that seabirds are important to Pribilof culture and Aleut culture (Table 4.2, 93-96% agreement). On St. Paul, only two people disagreed with the statement, “Seabirds are important to Priblovian culture,” and the

same two also disagreed with the statement, “Seabirds are important to Aleut culture.” Overall, there was a decline from the general to the specific: there was near universal agreement that seabirds were important to Priblovian and Aleut culture, but only 71%, although still a large majority, agreed that seabirds were important to them personally. Seabirds were relied upon by about a third of the households, and most respondents agreed that they are important to the subsistence economy of the islands. We saw higher agreement for the importance of seabirds to various social groups (e.g. Priblovians, Aleuts), and less agreement that seabirds are personally important or personally used. In addition, personal importance depended on gender of respondent (males’ mean Likert response: 4.2 ± 0.2 , females’: 2.9 ± 0.6 ; $t = -2.23$, $df = 12$, $p = 0.045$). Ethnicity (Aleut/non-Aleut) and income level were not significant (all $p > 0.57$). Age was not a significant predictor of personal seabird interest ($F_{3,47} = 1.77$, $p = 0.16$), but those in the 18-30 year old age group were much less likely to consider seabirds personally important than other age groups (Figure 4.1). The finding of lower seabird importance to younger respondents was corroborated by the interviews, where several older interviewees expressed a desire for young people to share the seabird harvest with their elders, but claimed that the younger generation does not hunt seabirds, so this resource is unable to be shared.

Interviews demonstrated that seabird observations and harvesting had been an important part of family life and growing up. Several interviewees remembered harvesting least auklets (*Aethia pusilla*) as children and described it as a good way to get children involved in subsistence activities and helping provide for the family. Joining the

adult seabird hunt was described as a rite of passage, with one interviewee remembering fondly the gift of “a ten-gauge at ten” so that he could help his father hunt sea ducks and kittiwakes. Others remembered the teachings of parents and elders when describing hunting practices and reminiscing about their early experiences.

Seabird subsistence was also part of the Aleut identity. When the Pribilofs were still managed as an independent or government-controlled seal harvesting business, or what an interviewee described as “the government days,” seabirds were a primary source of protein to the Aleut population. Off-island groceries were not routinely available to the non-white population of the island. One interviewee described the red-faced cormorant (*Phalacrocorax urile*) as “the Aleut turkey,” because only white officials were allowed a turkey at Thanksgiving.

4.4.3 Current seabird use (Table 4.3)

The results for questions aimed at describing current seabird use mirrored the results for seabird importance: most respondents agreed that seabirds should be harvested, indicating support for seabird use and importance in the abstract, but less than half of respondents indicated that they prefer to consume seabird protein over other sources of locally available food. Although it was not significant, reliance on seabird subsistence tended to increase with age. In the lowest age category (18 to 30 yrs old) 0% indicated household reliance. This jumped to 30% of respondents aged 31 to 45 yrs, 36% of those 46 to 60 yrs old, and 43% of those over 60. In addition, on both islands there was a roughly even split between respondents agreeing with the statement, “I prefer to eat seabird meat to other forms of protein,” and those agreeing with, “I only eat seabird

products when there is nothing else.” But on both islands, slightly more respondents agreed with the “last resort” option than with that for “preference.” This was especially notable in the age group 45 to 60, where 33% said they preferred seabird meat, and 48% said they would eat it only as a last resort. However, these results should be interpreted cautiously, as 8 respondents (16% of total surveys) somewhat agreed or agreed with both the “last resort” and the “preference” statements. In interviews, most interviewees said they preferred food from the store, to seabird meat, and that bird harvesting was most important in the past, when there was no store, or for large families who needed the meat to augment their diets.

4.4.4 Seabird knowledge (Table 4.4)

Seabird knowledge was strongly positively related to personal importance of seabirds ($t = 5.19$, $df = 49$, $p < 0.0001$). Those who agreed with the statement, “I know a lot about the seabirds of these islands,” also agreed that, “Seabird are important to me personally,” indicating a potential mechanism for knowledge fostering personal importance, or personal importance driving knowledge-seeking. Questions aimed at eliciting respondents’ knowledge of seabirds and their own evaluation of that knowledge (i.e. do they think they are knowledgeable about seabirds and do they wish to know more) also provided the first real differences between the islands. On both islands, 50-60% of respondents believe that current harvest regulations are appropriate, and this mirrors our interview findings where people described harvest levels as low and never complained that regulations restricted their abilities to acquire what they needed. However, on each island there was a roughly even split between those indicating harvest

regulations were fine and those indicating they should be changed. This confusion was reflected in interviews as well; some interviewees told the interviewer, “There are no rules” for harvest, while others said the rules were good, because they prevented overharvesting. Residents of the two islands also differed in their perception of their own seabird knowledge. On St. Paul, about 60% agreed that they knew a lot about seabirds and would like to know more, and about 18% disagreed with those statements. However, on St. George, all respondents agreed, “I know a lot about the seabirds of these islands,” and, “I would like to know more.” Agreement rates were 75% and 90% respectively. Although percentages reporting reliance on seabird harvest were comparable (35% rely on St. Paul, 30% on St. George), St. George residents appear more interested in seabird knowledge than do St. Paul residents.

Because we targeted interviewees who were engaged in harvesting or were elders who remembered days of more harvesting in the past and we selectively interviewed people who were interested in our project, a great deal of harvest-related knowledge was shared. The most commonly harvested birds were the black- and red-legged kittiwakes (*Rissa tridactyla* and *R. brevirostris*), the common and thick-billed murre (*Uria aalge* and *U. lomvia*; eggs and adults), and the least auklet. Red-legged kittiwakes were more desired than black-legged. Interviewees preferred to harvest kittiwakes as they fledge or when they first arrive to the breeding colony in the early summer. Recently arrived birds were described as less fishy-tasting. Another version of this preference was to hunt adults before eggs are laid, so early in the breeding season.

Hunting techniques varied by species. One interviewee told us kittiwakes were shot over the water and blown back to land. Least auklets were usually described as being hunted with nets or sticks thrown into low-flying flocks. Some interviewees described least auklets as being too much trouble to harvest these days or only worth it so children can practice.

4.4.5 Economic outlook (Table 4.5)

Our surveys also explored perceptions of economic conditions and tourism. Economic outlook was equally poor on both islands, where for both communities the margin of error for per capita or household income overlaps the Alaskan poverty line (Alaska Department of Commerce, Community, and Economic Development at <http://commerce.alaska.gov/cra/DCRAExternal/community>). Overall 88% of respondents said the economic situation on the Pribilofs was getting worse, while only 10% felt it was improving. One interviewee said that seabird harvest was tied to the economy, with more harvesting occurring when there is less money available in the cash economy. Tourism was regarded favorably, with 87% believing it to be important to the economy of the islands. To our binary set of questions (there is too much tourism/there is not enough tourism) responses indicated 73% disagreement that there is too much tourism and 81% agreement that there is not enough, indicating consistent high levels of support for increasing tourism. Several interviews also indicated interest in expanding tourism, involving locals as guides, or collaborating to share knowledge with scientists. One interviewee described expanded tour guide opportunities positively saying people

would, “be really into that.” Others expressed interest in a children’s summer camp that could enable kids learn about seabirds.

4.5 Discussion

Our results support the prediction of a vulnerable community with strong interconnectedness and value for its environment and natural resources. These findings are also consistent with previous research: subsistence is declining and economic outlook is poor (Huntington et al. 2009). Economic outlook was grim, and most interviews also mentioned the economic contribution of subsistence harvest and the need for more economic opportunities on the islands. To contrast with this evidence of vulnerability, we found overwhelming support for the importance of seabirds as a cultural resource to the Aleuts, to the people of the Pribilofs, and to most respondents personally. The strongest aspect of this importance was the way seabird usage was a family experience and value. All memories of seabird harvesting were of family learning, coming of age, and ways in which children were taught to be valuable members of the community. For example, least auklet hunting was a way for children to contribute protein to the family, learn traditional harvesting techniques, and bond socially with family and community members (Orbach and Holmes 1983, and this study). However, the disconnect between values and practice found by Huntington et al. (2009) still stands. Less than 50% of households agreed with the statement, “My household relies on seabird subsistence.” When asked about seabird subsistence in general, the discussion always quickly turned to memories of hunts and harvests, but in most survey and interviews they were just that:

memories. Very little seabird subsistence occurs on the Pribilofs today, which has resulted in no conflict between seabird subsistence regulation and current practices, unlike fur seal subsistence and commercial harvests, which have been contentious in the past. The lack of discord over seabird subsistence is also in contrast to other Bering Sea communities where harvest demands remain very high and bird populations may be threatened (Artukhin 1991, Artukhin pers. comm.). Tourism development that benefits the local economy could keep harvest and conflict levels low while improving local economic conditions. We found few people who claimed to prefer seabird food, although elders expressed a desire for sharing the harvest. According to interviewees, seabird subsistence has declined as it was supplanted by the increased availability and ease of store-food access. Despite lack of current usage, survey results expressed knowledge of seabirds and a desire to learn more. The presence of current knowledge was also supported in the interviews, where comprehensive information on when and how to harvest seabirds was revealed. Developing seabird tourism could address the desire to learn more about seabirds, improve the local economy, allow the current seabird knowledge to be shared with youth and a wider tourist audience, and continue the current good relationships between subsistence users and regulators.

So, why is harvest low when interest in the resource and claims of knowledge are high? Our results indicate that this disconnect is driven economically and socially. Store food is more available than it has been to previous generations and may make the benefits of seabird subsistence less appealing, although subsistence fisheries and reindeer hunting still continue at high levels. In addition, the food from the store is easy to obtain,

requiring little effort and only cash as a tool to acquire it. However, several interview respondents indicated that seabird subsistence is preferred when economic times are hard, which was true of Huntington et al.'s (2009) findings on St. George as well. On St. Paul, seabird subsistence is more often undertaken for cultural rather than nutritional or economic reasons, a pattern seen in other communities as well (Merkel 2010). Socially, although interest in seabirds is high, reductions in the number of households participating in seabird subsistence mean that fewer children are learning how to harvest as they grow up, also commonly seen in modernizing northern communities (Moerlein and Carothers 2012). Only about a third of survey respondents relied on seabird subsistence at all, and rates of harvest may be much lower since sharing expands the use of the resource to households that may not harvest it themselves. Seabird reliance levels increased with age, demonstrating that the knowledge transfer to enable harvesting by younger generations may have stopped. Those who agreed that, "I know a lot about the seabirds of these islands," also considered seabirds personally important to them. Younger respondents also attached less importance to seabirds, indicating a break in the links of knowledge transfer, as has been seen in other Arctic communities (Moerlein and Carothers 2012). A connection here, between knowledge and importance is a point of vulnerability: seabirds will be less important to generations not raised to their importance as subsistence and cultural resources. Removal of these knowledge and experiential connections weakens the socio-ecological system, removing fallback options, lowering adaptive capacity, and decreasing resilience. This is true whether personal importance drives increased knowledge, or vice versa. In fact, it is likely that seabirds are more

important to those who have been taught about them, and also that those who consider seabirds important have learned more about them. The creation of interest and knowledge via education is an important way to strengthen a vulnerable system. An interest in the local environment and traditional ways of life that tie social systems to ecosystems will foster the strong community ties that help preserve remote communities. They are also a source of the adaptive capacity that provides the means for self-preservation. Trends toward modernization make it unlikely that a culture relying heavily on seabird subsistence for calories will return; but that does not mean seabirds do not have economic and cultural potential for these communities.

Interest in expanding tourism as an economic opportunity was expressed in interviews, and has been previously suggested in the literature (Young 1987; Sherwonit 1994). These results indicate that currently most knowledge of the system is of when and how to harvest birds. In a management sense, this indicates knowledge of when birds arrive (phenology), when and what the birds consume (references to a “fishy” taste being seasonally determined), and life history traits (e.g. when and how often birds will replace eggs). However, if a tourism industry is to be developed around the seabirds as an ecotourism draw, the development of human capital in the communities will be required, in order to develop paths of communicating current local knowledge to wider audiences, encourage acquisition of skills and infrastructure to increase tourism opportunities for locals and outside tourists. Cruise tourism is already occurring at the islands, but the involvement of locals is limited. Future development is likely to be of land-based tourism, which provides the most opportunity for extended stays, involvement in cultural

activities and education, and access to bird colonies that would maximize proximity and minimize disruptions. Cruise ships can disrupt foraging seabirds; and for the safety of both humans and birds, ships should not approach too closely to breeding colonies and foraging areas (Velando and Munilla 2011). Yet land-based tourism development will face uncertain air service, due to weather conditions, and the relatively high expense of rural accommodations. Challenges due to unpredictable weather are common in polar tourism development and may need to be addressed here as well (Stewart et al. 2007).

Tourism development in fragile polar ecosystems is a tricky proposition, and the careful involvement of communities is essential. It is crucial that development be locally owned and operated if the economic benefit is to remain in these communities and not be shunted to distant tour operators; heedless use by outside interests could marginalize local people and culture while also cutting out the local economy (Notzke 1999). The goal of a new tourism base in the Pribilofs would be to communicate local knowledge to a wider audience. In addition, that knowledge must be expanded with the additional knowledge of life history, systematics, and ecology that would interest bird-watching tourists.

Tourism is often seen in remote areas as a way to develop the local economy while also re-engaging youth with their own culture and traditions of land use (Chanteloup 2013).

Interviewees responded positively to questions about developing an ecotourism industry and also offered their own suggestions: for a summer camp that teaches children about local seabirds or for opportunities to share their own seabird knowledge with seabird researchers while learning about the seabirds from scientists' perspectives as well. Some

collaboration and exchange has already begun with the founding and expansion of the Seabird Youth Network (<http://www.seabirdyouth.org/>).

4.5.1 Conclusion

The economic situation in the Pribilofs is dire (Huntington et al. 2009) and subsistence continues to decline (Fall et al. 2013). The communities are vulnerable to continued economic change due to their peripheral location in a rapidly changing environment (Dryzek and Young 1985), reliance on external economic drivers, and history of exploitation and few economic opportunities (Young 1987). Yet the communities retain strong interconnectedness and place value on their environment and on seabirds. Tourism has large potential in this system and there is interest by community members (this study; Sherwonit 1994). However it will need to be managed carefully; local decision-making and control of tourism expansion are key (Sherwonit 1994; Mercurieff 1995). With input and care, seabirds are a highly sustainable resource and tourism could be managed to maximize economic benefit and minimize environmental impact.

4.6 Figures

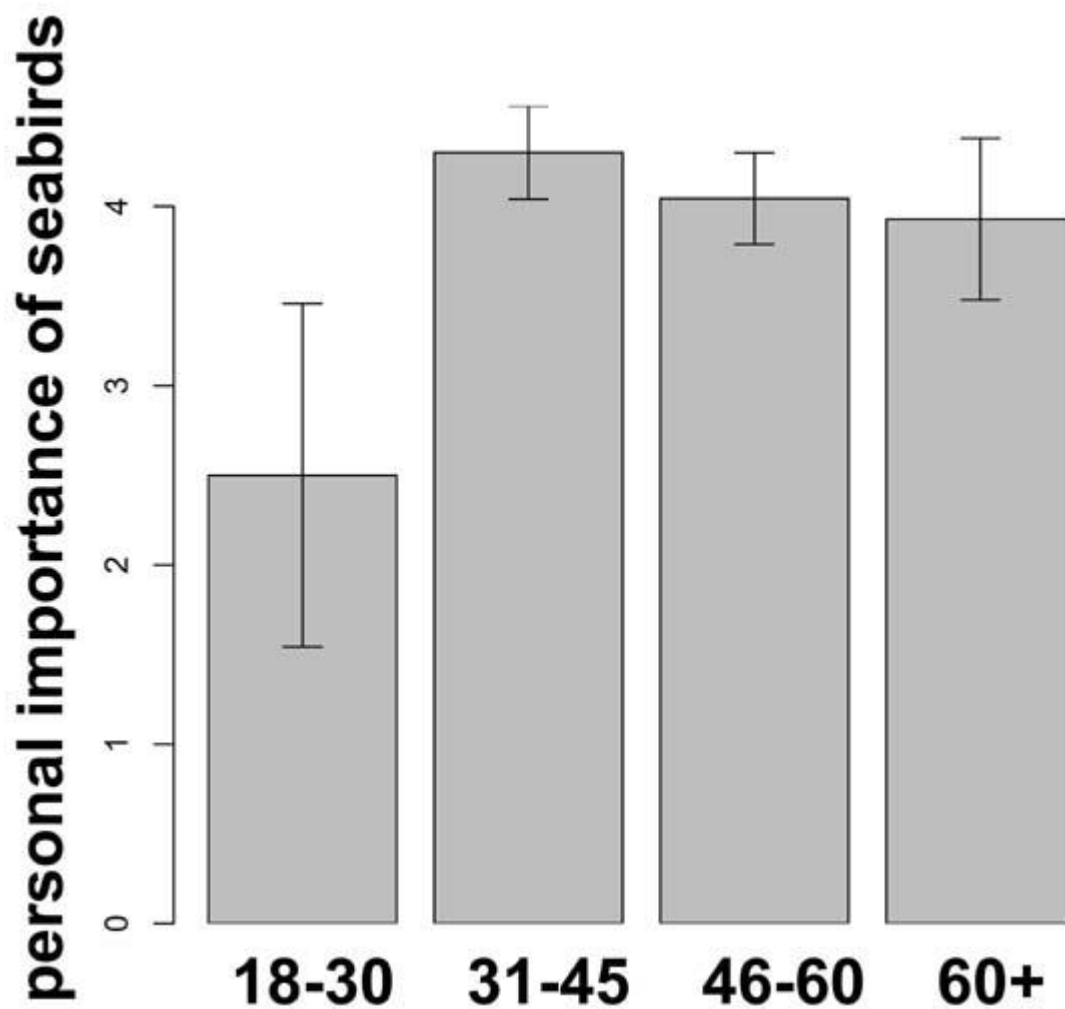


Figure 4.1 Importance of seabirds by age of respondent. Seabirds were consistently marked as more important by older members of the community.

4.7 Tables

Table 4.1 Demographic parameters. Census numbers are from the 2010 federal census, archived by the Alaska Department of Commerce, Community, and Economic Development at <http://commerce.alaska.gov/cra/DCRAExternal/community>, except for the “grew up on the Pribilofs” category, where they are from a 1994 Alaska Department of Fish and Game subsistence survey of households. Note, the 2010 census numbers reflect the entire population, where as our numbers reflect only heads of households responding to our survey. The differences in whole population versus heads of households are particularly noticeable in age and gender categories

Query	Category	St. Paul			St. George		
		Responses	Percent	Census	Responses	Percent	Census
Gender	male	24	80	53	16	73	58
	female	6	20	47	6	27	42
Ethnicity	Aleut	27	87	82	21	95	88
	non-Aleut	4	13	18	1	5	12
Income	< 25K	4	13		7	32	
Level	25-50K	7	23		7	32	
	50-100K	11	35		4	18	
	100+ K	4	13		0	0	
	<i>no response</i>	5	16		4	18	
Age	18-30 yrs	3	10	17	1	5	18
	31-45 yrs	7	23	22	2	10	16
	46-60 yrs	11	37	19	12	57	28
	60+ yrs	9	30	12	6	29	15
	<i>no response</i>	1	3		0	0	
Origin	grew up on Pribilofs	27	87	60.6	20	91	68.3
	not on Pribilofs	4	13		0	0	
	<i>no response</i>	0	0		2	9	

Table 4.4 Survey responses to statements assessing knowledge of seabird biology and harvest regulations. For each island the

sample size (n) responding to each question is given, along with the responses broken down according to the Likert scale: 1 =

Disagree; 2 = Somewhat Disagree; 3 = Neither; 4 = Somewhat Agree; and 5 = Agree. For each statement the percent of responses

agreeing and disagreeing is provided for each community. The last column indicates the percentage of responses in agreement with

the statement in the entire sample.

Seabird Knowledge	St. Paul								St. George							Both	
	n	1	2	3	4	5	Disagree (%)	Agree (%)	n	1	2	3	4	5	Disagree (%)		Agree (%)
Statement																	
Current harvest regulations are appropriate.	27	3	2	2	5	9	8	19%	63%	18	1	1	6	1	9	11%	56%
Current harvest regulations should be changed.	27	4	3	3	9	5	6	26%	41%	18	8	1	6	1	2	50%	17%
I know a lot about the seabirds of these islands.	31	3	3	3	6	11	8	19%	61%	20	0	0	5	8	7	0%	75%
I would like to know more about seabirds.	30	4	1	6	9	10	10	17%	63%	20	0	0	2	4	14	0%	90%
Seabirds are important to me personally.	31	6	0	3	7	15	15	19%	71%	21	1	0	5	3	12	5%	71%
Some kinds of seabird are doing better than others.	29	3	2	8	4	12	12	17%	55%	19	2	1	4	7	5	16%	63%

Table 4.5 Survey responses to statements assessing tourism attitudes and economic outlook. For each island the sample size (n)

responding to each question is given, along with the responses broken down according to the Likert scale: 1 = Disagree; 2 =

Somewhat Disagree; 3 = Neither; 4 = Somewhat Agree; and 5 = Agree. The last statement was not done on the Likert agreement

scale: A = worse; B = stable; and C = improving. For each statement the percent of responses agreeing and disagreeing (or claiming

worse vs. improving) is provided for each community. The last column indicates the percentage of responses in agreement with the

statement in the entire sample. For the last statement, it indicates those who felt the economy was getting worse.

Economic Outlook		St. Paul							St. George							Both	
Statement	n	1	2	3	4	5	Disagree (%)	Agree (%)	n	1	2	3	4	5	Disagree (%)	Agree (%)	Agree (%)
Tourism is important to the Pribilovian economy.	31	2	1	1	7	20	10%	87%	21	2	0	1	3	15	10%	86%	87%
There is too much tourism on the Pribilofs.	31	1	8	6	2	0	74%	6%	21	11	4	4	1	1	71%	10%	8%
There is not enough tourism on the Pribilofs.	31	1	3	3	4	20	13%	77%	22	0	1	2	4	15	5%	86%	81%
Statement	n	A	B	C	-	-	Worse	Better	n	A	B	C	-	-	Worse	Better	Worse
Is the economic situation on the Pribilofs improving or getting worse?	28	2	0	3	-	-	89%	11%	20	17	1	2	-	-	85%	10%	88%

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Conclusion

Major Findings

Biological age is an important emerging concept in ecology. It is often compared to a “weathering” process (Tsuji et al. 2002, Aviv 2006, Alviggi et al. 2009, Geronimus et al. 2010) through which the soma becomes more degraded due to environmental factors or genetic predispositions to various rates of decay . It can also be characterized as residual lifespan (Martin and Festa-Bianchet 2011), or as an aging biomarker which captures the organism’s proportional progress through life (Monaghan and Haussmann 2006). This thesis has addressed telomere length in relation to chronological age, physiology, and behavior of a long-lived seabird, the thick-billed murre (*Uria lomvia*). Long-lived seabirds are excellent candidates for life history and behavioral studies of telomere length as they, like most birds, live exceptionally long for their body size (Holmes and Austad 1995) and, even for birds, exemplify the “slow-lived” paradigm of low fecundity and high adult survival (Gaston and Jones 1998).

In chapter one, we compared known chronological ages to telomere length in thick-billed murre chicks and adults. We found that chicks had longer telomeres than adults, but loss rates among adults were negligible. However, although telomere length did not differ between the sexes as chicks, adult females had significantly lower telomere length than males. This finding is in contrast to the patterns observed in humans and many other species studied, where adult males have shorter telomeres than females (Barrett and Richardson 2011); even in other seabird species females had longer telomeres than males (Foote et al. 2011). The difference in murre (i.e. that females have

shorter telomeres) may be due to male-biased parental investment patterns that result in selection for longer life in males (Young et al. 2013), or to genetic and hormonal differences in mutation accumulation and protection against aging mechanisms (Kyo et al. 1999, Horn et al. 2011). Regardless of the cause, this difference implies that monomorphism in size and plumage may not extend to aging patterns and physiological mechanisms and that sex needs to be accounted for in studies of biological aging.

The second chapter addressed physiological and reproductive investment patterns in thick-billed murres of unknown age by environmental quality (proxied by colony), sex, and biological age. Biological age was measured as telomere length, as telomeres incorporate chronological age along with non-linear and individual-level aging processes. Our two distinct hypotheses were 1) that biologically older birds, with shorter telomeres, would be in poorer state and invest less (i.e. detrimental aging) or 2) that biologically older birds would be in higher physiological state and invest more in their offspring (i.e. beneficial aging). The first hypothesis predicts senescence, while the second is consistent with theories of constraint, restraint, and terminal investment (Dugdale et al. 2011). We found that behavioral investment was independent of biological age, implying that maintenance of consistent levels of parental care is prioritized, and reproductive costs, which may increase with age (Clutton-Brock 1984), are paid physiologically instead of behaviorally. The first hypothesis, that older birds would be more stressed, was supported on Bogoslof, a food-rich colony. The second hypothesis, that older birds would show lower stress levels, was supported on St. Paul, the island with overall poor foraging conditions. Under the best foraging conditions (Bogoslof) older birds were

more stressed; under poor conditions (St. Paul) they were less stressed than young birds, and at intermediate conditions (St. George) there was no age-related pattern. These findings, in conjunction with the gradient of colony conditions, led to the development of our “senescence and experience conceptual model” (chapter 2). This model states that when conditions were good, experience had no apparent benefit – i.e. when food was readily available, the skills and experience of age did not provide an added edge. There was support for both detrimental and beneficial aspects of aging and the degree to which they are expressed was environmentally determined. It is important to emphasize the role that environment plays in determining the expression of phenotype. Not only does behavior and phenotypic fitness change through time (i.e. with age, Lecompte et al. 2010), but also through space (Elliott et al. 2010).

Chapter three builds on the findings and framework of chapter two, to look at how the effects of biological age, sex, and environment (colony) affect foraging habitat selection and prey selection. Here, we found that each driver played a pivotal role in determining habitat use. Foraging behavior indicated that older birds retain their ability to use the environment efficiently, which was consistent with previous findings that older murres remain behaviorally flexible, despite paying physiological costs (Ch 2, Elliott et al. submitted). However, age did affect spatial and temporal habitat use, as well as prey selection. Females and males aged differently in spatial use of the environment, emphasizing the importance of sex to aging patterns behaviorally as well as physiologically. Prey selection was related to colony; changes in murre trophic level depended on age, but their direction also depended on habitat quality. Support for the

increased foraging ability of older birds indicated that experience outweighing senescence, especially for prey selection. Mechanisms consistent with senescence and experience appear to be working simultaneously, allowing organisms to modify behavior depending on environmental conditions as they age.

The findings of the first three chapters indicate that biological aging processes play an important role in determining organisms' fitness, behavior, and reaction to the environment. Further, the relationship with population processes makes biological age a demographically relevant state. It ought to be possible to parameterize life history models using biological age states, comparable to the way age classes are currently used in matrix models. A fundamental difference is that transitioning between age class x to $x+1$ is a given in chronological age models, whereas state transitions for biological age include a) the possibility to remain in the same state, b) the possibility of becoming biologically "younger," and c) the opportunity for different rates of aging (e.g. given two organisms of biological age x , one organism may age into stage $x+1$, while another enters $x+2$).

In a similar vein, this work also lends itself to demographic descriptions of colonies at a given time of sampling. If telomere dynamics are well established for a given species (or population) it ought to be possible to use average telomere length to predict dominant behavioral patterns, and potentially colony health. Intra-specific comparisons would be the easiest, but if telomere patterns are well-known for a group of species, patterns relative to species-specific norms may be comparable. Care would need to be taken since telomere lengths are species-specific and are not directly comparable.

Such biological age species surveys could be of use to managers or others looking to analyze effects of conditions on different species.

Despite the lack of direct comparability across species, closely-related species could also provide fodder for work on the evolutionary origins and effects of life history traits and demographic parameters. Studies of clades of relatively recently diverged species may allow more direct comparisons of telomere lengths and the differences between groups may be able to be linked to phylogenetics or evolutionary differences in lineages based on their life history. David Lack's seminal work, *Ecological Adaptations for Breeding in Birds* (Lack 1968), by necessity includes little work on the effects of aging (chronological or biological) since such studies were rare at the time. However, the development of biological aging as a tool for predicting behavior and fitness could lead to comparable studies about the role of aging in the evolution of that behavior and fitness in birds or wider taxa.

The first three chapters explored telomere dynamics and the relationships of biological age to behavior and physiology in a single species. Although telomeric ecology is expanding in its use of telomere length to predict lifespan or survival, studies where behavioral effects are measured are still rare. Our work uses telomeres as an ecophysiological tool, like corticosterone levels or immune responsiveness. Behavior of birds within the ecosystem is predicted using telomere length, without committing to causality. Birds may lose telomeres because of behavioral choices or may make behavioral choices because of phenotypic changes reflected in the telomere measurement.

This work ties ecology, behavior, and physiology to genetic and molecular studies of aging.

In addition, this thesis ties the behavior and physiology of long-lived species to the wider social-ecological system; the fourth chapter dealt with the role of seabirds as a resource with cultural and economic value to the people of the Pribilofs. A common theme throughout our interviews and survey results was overwhelming support for seabirds as a cultural resource. Our work confirmed previous findings that seabird subsistence activities are declining in these communities (Fall et al. 2013). Though few respondents continued to harvest seabirds, a large majority agreed that seabirds were important to the Pribilofs, Aleuts, and to the respondents personally. Seabirds are remembered as bringing families together, as providing added nutrition in hard times, as symbols of defiance in the face of oppression from outsiders, and as an important part of growing up on the Pribilofs. In addition, respondents agreed that the economies of the islands are doing poorly (see also Huntington et al. 2009) and that tourism increases would be welcomed. Such development must be initiated by the people of the Pribilofs if it is to benefit local economies and reconnect people to seabirds as a cultural resource. The most common suggestion from our interviews was that children could become more involved in seabird education. This has already begun, using such platforms as the Pribilof Marine Science Camp and the Seabird Youth Network, both of which link natural systems and current research to science curricula for local children. These educational opportunities and the love of learning and of seabirds developed therein lay

the best possible foundation for future expansion of seabird-human relations and for future collaboration between researchers and the local people.

The communities are vulnerable to continued economic change due to their peripheral location in a rapidly changing environment (Dryzek and Young 1985), reliance on external economic drivers, and history of exploitation (Young 1987). Yet the communities retained strong interconnectedness and place value on their environment and on seabirds. Tourism has large potential in this system, and there was interest by community members in developing this potential (Ch. 4, Sherwonit 1994). However it will need to be managed carefully; local decision-making and control of tourism expansion are key (Merculieff 1995, Notzke 1999). With input and care, seabirds are a highly sustainable resource, and tourism could be managed to be low-impact.

Future Research Directions

This work has provided a lot of groundwork in telomere dynamics in relation to behavior and physiology of a long-lived seabird. As an emerging field, telomeric ecology still has a lot of unanswered questions. For example, the sex differences that we observed in adult murre telomere length are tantalizing. More work could be done comparatively to see how widespread this phenomenon is. A large comparative study of telomere length between adults of many species would allow analysis of life history or phylogenetic patterns. It would likely be advisable to confine such an analysis to within one taxon, especially one with diverse patterns of mating systems and lifespans. Birds

represent such diversity, and are therefore good candidates for such a comparison, or even at lower levels such as the Charadriiformes or Passeriformes.

The findings presented in this thesis also have bearing on the effects of reproductive effort and investment on aging and lifespan; however they do not directly test the causality of those projected effects. Although these experiments are difficult to carry out, it should prove fruitful to examine how increased reproductive effort affects telomeric decay and thus survival. Experimental designs which manipulate effort (e.g. handicapping to increase effort or manipulating chick needs to decrease effort) could be a first step towards controlling for variation in individual quality and annual variation that currently confound many observational studies. Captive studies would be useful to determine fine-scale effects of the cost of reproduction or immune activity on telomere loss and lifespan. Use of non-model systems in approximately natural conditions would expand the usefulness of such studies. Model systems, especially laboratory rodents, have undergone such extensive artificial selection or are chosen because they are so fast-living that their utility in expanding our understanding of the range of aging in natural environments and slower-lived organisms is limited.

The middle chapters of this thesis address the drivers of change with age: experience and senescence. Experience is primarily beneficial aging, providing knowledge of the environment and how to extract resources and produce offspring efficiently. Senescence is the reverse, detrimental aging that reflects increased mortality and the decay of somatic systems. This research demonstrates that the effects of one process do not swamp out the other, but that environment, and likely individual

characteristics determine whether time improves or worsens performance. Future work could also continue to address this tradeoff. Which conditions are best suited to favor experience over senescence and why? Does the environment select for phenotypes best able to modulate experience and senescence responses to the habitat quality presented? Or does plasticity fit a “good” phenotype to excel in any environment? Longitudinal tracking of individuals, as they accumulate experience and as the environment fluctuates along with their own aging processes, would be an excellent way to relate the ultimate measure of success – lifetime fitness with measurable demonstrations of experience or senescence.

Interdisciplinary work, like that comprising chapter four, is becoming more and more common, especially as ecology, conservation, and biology start to work more closely with social-ecological systems instead of nature as separate from humans (Chapin et al. 2009). Working and taking courses in this field has been a valuable part of this thesis. These experiences taught me new ways of thinking about the connections between humans and the world, exposed me to other ways of knowing, gave me access to the resilience and sustainability framework of terminology and thought, and showed me that the days are gone when researchers could remain entirely departmentalized. The Bering Sea Integrated Ecosystem Research Project, in which I participated during this degree, was an excellent example of the type of large-scale, multi-level interdisciplinary research projects that can address ecosystem-level questions in our changing world. The ability to reach across the disciplinary divides and understand the importance of social-

ecological research is one of the best tools derived from this work. I hope to continue such collaborations and involvement in comprehensive projects in the future.

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