AN ABSTRACT OF THE THESIS OF

Nicholas R. Hatch for the degree of Master of Science in Wildlife Science presented on December 5, 2011.

Title: Foraging Ecology and Reproductive Energetics of the Kittlitz's Murrelet (*Brachyramphus brevirostris*) in Southeast Alaska.

Abstract approved:

_____

Daniel D. Roby

The Kittlitz's murrelet (*Brachyramphus brevirostris*) is a species of conservation concern over the entirety of its known range, which spans coastal Alaska and northeastern Russia. Concerns about the status of the species have been raised due to evidence of population declines in key breeding areas, low reproductive output, and perceived threats to adult survival. A general lack of information related to vital rates and natural history for this species has hampered efforts to address potential threats and drivers of population decline. This thesis addresses the hypothesis that foraging conditions and nutritional stress may be related to the observed low reproductive output and apparent population declines. I used stable isotope analysis of Kittlitz's murrelet feathers and blood to assess foraging habits during four separate periods across the annual cycle. I also used stable isotope signatures ($\delta^{15}N$ and $\delta^{13}C$) in

feathers from museum specimens collected in southeastern Alaska during 1907–1984 to investigate potential long-term trends in food habits and foraging ecology. I found that $\delta^{15}N$ progressively increased by 5‰ between the vernal pre-alternate molt and the autumnal pre-basic molt, equivalent to an increase of 1.5 trophic levels for assimilated prey, whereas seasonal patterns in $\delta^{13}C$ suggest shifts in foraging habitat between breeding and non-breeding periods. These results indicate that the pre-breeding diet was comprised primarily of low trophic level prey from offshore habitats, such as macrozooplankton and/or larval fish. During the summer breeding season, Kittlitz's murrelets gradually switched to consuming higher proportions of planktivorous fish from nearshore habitats. By the post-breeding period, during the pre-basic molt, the diet was comprised almost exclusively of higher trophic level prey, presumably forage fish, from offshore habitats. Based on stable isotope signatures of murrelet feathers from museum specimens, these seasonal patterns were evident during the past century (1907-2009). $\delta^{13}C$ in feathers grown during pre- and post-breeding (pre-alternate and pre-basic molts, respectively) became significantly more depleted over the last century, however, suggesting either a gradual change in diet and/or foraging habitat or a long-term shift in the isotopic composition of prey.

I investigated potential energy constraints on reproduction in Kittlitz's murrelets by constructing a bioenergetics model to estimate energy budgets for breeding adult Kittlitz's murrelets under different scenarios of prey energy content and commuting distance between foraging areas and nest sites. Estimated field metabolic

rate (FMR) of breeding Kittlitz's murrelets during the chick-rearing period exceeded the hypothetical maximum sustainable working capacity (MSWC; 4 times basal metabolic rate [BMR]) under empirically derived scenarios of prey energy content and commuting distance. This suggests that, under conditions of low energy content in available prey and/or long commuting distances to inland nest sites, Kittlitz's murrelets would be required to expend energy at a rate that, if maintained over an extended period, could be detrimental to subsequent adult survival and overall fitness. In addition, energy expenditure rates at the high end of the estimated range may exceed the rate at which food energy can be assimilated by adult murrelets. Metabolism of fat reserves, as indicated by mass loss during the breeding season, may be a partial, although limited, solution to periods of high energy demand for breeding adults.

This thesis research is the first to indicate that Kittlitz's murrelets rely on distinctly different prey resources during different periods of the annual cycle. The previously unappreciated seasonal complexity of Kittlitz's murrelet foraging ecology offers a new perspective on potential factors limiting survival and reproduction in this species of conservation concern. In addition, my research suggests an adaptive explanation for the low breeding frequency and low reproductive output of Kittlitz's murrelets that is related to the exceptionally high energy expenditure rates required to raise young at nest sites as much as 70 km inland from the coast and up to 2,500 m above sea level. Because of their high level of reproductive effort, Kittlitz's murrelets

may be more dependent on the high availability of high-lipid marine prey than other seabirds.

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Foraging Ecology and Reproductive Energetics of the Kittlitz's Murrelet (*Brachyramphus brevirostris*) in Southeast Alaska

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Nicholas R. Hatch, Author

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Dr. Daniel Roby (USGS – Oregon Cooperative Fish and Wildlife Research Unit, Corvallis, Oregon) and Michelle Kissling (USFWS – Juneau Field Office, Juneau, Alaska) contributed to the overall study design, analysis, and editing of all chapters of this thesis. Michelle Kissling secured funding, provided logistical support, and developed the foundation of research on which this study was based.

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FORAGING ECOLOGY AND REPRODUCTIVE ENERGETICS OF KITTLITZ'S MURRELET (*BRACHYRAMPHUS BREVIROSTRIS*) IN SOUTHEAST ALASKA

CHAPTER 1

GENERAL INTRODUCTION

AND BACKGROUND

Nicholas R. Hatch

The Kittlitz's murrelet (*Brachyramphus brevirostris*) is a small seabird endemic to Alaska and eastern Russia. This species belongs to the seabird family Alcidae, comprised of pursuit-diving planktivores and piscivores. Worldwide population estimates for Kittlitz's murrelets range between 30,900 and 56,800 individuals (USFWS 2010), with ca. 80% residing in coastal Alaska from LeConte Bay to the south, the Near Aleutian Islands to the west, and Barrow to the north (Day et al. 1999). Recent studies suggest this species has experienced precipitous, range-wide population declines of up to 18% per annum in the last 20 years, but have stabilized in recent years (Kuletz et al. 2011, Piatt et al. 2011; USFWS 2010). Kittlitz's murrelet is on the International Union for the Conservation of Nature (IUCN) Red List of critically endangered species (BirdLife International 2010), is considered one of the most endangered seabirds in the United States by the National Audubon Society (2006), and has been a candidate species for listing under the U.S. Endangered Species Act since 2001 (USFWS 2010). Due to its cryptic nature and remote distribution, however, in-depth study of the basic ecology of this species has been extremely challenging. This lack of information has hampered and limited efforts at management and conservation of the species.

Most seabird research is conducted during the breeding season, when adults tend to congregate in colonies where many individuals are relatively easy to study. However, the non-breeding season may be a period of relatively high adult and first-year subadult mortality. Also, the non-breeding period is when future breeding individuals prepare for reproduction by accumulating energy stores, forming pair

bonds, and, in some species, completing a full feather molt. Over-winter nutritional stress in seabirds may lead to delayed or aborted breeding attempts during the subsequent breeding cycle (Daunt et al. 2006). Therefore, the effects of over-winter stress may not manifest through direct mortality, but through reduced productivity in the following reproductive cycle. This in turn has major implications for population status through lowered fecundity and lower subsequent recruitment (Harris et al. 2007). The distribution and foraging habits of seabirds during winter are important components of life history that are not well known for the majority of seabird species. For declining seabirds, this information may be vital to effective conservation and restoration.

Like other *Brachyramphus* species, Kittlitz's murrelets have evolved an anti-nest-predator strategy unique among seabird taxa. Rather than nesting colonially or semi-colonially on coastal cliffs, or in burrows on offshore islands, Kittlitz's murrelets nest singly on the surface of the ground at remote sites up to 70 km from the coast and up to 2,500 m above sea level (Day et al. 1999; MLK, unpublished data). In many parts of their range Kittlitz's murrelets are closely associated with glacial systems and tend to nest in recently de-glaciated rocky outcrops, including nunataks, that have very limited, if any, established plant communities. In non-glaciated areas (Aleutian Islands and northern Alaska), murrelets nest on mountaintops or on high elevation scree fields similar in character to recently de-glaciated habitats. This preference for dispersed and remote nest sites in rugged terrain has made the study of breeding ecology difficult, resulting in a paucity of information on nesting. Prior to 2006, fewer than 50

nests of Kittlitz's murrelets had been documented, most discovered haphazardly by hikers (Day 1995, Day et al. 1999, Piatt et al. 1999). Since 2006, ca. 90 additional nests have been found through nest searching (Kaler et al. 2006; M.J. Lawonn, unpublished data; M. Kissling, unpublished data) or radio-tracking of adult murrelets (Kissling et al. 2007; A. Allyn, unpublished data; M. Kissling, unpublished data; S. Gende, unpublished data).

Kittlitz's murrelets are monogamous and lay a single large egg (20-25% of adult body mass) in a small depression near the top of scree fields, often just down slope of a large boulder (Day 1995; Day et al. 1999; Piatt et al. 1999; M. Kissling, unpublished data). Breeding adults share incubation duties, trading 24-48 hour incubation shifts until hatching, roughly 30 days after laying (Day et al. 1999; M. Kissling, unpublished data). The chick is provisioned with up to 10 whole fish per day, delivered one at a time by one or both parents (Day et al. 1999; M. Kissling, unpublished data). The nestling fledges after 24-30 days at the nest, making its first flight from the nest site to the ocean. Once on the water, it is presumed that fledglings head out to sea with no post-fledging parental care (Day et al. 1999). Adults start to leave the breeding grounds in mid- to late-July, with few individuals remaining by mid-August (Kissling et al. 2007). Post-fledging activities of adults are not well known. It has been suggested that post-breeding adults fly offshore to the Gulf of Alaska and remain there for the remainder of the non-breeding season (Day et al. 1999). Recent evidence, however, suggests larger post-breeding movements out of the Gulf of Alaska may be quite common (M. Kissling, unpublished data).

Many seabird species and other top marine predators in the North Pacific have experienced population declines over the past 30 years (Anderson and Piatt 1999). Numerous studies have related these declines to changes in food web dynamics that result in declines in the primary prey types for these top predators (Atkinson et al. 2008, Cairns 1987, Kitaysky et al. 1999, Jodice et al. 2006), particularly during the breeding season (Kitaysky et al. 2006). There is mounting evidence that climatic events, such as shifts in large-scale oceanographic regimes and/or anthropogenic perturbations of the marine ecosystem through intensive fishing pressures, are driving these food web shifts in many regions (Anderson et al. 1997, Anderson and Piatt 1999). Recent studies suggest that Kittlitz's murrelets are one of these declining species, but there is no direct evidence for the primary mechanism of the decline (USFWS 2010). While the ultimate causes for the decline remain unclear, it has been suggested that changes in the distribution and availability of forage fishes may be related to declines in this and other piscivorous seabirds in the Gulf of Alaska (USFWS 2010).

Kittlitz's murrelets are neritic foragers during the breeding season, feeding mostly on schooling forage fishes, such as Pacific sand lance (*Ammodytes hexapterus)*, juvenile Pacific herring (*Clupea pallasi*), and capelin (*Mallotus villosus*), as well as macrozooplankton, such as euphausiids and copepods (Day et al. 1999). However, the food habits and nutritional requirements for Kittlitz's murrelets are poorly understood. The quality of prey items can vary among prey types, habitats, and seasons (Jangard 1974, Hislop 1991). Robards et al. (1999) showed that the lipid content and total

energy density of Pacific sand lance varied seasonally, but tended to coincide with seasonal peaks in energy demands of their predators. There is evidence that the timing of seasonal peaks in primary productivity may influence the timing of productivity at higher trophic levels (Henson and Thomas 2007). For seabirds that have a specific temporal window in which to produce young, shifts in the timing of productivity may lead to poor reproductive success due to asynchrony with prey resources (trophic mismatch; Safina et al. 1988, Aebischer et al. 1990, Monticelli et al. 2008). Understanding the temporal variability in prey resource utilization is integral to determining how energetic bottlenecks may affect predator populations and, ultimately, the mechanisms of their decline.

There is strong evidence that Kittlitz's murrelets are experiencing low rates of reproduction and recruitment in many core population areas (Van Pelt and Piatt 2003; Kaler et al. 2009; M. Kissling, unpublished data). In Prince William Sound, Day and Nigro (2004) found little evidence of successful reproduction over a 3-year study period. This may have been due to poor food resources prior to the breeding season, leading to a failure to achieve the threshold physiological condition for breeding. Conversely, individuals may have initiated breeding, but failed during either the incubation or chick-rearing period. Kaler et al. (2009) reported low (and potentially unsustainable) reproductive success on Agattu Island, Aleutian Islands, USA, presumably due to nest abandonment and insufficient nestling provisioning rates. If food resources are not sufficiently available at the critical time, then natural selection

may favor individuals that forego or abort reproduction and thereby enhance residual reproductive value.

This thesis aimed to investigate two different aspects of Kittlitz's murrelet ecology, both of which are integral to our understanding of how to manage, restore, and conserve this species. In Chapter 2, I investigated the foraging habits of Kittlitz's murrelets using stable isotope analysis to assess variability in the diet of adult Kittlitz's murrelets over 3 different temporal scales: (1) inter-seasonal, (2) inter-annual, and (3) long-term (over the last century). In Chapter 3, I (1) construct a bioenergetics model to estimate the overall metabolic demands of breeding Kittlitz's murrelets and (2) use this model to test the sensitivity of adult energy expenditure rates to the observed variation in commuting distance between foraging areas and nest sites and in the energy content of prey delivered to nestlings, as it influences energy provisioning rates to the nest. Chapter 4 provides a general summary, synopsis, conclusions, and some ideas for future research.

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CIRCANNUAL PATTERNS IN THE FORAGING ECOLOGY OF KITTLITZ'S MURRELETS (*BRACYRAMPHUS BREVIROSTRIS*) AS INFERRED FROM STABLE ISOTOPE ANALYSIS

CHAPTER 2

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Abstract

We investigated seasonal changes in the foraging ecology of Kittlitz's murrelets (*Brachyramphus brevirostris*) using stable isotope signatures ($\delta^{15}N$ and $\delta^{13}C$) from feathers and blood. Murrelets foraged relatively further offshore and at a lower trophic level (zooplanktivory) during pre-breeding, and then moved inshore and foraged on a more diverse diet including zooplankton and forage fish during both the early (May/early June) and late (late June/July) breeding season. Post-breeding season, murrelet tissues were depleted in carbon and highly enriched in nitrogen, suggesting a post-breeding migration from nearshore summering areas to isotopically distinct wintering areas and consumption of high trophic level forage fish. Based on stable isotopes from museum specimens, these seasonal patterns were relatively consistent during the past century (1907-2009). Carbon isotope signatures during pre- and post-breeding became significantly more depleted over the last century, however, suggesting either a gradual shift in diet and foraging habitat or a change in the isotopic composition of prey over the long-term. The most striking finding from this study was that the foraging strategies of Kittlitz's murrelets differed markedly with season and birds over-wintered in regions and fed on prey that were isotopically very distinct from those used during the breeding season.

Introduction

Seabirds rely on ephemeral and irregularly distributed food resources that can vary in availability both seasonally and inter-annually (Piatt et al. 2007, Ronconi 2008). During the breeding season, nesting seabirds are constrained to foraging within commuting distance of their nest site, thereby potentially limiting options for foraging on certain prey types and in certain marine habitats. Outside of the breeding season, during the inter-nesting period, seabirds are not constrained spatially, but may encounter adverse environmental conditions, lower prey availability, or more patchily distributed food resources (Fort et al. 2009). The inter-nesting period is when adults prepare for reproduction by accumulating adequate nutrient stores (Sorensen et al. 2009) and, in some species, by completing a full feather molt (Pyle 2009). Over-winter nutritional stress may lead to delayed or aborted breeding attempts during the subsequent breeding cycle (Daunt et al. 2006, Sorensen et al. 2009), thereby reducing productivity (Baird 1990, Hatchwell 1991, Chastel et al. 1995). Over-winter distribution, habitat use, and diet composition are key components of seabird life histories and, for declining seabirds, this information may be vital to conservation and restoration.

Stable isotope analysis (SIA) has become a prominent tool in the study of the foraging ecology of various marine taxa (see review by Bond & Jones 2009) and avoids some of the pitfalls of more commonly used techniques, such as foregut content analysis (Barrett et al. 2007) and direct observation of prey being

captured and consumed. Ratios of stable isotopes of nitrogen in consumer tissue ($^{15}N/^{14}N$) indicate relative trophic level (DeNiro & Epstein 1978, Steele & Daniel 1978). In marine environments, these ratios have been shown to enrich by 3 – 4 parts per thousand (‰) per trophic level due to preferential excretion of the lighter isotope during tissue synthesis (Hobson et al. 1994, Kelly 2000, Wisegarver 2008). Stable carbon isotope ratios ($^{13}C/^{12}C$) are used to infer foraging location because they become progressively depleted across a nearshore/offshore gradient due to differences in primary production between nearshore and offshore zones (DeNiro & Epstein 1978, Rau et al. 1983, Peterson & Fry 1987, Kelly 2000). Thus, consumers foraging further offshore will have a depleted (more negative) stable carbon isotope signature compared to those foraging in a nearshore environment (Hobson & Welch 1992, Hobson et al. 1994). Using stable isotope signatures of both consumer and prey, it is possible to determine the relative trophic level, foraging habitat, and general diet composition of consumers.

SIA has been used to infer diet in sensitive species (e.g., Balearctic shearwater [*Puffinus mauretanicus*]; Navarro et al. 2009), diet during the non-breeding period (e.g., Wilson's storm-petrel [*Oceanites oceanicus*]; Quillfeldt 2002), and long-term shifts in diet (e.g., marbled murrelet [*Brachyramphus marmoratus*]; Becker & Beissinger 2006, Norris et al. 2007). Dalerum and Angerbjorn (2005) outlined three methods for assessing temporal variability in diet composition using SIA by (1) longitudinal sampling of the same tissue from an

individual consumer (e.g., sampling blood repeatedly from one individual); (2) serial sampling of a tissue that is grown continuously over the lifespan of the consumer (e.g., vibrissae or baleen); and (3) one-time sampling of multiple tissues with different periods of synthesis (e.g., different feather types) or with different rates of isotopic turnover (e.g., muscle vs. bone) from the same individual.

The Kittlitz's murrelet (*Brachyramphus brevirostris*) is a small member of the seabird family Alcidae that is endemic to coastal Alaska and eastern Russia. The Kittlitz's murrelet, like other *Brachyramphus* murrelets (of which there are 2 other extant species), are unique among the Alcidae in that they nest solitarily, and in Kittlitz's murrelet the preferred nesting habitat is recently de-glaciated or non-vegetated rocky slopes, possibly far from the sea (up to 70 km; Day et al. 1999). During the breeding season, Kittlitz's murrelets are often observed foraging near shore in coastal regions or in deep, protected bays and glaciated fjords characterized by cold, low-salinity waters with high turbidity, and proximity to suitable nesting habitat (Day et al. 1999, Arimitsu et al. 2009). Winter distribution and marine habitat use are not well known other than a general movement away from protected bays and fjords that are occupied during the breeding season (Day et al. 1999).

Due to their cryptic habits, both during nesting and at sea, there is a paucity of information pertaining to the diet of Kittlitz's murrelets, especially during the non-breeding season. Gut contents of Kittlitz's murrelets collected during summer

in Alaska suggest they forage on both neritic forage fishes and macrozooplankton, but are closer to a secondary carnivore (foraging on planktivorous fish) than a primary carnivore (foraging on herbivorous zooplankton; Mearns et al. 1981, Sanger 1987). Using stable isotope signatures of muscle tissue collected during the late breeding season, Hobson et al. (1994) confirmed these results and estimated that murrelets foraged on ~70% fish and ~30% zooplankton during the breeding season. A single sample of foregut contents from a Kittlitz's murrelet collected in winter was dominated by macrozooplankton at the time of collection (Day et al. 1999), suggesting that Kittlitz's murrelets may occupy a different trophic level outside the breeding season.

The Kittlitz's murrelet is a candidate for listing under the U.S. Endangered Species Act primarily due to reported population declines and potential threats in core breeding areas across the known range of the species (USFWS 2010). Declines in local populations between 63% and 85% have been reported in Lower Cook Inlet (-84% between 1993 − 1999; Kuletz et al. 2011a), Prince William Sound (-63% between 1989 – 2004; Kuletz et al. 2011b), and Glacier Bay, Alaska (-85% between 1991 – 2000; Piatt et al. 2011). Similarly, there is complimentary evidence of low reproductive success in several key nesting areas (e.g., Day & Nigro 2003; Kaler et al. 2009; MLK, unpublished data). The mechanisms and causes of these declines are unknown, but changes in prey resources have been

suggested as a primary driver for declines in numerous apex predators in the Gulf of Alaska (Agler et al. 1999, Anderson & Piatt 1999).

We investigated diet composition and trophic position of Kittlitz's murrelets using SIA at three temporal scales: (1) inter-seasonally, (2) inter-annually, and (3) long-term (inter-decadal) as a means of assessing longitudinal changes in foraging habits. Specifically, we characterized murrelet diet using stable isotope signatures of tissues synthesized during four different periods in the annual cycle: pre-breeding, early breeding, late breeding, and post-breeding. We then compared variability in seasonal changes across years (2006-2009) and decades (1907-2009). We also examined the relationship between diet and explanatory factors related to reproduction, including gender and, in females, vitellogenin (VTG), a yolk precursor protein (Vanderkist et al. 2000).

Materials and Methods

Study Site

We conducted field work in Icy Bay, Alaska, USA (59°58'16.93"N, 141°23'3.23"W), a tidewater fjord located on the coast of the Gulf of Alaska ca. 100 km west of Yakutat, Alaska (Figure 2.1). Four tidewater glaciers and one piedmont glacier, the largest in the world, feed into the head of the bay, strongly influencing the oceanographic character of the marine environment by reducing

sea surface temperatures, reducing salinity, and increasing primary productivity through increased transport of terrestrial nutrients (Hood et al. 2009).

Murrelet Sample Collection

In Kittlitz's murrelets, individual feathers are grown over a period of about 10-15 days (Sealy 1975, Pyle 2009) and are isotopically inert once grown (Hobson and Clark 1992). Thus, the isotopic signature of feather material is a reflection of the diet during the few weeks prior to molt. Murrelets undergo a partial pre-alternate molt in March-April (pre-breeding period), during which dark-tipped breast feathers are grown prior to arriving on the breeding grounds (Sealy 1977). In August-September (post-breeding), murrelets grow all-white body feathers and replace primary and secondary flight feathers during the pre-basic molt (Sealy 1977, Pyle 2009). Similarly, red blood cells are continually being replaced, with a turnover rate of roughly 30 days (Hobson and Clark 1992). Thus isotopic signatures of blood reflect diet during the 20-30 days prior to blood sampling.

We collected blood and feather samples from adult Kittlitz's murrelets during May-August in 2006-2009. We captured Kittlitz's murrelets on the water at night from 4.5-m inflatable boats using high-powered spotlights and salmon dip-nets (Whitworth et al. 1997). We captured murrelets during two sessions: (1) early breeding season (7 May – 3 June), which coincides with egg-laying and incubation; and (2) late breeding season (18 July – 3 August, only during 2008-

2009), which coincides with chick-provisioning (Day 1996). From each captured bird, we collected 2-3 cm of the tip of the fifth secondary flight feather (2008-2009 only), 4-5 dark-tipped breast feathers, 2-4 white breast feathers (2006-2007 only), and 1 ml of whole blood, along with standard morphometric data. We sexed murrelets using PCR chromosome analysis (Zoogen Services Inc., Davis, CA) and determined reproductive status of females using assays of VTG following Vanderkist et al. (2000; T. Williams, Simon Fraser University); we assumed the same threshold value developed for marbled murrelets (egg producing female VTG score > 0.96 mg μl^{-1}) to hold for Kittlitz's murrelets.

To investigate diet at the inter-decadal scale, we relied on museum specimens from 15 museum collections for feather samples (see Acknowledgments for specific information on sources). Because no Kittlitz's murrelets were previously collected in Icy Bay, however, we obtained murrelet samples collected from the northern Gulf of Alaska region, including Glacier Bay and Yakutat Bay, and assumed that baseline isotopic signatures were similar across this ocean zone (Schell et al. 1998). Combined with the samples collected from Kittlitz's murrelets in Icy Bay, our dataset spanned nearly a 100-year period (historical samples: 1907-1972; contemporary samples: 2006-2009) of isotopic inference.

Prey Sampling

We collected potential prey items in Icy Bay during the breeding season using beach seine, dip-net, or opportunistic collection from nearby colonies of piscivorous seabirds. We selected beach seine sampling locations to target known prey species of the Kittlitz's murrelet: Capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus)*, and Pacific herring (*Clupea pallasi)*, or those forage fish species observed in murrelet foraging habitat. Following the methods of Arimitsu et al. (2003), we sampled the nearshore environment using a nylon beach seine that was 36.6 m in length, 2.4 m deep at the midpoint, tapering to 0.5 m deep at the wings, with a mesh size of 6 mm at the center and 28 mm at the wings, and deployed from a 4.5-m inflatable skiff. We sampled invertebrates using a 0.5 m diameter by 1.5 m long plankton ring net with 550 μm mesh at depths of 10-25 m. For SIA we selected 5 - 7 individuals per prey species or prey age class known to be consumed by Kittlitz's murrelets.

Stable Isotope Analysis

To remove any potential error due to surface contaminants, murrelet feathers were cleaned using a 24-hr soak in 2:1 (v:v) chloroform:methanol, rinsed with clean solvent, and then air-dried for another 24 hr. Whole blood was lyophilized for 24 hr and ground to a fine powder.

Lipids are generally depleted in ^{13}C compared to other tissue components and lipid content tends to vary among individuals due to differences in physiology

or environment (DeNiro & Epstein 1978, Hobson & Clark 1992, Logan & Lutcavage 2008). To account for this, and to simplify comparisons between the murrelet consumer and potential prey, we extracted total lipids from all prey samples. Samples of 1.0 - 1.5 g of fish lateral muscle were lyophilized, leaned by soaking for 24 hr in 2:1 chloroform:methanol, rinsed with clean solvent, and air-dried to constant mass for up to 24 hr. Invertebrate samples were treated similarly after soaking in a 10% HCL solution to remove carbonates, rinsed in distilled water, and air-dried to constant mass for up to 24 hr (Thompson & Furness 1995). Samples of ca. 1 mg (measured to ± 0.0001 mg) of feather, blood, or prey were loaded into tin capsules and analyzed for isotope composition at the Stable Isotope Laboratory, College of Oceanic and Atmospheric Sciences (COAS), Oregon State University. Encapsulated samples were combusted at > 1000°C in a Carlo Erba NA15—elemental analyzer, feeding a DeltaPlus XL continuous flow mass spectrometer. Measurement error for this analytical system has been estimated at ± 0.1‰ for $\delta^{13}C$ and ± 0.3‰ for $\delta^{15}N$ (J. McKay, COAS Stable Isotope Laboratory manager, Oregon State University, pers. comm.).

Stable isotope signatures are reported as parts per thousand (‰) using delta (δ) notation determined using the equation:

$$\delta\mathbf{X} = [(\mathbf{R}_{sample}/\mathbf{R}_{standard})\text{-}1] \times 1000,$$

where **X** is ^{13}C or ^{15}N, and **R** is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standard reference materials for $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were atmospheric N_2 gas and

Pee Dee Belemnite, respectively. To account for variable rates of isotopic discrimination between different tissues, we used published values from common murres (*Uria aalge*; Becker et al. 2007) and rhinoceros auklets (*Cerorhinca monocerata*; Sears et al. 2009). For cross-tissue comparisons, isotopic signatures were normalized to isotopic values of prey.

Statistical Analysis

We tested isotopic signatures of carbon and nitrogen from Kittlitz's murrelets for normality using Kolmogorov-Smirnov tests, and for homogeneity of variance using Levene's test. We tested for effects of season, year, and sex on nitrogen and carbon isotope signatures using repeated measures ANOVA. We used linear regression to assess temporal trends in pre- and post-breeding carbon and nitrogen isotope signatures for feather samples collected between 1907 and 2009. Results were considered significant at $P \leq 0.05$. All statistical analyses were conducted using the statistical language R (R Development Core Team 2009).

Isotopic signatures of white breast feathers and secondary flight feathers collected from the same murrelet were not significantly different (paired t-test, $t = 0.02$, $P > 0.1$, $N = 21$), suggesting the two feathers types were grown during the same period (autumnal pre-basic molt). Consequently, stable isotope signatures from secondary feathers and white breast feathers were both considered to reflect diet composition during the post-breeding, pre-basic molt.

One individual Kittlitz's murrelet whose blood was sampled during the early breeding season (2009) had an extremely low average stable carbon isotope signature (mean $\delta^{13}C$ = -25.5‰, SD = 0.4, N = 3), considerably more depleted than any other sample. The pre-breeding and post-breeding signatures from this individual, however, were similar to the mean (within 1 standard deviation) for each respective season. Thus, it is possible that this sample was somehow contaminated or this individual was foraging on prey that reared in freshwater (e.g., mean $\delta^{13}C$ for coho salmon (*Oncorhynchus kisutch*) smolts = -31.9‰), in addition to marine prey, during this period, thereby lowering the integrated blood isotopic signature for carbon (Hobson 1990). The blood sample from this individual murrelet was removed from further analyses because it was a significant outlier.

Results

We sampled 272 Kittlitz's murrelets using the live-capture method during 2006 – 2009, with the majority of birds (77%; 211 of 272) captured in either 2008 or 2009 (Table 2.1).

Mean fractionation-corrected stable isotope signatures for nitrogen in contemporary Kittlitz's murrelet tissues ranged from relatively low values in spring (pre-breeding $\delta^{15}N$ = 9.95‰, SE = 0.10, N = 207), to significantly enriched

values in late summer (late breeding $\delta^{15}N$ = 12.02‰, SE = 0.09, N = 79), to the highest values observed in fall (post-breeding $\delta^{15}N$ = 14.46‰, SE = 0.04, N = 237; Table 2.1). These differences in isotope values correspond to trophic level (TL) differences of 0.69 TL (pre-breeding to late breeding) and 0.81 TL (late breeding to post-breeding), with a total seasonal enrichment across the entire season equivalent to 1.5 TL, based on an isotopic enrichment value of about 3.0‰ per trophic level for the Gulf of Alaska (Hobson et al 1994). Mean fractionation-corrected stable isotope signatures of carbon in the same tissues were relatively low (depleted in ^{13}C) in spring (mean $\delta^{13}C$ = -19.76‰, SE = 0.06, N = 207), increased to a high in late summer (late breeding $\delta^{13}C$ = -18.22‰, SE = 0.05, N = 79), and were the lowest in fall (post-breeding $\delta^{13}C$ = -20.71‰, SE = 0.07, N = 237; Table 2.1, Figure 2.2).

Inter-Seasonal Variability

Isotopic signatures of Kittlitz's murrelets differed significantly among seasons (repeated measures ANOVA; carbon: $F_{2,453} = 124.18$, $P < 0.01$; nitrogen: $F_{2,453} = 1635$, $P < 0.01$; Table 2.4, Figures 2.2 and 2.3). There was a significant year/season interaction for $\delta^{15}N$ but not for $\delta^{13}C$ (Table 2.4). Nitrogen isotope signatures were most depleted in spring (corrected pre-breeding mean $\delta^{15}N$ = 9.95‰, SE = 0.10, N = 207), indicating that trophic level of the diet was lowest during pre-breeding. Mean pre-breeding carbon isotope signatures suggested

offshore foraging (corrected pre-breeding mean $\delta^{13}C$ = -19.76‰, SE = 0.06, N = 207). Nitrogen isotope signatures in feathers grown during the pre-breeding (pre-alternate) molt were correlated with those in blood during early breeding (corrected values, $r^2 = 0.50$, $P < 0.05$), indicating that murrelets were foraging on similar prey during the pre-breeding and early breeding periods within a particular year or there was some carry-over in isotopic inference from one period to the next. This correlation was not as strong for carbon isotope signatures ($r^2 = 0.17$, $P = 0.05$), however, suggesting that murrelets in the early breeding season were foraging closer to shore than during the pre-breeding period (corrected early breeding mean $\delta^{13}C$ = -18.92‰, SE = 0.11, N = 69). During the late breeding period, when murrelets were presumably provisioning nestlings (if they were actively nesting), nitrogen and carbon isotope signatures were enriched compared to the early breeding season (corrected late breeding mean $\delta^{15}N$ = 12.02‰, SE = 0.09, N = 78; $\delta^{13}C$ = -18.22‰, SE = 0.05, N = 79), suggesting a switch to a diet with a higher proportion of nearshore fish. During fall, the nitrogen isotope signature was highly enriched (corrected mean $\delta^{15}N$ = 14.46‰, SE = 0.04, N = 237), while carbon was highly depleted ($\delta^{13}C$ = -20.71‰, SE = 0.07, N = 237), signifying a diet dominated by high trophic level prey (forage fish) from offshore and/or remote from the breeding grounds.

Historical Sampling

The seasonal patterns in both $\delta^{15}N$ and $\delta^{13}C$ were consistent from 1907 – 1984. The mean difference between pre-breeding and post-breeding values of $\delta^{15}N$ ranged from 1.14 – 5.48 (trophic level equivalent of 0.38 TL – 1.82 TL assuming $\delta^{15}N$ 3.0‰ per trophic level), which encompasses the seasonal differences observed from 2006 – 2009 (mean = 4.51 or 1.50 TL). Mean isotopic signatures of nitrogen declined between 1907 and 2009 for feathers grown pre-breeding ($\delta^{15}N = -0.015 * (YEAR) + 39.21$, $R^2 = 0.11$, $P < 0.001$; Table 2.3, Figure 2.4A), but not for feathers grown post-breeding ($\delta^{15}N = -0.0021 * (YEAR) + 18.60$, $R^2 = 0.01$, $P = 0.12$; Table 2.3, Figure 2.4B). Mean $\delta^{13}C$ also declined from 1907 to 2009 for feathers grown pre-breeding ($\delta^{13}C = -0.022 * (YEAR) + 23.92$, $R^2 = 0.64$, $P < 0.001$; Table 2.3, Figure 2.4C), as well as for feathers grown post-breeding ($\delta^{13}C = -0.025 * (YEAR) + 28.79$, $R^2 = 0.65$, $P < 0.001$, Table 2.3, Figure 2.4D).

Gender and Breeding Status

We did not detect significant gender differences in isotopic signatures for either nitrogen or carbon, either among years (2006-2009) or among seasons within a year (Kruskal-Wallis test, $P > 0.05$, Table 2.2). This suggests that there were no differences between the sexes in diet or foraging habitat among all years of the study. There were no differences in nitrogen or carbon stable isotope signatures between female murrelets that were physiologically prepared to lay

eggs and female murrelets that were not prepared to lay ($P > 0.05$ for all seasons and both isotope signatures), based on VTG levels in blood.

Discussion

Seasonal Variability

Stable isotope signatures revealed significant inter-seasonal variability in the diet of Kittlitz's murrelets between and among pre-breeding, breeding (early and late), and post-breeding periods. These inter-seasonal differences in diet were consistent not just during the contemporary study period (2006-2009), but also for the longer time series (1907-2009). The magnitude of the seasonal shift in stable nitrogen isotope signatures is equivalent to an increase of more than one whole trophic level (TL) from pre-breeding diets to post-breeding diets (assuming trophic enrichment of 3 – 4‰ per TL; Hobson et al. 1994). This change in diet is presumably the result of changes in the relative availability and profitability of different prey types during the annual cycle. In spring (pre-breeding), murrelets may take advantage of abundant zooplankton swarms offshore following the spring bloom (Brodeur et al. 1996, Coyle & Pinchuk 2005). During the early breeding season, when murrelets are restricted to foraging within commuting distance of upland nest sites (Day et al. 1999), foraging habits shift to a reliance on

prey with more enriched carbon, which suggests that murrelets are foraging on zooplankton closer to shore. As the breeding season progresses and nesting murrelets transition from incubation to chick-rearing duties, the diet shifts to greater quantities of higher trophic level prey, presumably forage fish, which are used for provisioning nestlings, as well as for self-feeding. Kittlitz's murrelets are not known to provision nestlings with zooplankton (Day et al. 1999; NRH, pers. obs.).

Prey switching during the breeding season has been observed in colonial seabirds as availability of prey within foraging distance of the breeding colony changes with oceanographic conditions (Ito et al. 2009), and with stage-specific foraging preferences that are relatively consistent between years or locations (Williams and Buck 2007, Hedd et al. 2010). Optimal foraging theory suggests that murrelets will forage on prey that maximize net energy gain, after compensating for energy expended during foraging (Pyke et al. 1977, Lacher et al. 1982).

Annual Variability

Overall, our results clearly showed that the foraging habits of Kittlitz's murrelets followed the same seasonal pattern each year. Mean stable isotope signatures during a particular season did vary somewhat among years, however, especially during pre- and early breeding. This could be explained by variability

in where murrelets foraged, based on spatial differences in baseline stable isotope signatures of prey, or what prey they consumed, suggesting differences in the proportion of major prey types consumed at the same trophic level (e.g., proportion of euphausiids vs. copepods) or annual variability in the stable isotope signatures of prey (Williams and Buck 2007). Annual differences in feather stable isotope signatures may also be related to the timing and location of molt, which appears to be highly asynchronous in the vernal pre-alternate molt (MLK, unpubl. data; NRH, pers. obs.). Presumably, murrelets undergo pre-alternate molt offshore but close to breeding sites. For the majority of birds examined in this study, the pre-alternate molt was initiated prior to arrival on the breeding grounds in early May (Sealy 1977), but in some birds, pre-alternate molt continues through May and even into June. It is unclear whether this is due to delayed initiation of the molt process or a protracted molt period in some birds. However, either scenario could potentially result in variation in where murrelets forage or what they consume during pre-alternate molt, thus leading to the observed differences in pre-breeding stable isotope signatures.

Gender and Breeding Status Differences

This study revealed no evidence of sexual differences in the food habits of Kittlitz's murrelets during any season or year. During the breeding season, murrelets are thought to maintain strong pair bonds and are often observed in pairs

(Day et al. 1999; NRH, pers. obs.), which suggests that both members of a pair have similar foraging habits during summer. Little is known about Kittlitz's murrelet social behavior outside the breeding season. The similarity in both carbon and nitrogen isotope signatures between the sexes suggests no major differences in food habits or foraging habitats throughout the annual cycle.

The physiological and energetic cost of egg production is large for any semi-precocial or precocial seabird (Kendeigh 1970). This is particularly so in Kittlitz's murrelet, which lay a single egg that is about 20% of adult body mass (Day et al. 1999). The energetic cost for a female to produce a 45-g egg is estimated to be 428 kJ (assuming egg synthesis efficiency of ~73% and an energy density for eggs of 5.5 kJ/g wet mass [Furness 1978]), roughly equivalent to 80% of the daily energy requirements of a breeding Kittlitz's murrelet during incubation (Chapter 3). Despite the increased energetic burden of egg production, there appears to be no significant difference in diet composition either prior to egg production (pre-breeding) or during egg production (early breeding) between breeding (elevated VTG) and non-breeding females. Thus, it appears that Kittlitz's murrelets in Icy Bay are consuming similar prey during the breeding season regardless of breeding status or sex.

Foraging Location

Isotopic gradients spanning large geographic areas have been used to estimate migration pathways and regions of resource use in organisms that are difficult to track using standard methods (Hobson 1990, Witteveen 2008). In general, $\delta^{13}C$ in the marine realm becomes progressively more depleted across a gradient from nearshore to offshore. Within the Gulf of Alaska region, $\delta^{13}C$ tends to be enriched in nearshore environments and pelagic waters of protected bays that do not experience significant mixing with offshore, oceanic waters, which tend to exhibit more depleted $\delta^{13}C$ (Kline 2009). These gradients have been confirmed through the food web; for example, Witteveen (2008) sampled skin tissue from foraging humpback whales (*Megaptera novaeangliae*) in different regions of Alaskan waters. These results suggested a gradient in $\delta^{13}C$ from more enriched values in southeastern Alaska (mean $\delta^{13}C$ = -17.2) to progressively more depleted $\delta^{13}C$ to the west and north (northern Gulf of Alaska mean $\delta^{13}C$ = -17.6, western Gulf of Alaska mean $\delta^{13}C$ = -18.5, Bering Sea mean $\delta^{13}C$ = -18.5). These geographic trends were supported in similar studies of carbon stable isotope signatures in zooplankton (Schell et al. 1998) and marine mammals (Hobson and Sease 1998, Hirons and Schell 2001).

Seasonal differences in $\delta^{13}C$ of Kittlitz's murrelets were consistent among years, suggesting that murrelets moved among isotopically distinct regions in a predictable order. Depleted carbon in breast feathers indicated offshore foraging habitats during pre-alternate molt leading up to the breeding season. Murrelets do

not arrive *en masse* to Icy Bay until the first or second week of May (NRH, pers. obs.). Carbon stable isotope signatures were most enriched in blood samples collected in July (late breeding), when murrelets are resident in Icy Bay and consume forage fish with isotopic signatures reflecting a carbon-enriched, nearshore habitat. Carbon stable isotope signatures were most depleted during post-breeding, after murrelets had departed Icy Bay, indicating that murrelets were not resident in habitats isotopically similar to those utilized during breeding through the autumnal (pre-basic) molt. Moreover, post-breeding carbon stable isotope signatures were significantly more depleted than during any other seasonal sampling period, suggesting that murrelets underwent molt far offshore and/or in a region that was quite isotopically different from the breeding grounds.

Population Level Implications

There are insufficient data to reliably estimate historical population size or any population trends for Kittlitz's murrelets during the period of this study (1907-2009; USFWS 2010). Associations between changes in food habits, as inferred from stable isotope signatures, and population declines have been described in the congeneric marbled murrelet from California, USA and British Columbia, Canada (Becker and Beissinger 2006, Norris et al. 2007). It is evident that long-term changes in the diet of marbled murrelets from the California Current System, inferred from a decline in mean nitrogen stable isotope signatures in murrelet

feathers, have occurred concurrent with significant population declines (Becker and Beissinger 2006). In California, these changes in diet and corresponding population declines have been attributed to the long-term effects of the over-exploitation and subsequent collapse of the California sardine (*Sardinops sadax*) fishery in the mid-20th Century (Becker and Beissinger 2006). In marbled murrelets, the change in trophic level was apparent because it appeared that, unlike Kittlitz's murrelets, marbled murrelets foraged on both zooplankton and forage fish during the pre-breeding (pre-alternate molt) period (Becker and Beissinger 2006). The overall depletion in nitrogen isotope signatures for marbled murrelets was interpreted as reflecting a decline in the proportion of higher trophic level prey consumed and an increase in consumption of lower trophic level prey. On the other hand, Kittlitz's murrelets appear to be adapted to or limited to foraging on zooplankton in spring, perhaps due to relative availability; the observed longitudinal change in nitrogen isotope signatures during pre-breeding was within the range of a zooplanktivore throughout. Consequently, the long-term trend in nitrogen isotope signatures may be the result of shifts in the species composition of zooplankton prey or changes in the isotopic signatures of the zooplankton prey themselves, perhaps due to changes in isotopic composition of primary producers.

Long-term trends in the isotopic profiles of the Bering Sea and Gulf of Alaska marine ecosystems have been the subject of numerous studies and these trends have been linked to declines in some apex predators (e.g., North Pacific

pinnipeds; Hirons et al. 2001, Cullen et al. 2001, Schell 2001). Schell (2000) attributed the observed depletion in carbon stable isotope signatures to an overall decline in productivity in the Bering Sea. Cullen et al. (2001), however, disputed this conclusion and asserted that the depletion of carbon stable isotopic signatures in the biota of marine environments could be explained by increased concentrations of fossil fuel-derived carbon in the atmosphere (the "Seuss Effect"). The depletion in $\delta^{13}C$ that can be attributed to the Seuss Effect has been estimated at around 0.16‰ per decade (Quay et al. 2003). We estimated that the rate of $\delta^{13}C$ depletion in Kittlitz's murrelet feathers over the past 100 years was 0.22‰ and 0.25‰ per decade for feathers produced during the pre-alternate molt and pre-basic molt, respectively (Figure 2.4C and 2.4D). Although it is difficult to attribute the observed long-term depletion in $\delta^{13}C$ of Kittlitz's murrelets to either the Seuss Effect or some other driver of isotopic change, these data add to the suite of marine predators in which this trend has been observed.

Kittlitz's murrelets are known to consume a diversity of prey, including zooplankton, larval fish, and forage fish (Day et al. 1999). Our results provide the first description of the seasonal differences in diet composition and foraging habitats used by this species and, within each season, we found evidence of a more specialized diet on either zooplankton or forage fish, rather than a generalist diet that consistently included a variety of both zooplankton and forage fish. Other members of the seabird family Alcidae from the North Pacific span the range of

prey utilization strategies, from pelagic-foraging planktivores (e.g., auklets [*Aethia* spp.]) to nearshore-foraging piscivores (e.g., pigeon guillemots [*Cepphus columba*]; Vermeer et al. 1987). *Brachyramphus* murrelets reside somewhere in the middle of this range; they rely on both small, lower trophic level prey (zooplankton) and larger, higher trophic level prey (forage fish), depending on the season. Hobson et al. (1994) assessed carbon and nitrogen stable isotopes in a suite of seabird species resident in the Gulf of Alaska (Figure 2.5). Summer stable isotope signatures of Kittlitz's murrelets in Icy Bay (this study, late breeding period) were very similar to those reported by Hobson et al. (1994) for Kittlitz's murrelets sampled from Kachemak Bay, Alaska during the same season (Figure 2.5). Stable isotope signatures for Icy Bay Kittlitz's murrelets during the pre-breeding and early breeding periods, however, were more similar to zooplanktivorous alcids, such as ancient murrelets (*Synthliboramphus antiquus*) or Cassin's auklets (*Ptychoramphus aleuticus*) (Figure 2.5; Hobson et al. 1994).

Post-breeding stable isotope signatures of Kittlitz's murrelet were characterized by mean stable nitrogen signatures significantly more enriched than in other Gulf of Alaska piscivorous seabirds, such as pelagic cormorants (*Phalacrocorax pelagicus*), common murres (*Uria aalge*), and pigeon guillemots (Figure 2.5). Mean carbon isotope signatures, however, were similar to those of Leach's storm-petrel (*Oceanodroma leucorhoa*), a species that generally forages far offshore in oceanic habitats (Huntington et al. 1996). This suggests that

following the breeding season, Kittlitz's murrelets move away from the breeding grounds and, during the presumably flightless period of pre-basic molt, forage on prey with a highly-enriched nitrogen isotope signature, prey not found near the breeding grounds. The large change in $\delta^{13}C$ from the breeding season to pre-basic molt may reflect a post-breeding migration to a different oceanographic region with a significantly less enriched carbon isotope signature, possibly outside the Gulf of Alaska. Recent data from 13 Kittlitz's murrelets that were satellite-tagged in Icy Bay suggest that at least some individuals undertake long distance and rapid post-breeding migrations of up to 1000 km to marine waters in the western Gulf of Alaska and the Bering Sea (MLK, unpubl. data). In the absence of any diet data for Kittlitz's murrelets in these areas, or any stable isotope signatures for murrelet prey collected from these areas during fall, the source of the unusual stable isotope signatures of post-breeding Kittlitz's murrelets is speculative. The satellite telemetry data, however, lend support to the hypothesis that during the post-breeding period Kittlitz's murrelets migrate to areas that are isotopically distinct from breeding areas.

Conclusions

Using stable isotope signatures in feathers and blood, we found differences in the foraging ecology of Kittlitz's murrelets at two temporal scales: inter-seasonal and

multi-decadal. From 2006 – 2009 we found very little variability at the inter-annual scale (within a trophic level), presumably caused by annual variability in the baseline isotope values of the base of the food web. We found no evidence of differences in foraging ecology between males and females or between breeding and non-breeding females. The most striking differences in stable isotope signatures of Kittlitz's murrelets were inter-seasonal differences in both nitrogen and carbon isotope signatures. Based on the isotopic evidence, Kittlitz's murrelets foraged offshore and primarily on macrozooplankton during the pre-breeding (pre-alternate molt) period. During the early part of the breeding season, when breeding adults share incubation duties at inland nest sites with their mate, murrelets foraged in the nearshore on a more diverse diet consisting of both fish and macrozooplankton. During the latter part of the breeding season, when breeding adults provision nestlings, murrelets foraged nearshore and predominantly on forage fish. After the breeding season Kittlitz's murrelets apparently migrated offshore or away from the breeding grounds and consumed higher trophic level prey, presumably forage fish that feed on carnivorous macrozooplankton, during the pre-basic molt.

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Figure 2.1. Map depicting the breeding range of the Kittlitz's murrelet in Alaska (blue shaded area), including the focal study area, Icy Bay, on the northern Gulf of Alaska coast (adapted from Day et al. 1999).

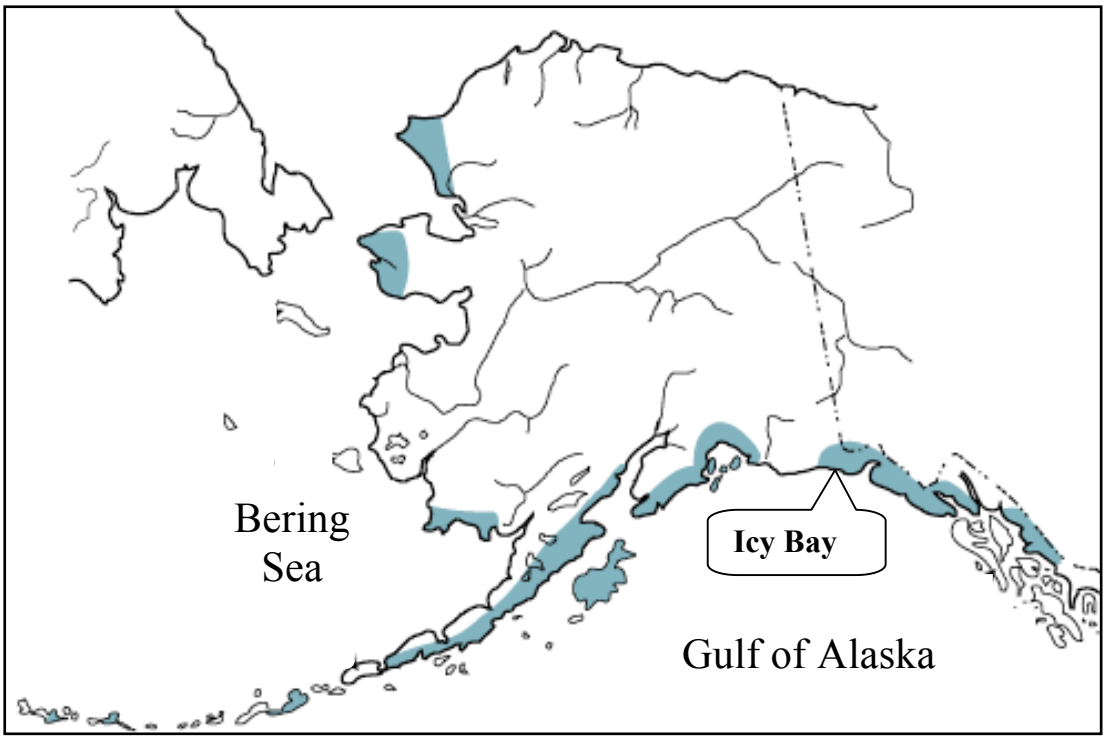


Figure 2.2. Fractionation-corrected stable isotope signatures of Kittlitz's murrelets plotted by period ("pre-breeding", "early breeding", "late breeding" and "post-breeding"; color/symbol). Ellipses represent 50th (inner) and 95th (outer) percentile distributions of the data by season. Values for carbon isotope ratios on the x-axis provide a relative indicator of nearshore vs. offshore foraging. Black lines on the y-axis indicate δ^{15}N values for common prey types, including juvenile Pacific herring (*Clupea pallasi*), Pacific sand lance (*Ammodytes hexapterus*), smelt spp. (Osmeridae), and euphausiid spp. (Euphausiaceae).

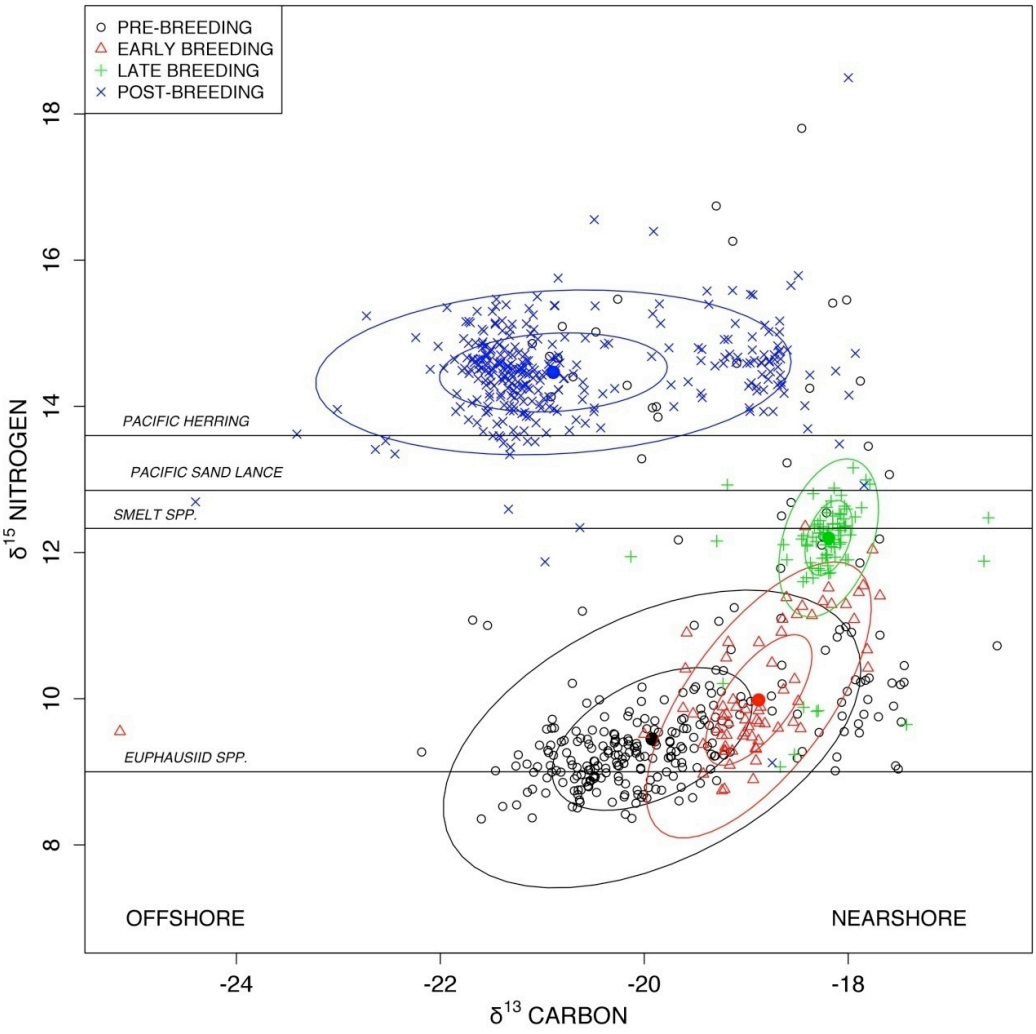


Figure 2.3. Boxplots depicting median (bold centerline), upper and lower quartiles (top and bottom of box), and 1.5 times the interquartile range of fractionation-corrected isotopic signatures for carbon and nitrogen in Kittlitz's murrelets during pre-breeding (dark-tipped breast feathers), early breeding (blood collected in May), late breeding (blood collected in July), and post-breeding (flight or white breast feathers) from Icy Bay, Alaska, 2006-2009.

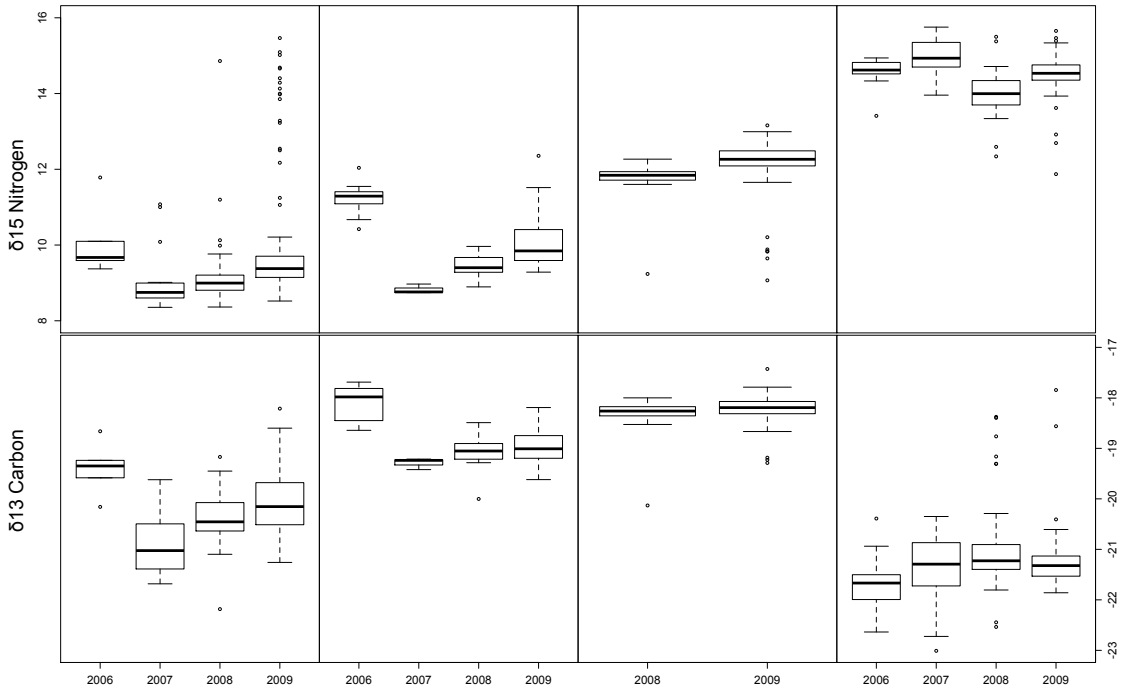


Figure 2.4. Long-term trends in mean stable isotope ratios for nitrogen and carbon in feathers of Kittlitz's murrelets from Icy Bay, Alaska (2006-2009) and other sites in the northern Gulf of Alaska (1907-1984). Plots A and B depict nitrogen stable isotope ratios as a function of year and plots C and D depict carbon stable isotope ratios as a function of year. Plots A and C depict the pre-breeding period and plots B and D depict the post-breeding period.

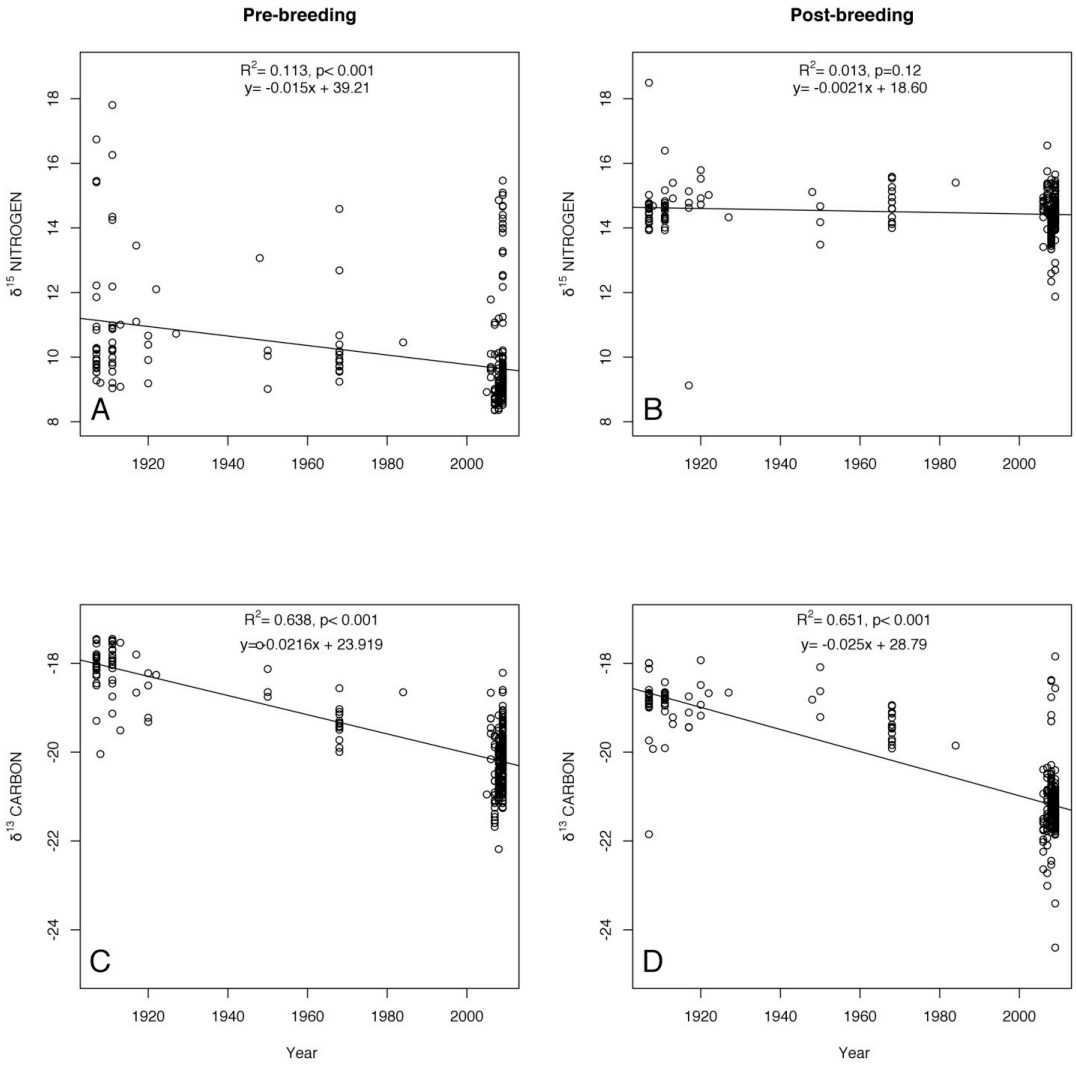


Figure 2.5. Carbon and nitrogen isotope signatures of Kittlitz's murrelets (this study; in red) during the pre-breeding, early breeding, late breeding, and post-breeding stages of the annual cycle, with comparable isotopic signatures from other seabirds collected during late breeding (Hobson et al. 1993; in black). To allow comparisons between studies and different tissues, all isotopic signatures were normalized to the level of prey using tissue-specific fractionation corrections. [**Species codes:** ANMU = ancient murrelet (*Synthliboramphus antiquus*), CAAU = Cassin's auklet (*Ptychoramphus aleuticus*), COMU = common murre (*Uria aalge*), GWGU = glaucous-winged gull (*Larus glaucescens*), HOPU = horned puffin (*Fratercula corniculata*), LESP = Leach's storm-petrel (*Oceanodroma leucorhoa*), MAMU = marbled murrelet (*Brachyramphus marmoratus*), PIGU = pigeon guillemot (*Cepphus columba*), PECO = pelagic cormorant (*Phalacrocorax pelagicus*)]

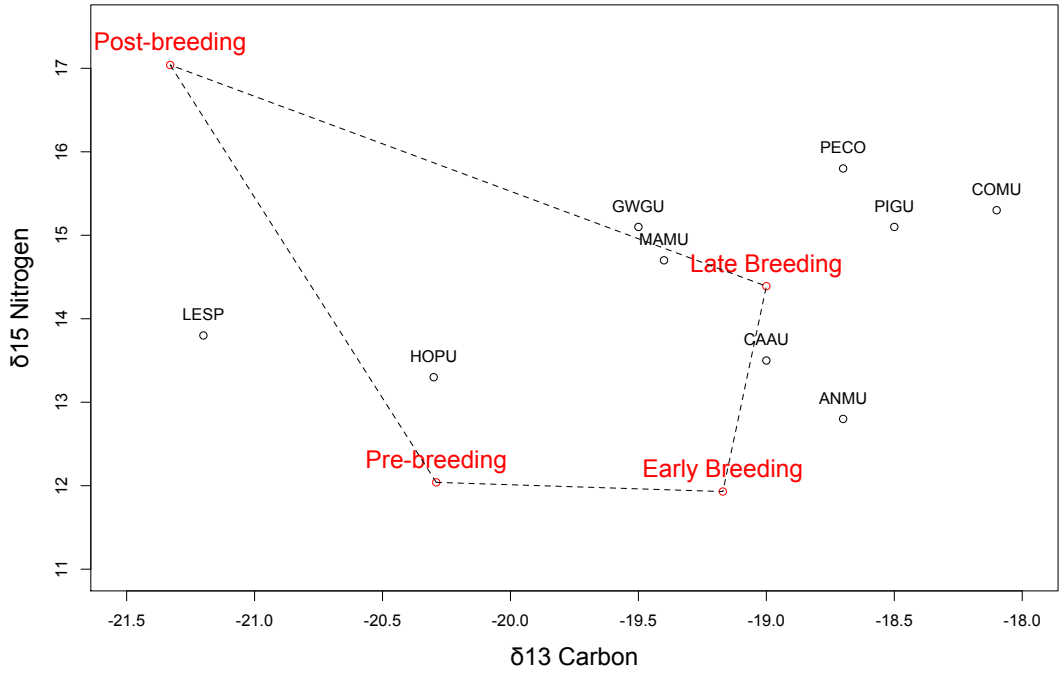


Table 2.1. Fractionation-corrected stable isotope signatures of Kittlitz's murrelets during pre-breeding, early breeding, late breeding, and post-breeding stages of the annual cycle, based on samples collected during 2005 – 2009 in Icy Bay, Alaska.

Year	Season	N	Tissue[1]	$\delta^{15}N$	SE	$\delta^{13}C$	SE
2005	Pre-breeding	1	DBF	8.92	NA	-20.95	NA
2006	Pre-breeding	6	DBF	10.03	0.36	-19.39	0.20
	Early breeding	14	BL	11.25	0.10	-18.10	0.09
	Post-breeding	12	WBF	14.56	0.12	-21.65	0.17
2007	Pre-breeding	18	DBF	9.05	0.19	-20.83	0.16
	Early breeding	3	BL	8.82	0.07	-19.29	0.07
	Post-breeding	21	WBF	15.03	0.12	-21.34	0.15
2008	Pre-breeding	57	DBF	9.15	0.12	-20.38	0.06
	Early breeding	14	BL	9.43	0.08	-19.09	0.09
	Late breeding	14	BL	11.67	0.19	-18.38	0.14
	Post-breeding	80	SF	14.02	0.05	-21.04	0.08
2009	Pre-breeding	131	DBF	9.91	0.14	-20.09	0.05
	Early breeding	38	BL	10.04	0.11	-19.13	0.17
	Late breeding	65	BL	12.10	0.10	-18.18	0.05
	Post-breeding	124	SF	14.53	0.04	-21.30	0.05
Average Across All Years	Pre-breeding	207	DBF	9.95	0.10	-19.76	0.06
	Early breeding	69	BL	10.11	0.10	-18.92	0.11
	Late breeding	79	BL	12.02	0.09	-18.22	0.05
	Post-breeding	237	SF	14.46	0.04	-20.71	0.07

[1]DBF = dark-tipped breast feather; WBF = white breast feather; BL = blood; SF = secondary feather

Table 2.2. Mean nitrogen and carbon stable isotope signatures of female and male Kittlitz's murrelets from Icy Bay, Alaska by season (data collected during 2006-2009). Values are corrected for differences in tissue-specific fractionation.

Season	Sex	N	$\delta^{15}N$	SE	$\delta^{13}C$	SE
Pre-breeding	Female	141	9.89	0.12	-19.78	0.06
	Male	138	10.03	0.17	-19.73	0.07
Early Breeding	Female	35	9.78	0.10	-19.26	0.22
	Male	29	10.35	0.09	-18.61	0.06
Late Breeding	Female	41	12.07	0.20	-18.23	0.07
	Male	37	11.95	0.28	-18.19	0.20
Post breeding	Female	147	14.48	0.06	-20.67	0.07
	Male	153	14.45	0.05	-20.68	0.08

Table 2.3. Fractionation-corrected stable isotope signatures of historical samples from Kittlitz's murrelets collected in the northern Gulf of Alaska during the pre-breeding and post-breeding periods, 1907 - 1984.

Year	Season	N	Tissue[1]	$\delta^{15}N$	SE	$\delta^{13}C$	SE
1907	Pre-breeding	23	DBF	10.97	0.45	-18.04	0.08
	Post-breeding	23	WBF	14.60	0.19	-18.89	0.15
1908	Pre-breeding	1	DBF	9.20	NA	-20.04	NA
	Post-breeding	1	WBF	14.68	NA	-19.93	NA
1911	Pre-breeding	18	DBF	11.45	0.60	-17.98	0.11
	Post-breeding	18	WBF	14.61	0.13	-18.84	0.08
1913	Pre-breeding	2	DBF	10.04	0.96	-18.52	0.99
	Post-breeding	2	WBF	15.15	0.24	-19.29	0.08
1917	Pre-breeding	3	DBF	12.28	0.96	-18.23	0.43
	Post-breeding	3	WBF	13.42	0.24	-19.18	0.17
1920	Pre-breeding	4	DBF	10.04	0.32	-18.82	0.27
	Post-breeding	4	WBF	15.24	0.25	-18.63	0.27
1922	Pre-breeding	1	DBF	12.10	NA	-18.26	NA
	Post-breeding	1	WBF	15.02	NA	-18.67	NA
1927	Pre-breeding	1	DBF	10.72	NA	-16.54	NA
	Post-breeding	1	WBF	14.33	NA	-18.66	NA
1948	Pre-breeding	1	DBF	13.07	NA	-17.60	NA
	Post-breeding	1	WBF	15.11	NA	-18.82	NA
1950	Pre-breeding	3	DBF	9.75	0.37	-18.51	0.19
	Post-breeding	3	WBF	14.11	0.24	-18.64	0.32
1968	Pre-breeding	15	DBF	10.45	0.39	-19.37	0.10
	Post-breeding	15	WBF	14.80	0.14	-19.39	0.08
1984	Pre-breeding	1	DBF	10.46	NA	-18.65	NA
	Post-breeding	1	WBF	15.40	NA	-19.85	NA

[1]DBF = dark-tipped breast feather; WBF = white breast feather

Table 2.4. Repeated measures ANOVA testing for effects of year, season, and sex on stable isotope ratios of nitrogen and carbon in Kittlitz's murrelet tissues collected in Icy Bay, Alaska during 2006-2009. Significant effects ($P < 0.05$) are in bold.

Factor	***SS***	***df***	***MS***	***F***	***P <***
$\delta^{15}N$					
YEAR	2.55	1.00	2.55	1.89	0.170
SEASON	2209.93	1.00	2209.93	1635.42	**2.2E-16**
SEX	3.65	2.00	1.83	1.35	0.260
YEAR*SEASON	**14.58**	**1.00**	**14.58**	**10.79**	**0.001**
YEAR*SEX	0.99	1.00	0.99	0.73	0.393
SEASON*SEX	3.62	2.00	1.81	1.34	0.263
YEAR*SEASON*SEX	0.01	1.00	0.01	0.01	0.922
Error	612.13	453.00	1.35		
$\delta^{13}C$					
YEAR	**9.75**	**1.00**	**9.75**	**9.47**	**0.002**
SEASON	**127.75**	**1.00**	**127.75**	**124.18**	**0.0004**
SEX	0.85	2.00	0.43	0.41	0.662
YEAR*SEASON	3.63	1.00	3.63	3.52	0.061
YEAR*SEX	0.79	1.00	0.79	0.77	0.380
SEASON*SEX	3.07	2.00	1.53	1.49	0.226
YEAR*SEASON*SEX	0.29	1.00	0.29	0.28	0.596
Error	466.03	453.00	1.03		

ENERGY BUDGETS AND POTENTIAL CONSTRAINTS FOR BREEDING IN KITTLITZ'S MURRELETS (*BRACHYRAMPHUS BREVIROSTRIS*)

CHAPTER 3

Nicholas R. Hatch, Daniel D. Roby, and Michelle L. Kissling

Abstract

We used a bioenergetics modeling approach to investigate potential energetic constraints for reproduction in the Kittlitz's murrelet (*Brachyramphus brevirostris*), a rare and declining seabird endemic to the North Pacific. Kittlitz's murrelets, like other seabirds in the family Alcidae, utilize energetically expensive foraging and flight modes. In addition, Kittlitz's murrelets frequently nest in high elevation, glaciated sites at considerable distance from marine foraging areas. Using time-activity data and estimates of activity-specific energy expenditure rates, we developed estimates of field metabolic rates (FMR) for breeding adult Kittlitz's murrelets. Estimated average FMR during incubation (482 kJ/day) was less than the hypothetical maximum sustained working capacity (MSWC, ~ 650 kJ/day). Average FMR during chick-rearing was 580 kJ/day (below MSWC) and exceeded MSWC when commuting distance between foraging area and nest site was at the high end of the empirical range (≥ 55 km) and when the energy density of fish prey was at the low end of the empirical range (< 4 kJ/g wet mass). Estimated FMR of adult murrelets during chick-rearing was most sensitive to (1) energy content of chick meals, (2) distance between foraging area and nest site, and (3) energy provisioning rate to the single nestling. Long commuting distances between marine foraging areas and alpine nest sites are energetically expensive, yet can be compensated for by selectively provisioning nestlings with energy-dense fish, thus optimizing the net energetic efficiency of provisioning offspring

while reducing commuting costs. However, when commuting distance increases above a certain threshold (generally above 55 – 60 km, depending on nestling energy demands), FMR increases above MSWC regardless of prey quality. High reproductive effort in Kittlitz's murrelets may explain the adaptive significance of some of the species' other life history traits, including apparently infrequent breeding attempts, low fledging success, and the species' overall low annual productivity.

INTRODUCTION

Reproduction is an energetically demanding endeavor for seabirds and, in many species, is the most energetically demanding period of the annual cycle (Ricklefs 1983). Seabirds have evolved various strategies for coping with the high energetic costs of reproduction, including reduction in clutch size and brood size (Lack 1968), development of techniques for efficiently storing energy (as in procellariiforms; Costa and Shaffer 2008), slow growth and development of embryos and nestlings (Starck and Ricklefs 1989), and physiological changes in adults during different periods of the annual cycle (e.g., seasonal changes in body mass; Croll et al. 1991).

Assessing the energetic costs associated with various components of seabird life histories is important for understanding potential energetic bottlenecks

that limit survival and productivity, and how these constraints may interact with environmental variability related to natural and anthropogenic change. Lack (1968) suggested that in many birds, breeding adults maximize reproductive output by working at maximum sustainable rates during reproduction and, due to high rates of energy expenditure and low food availability, seabirds can only raise a few slow-growing young compared to their terrestrial counterparts.

There are numerous methods for assessing energy budgets and energy expenditure rates of seabirds (reviewed by Fort et al. 2010). However, many of these approaches are not appropriate or are very difficult to implement in free-living birds and/or impossible to implement outside of a controlled, laboratory setting. Direct or indirect calorimetry (respirometry) techniques (reviewed by Ellis and Gabrielsen 2000) and the doubly labeled water method (reviewed by Shaffer 2011) provide measurements of energy expenditure rates of individuals at rest and while engaged in free-ranging activity, respectively. These methods require study subjects that can either be captured and held in captivity for a period or captured and then recaptured within a few days. For species that are (1) highly sensitive to capture and handling stress, (2) federally-listed with strict limits on handling, or (3) that are very difficult to capture, let alone recapture, the options for measuring metabolic rates are extremely limited. In these cases, it is possible to estimate rates of energy expenditure in free-living seabirds through indirect methods, using

time-activity budgets and allometrically-derived, activity-specific metabolic rates (Gaston 1985).

The seabird family Alcidae is characterized by energetically-costly flapping flight, small clutch size, low nestling growth rates, and variable nestling fledging strategies, all suggesting selection pressure that limits food provisioning to the nest by adults (Gaston and Jones 1998). Alcids are generally found in highly productive arctic, subarctic, and temperate marine ecosystems, where high thermostatic costs, together with relatively high commuting costs and long commuting distances, combine to increase overall reproductive effort compared to lower latitude seabirds (Birt-Friesen et al. 1989, Bryant 1997). These attributes suggest that alcids as a taxon may expend energy at or above their theoretical maximum sustained work capacity during parts of the breeding season (Drent and Daan 1980).

The Kittlitz's murrelet (*Brachyramphus brevirostris*) is a relatively rare alcid, endemic to coastal regions of the North Pacific (Day et al. 1999). There is considerable evidence that this species has undergone significant population declines in at least parts of its range since the 1970's (Kuletz et al. 2011a, Kuletz et al. 2011b, Piatt et al. 2011). Drivers of this apparent decline have not been identified to date, but based on available information it appears that reproductive output is low in core breeding areas (Prince William Sound, Glacier Bay, and Icy Bay, Alaska; USFWS 2010). Causes for poor reproductive success are not

obvious and, in particular, it is not clear whether most adult Kittlitz's murrelets initiate breeding and then fail, or if they simply do not attempt to breed in most years. One possible explanation for the observed low fecundity is that breeding adult Kittlitz's murrelets may be energy-limited, particularly during the nestling-rearing stage of the breeding cycle, when adults are self-feeding on macrozooplankton and forage fish, while provisioning their young with forage fish at upland nest sites up to 70 km from the nearest potential foraging area (Day et al. 1999). In some areas, low nestling survival has been attributed to exposure and starvation (Kaler et al. 2009), suggesting that adult Kittlitz's murrelets may experience difficulties provisioning food to their nestlings, at least in some years.

Kittlitz's murrelets are generalist marine predators, consuming mostly macrozooplankton or forage fishes, depending on the period of the annual cycle (see Chapter 2). They are commonly observed foraging near the face of tidewater glaciers, near the outflow from glaciers, and in the tidal features caused by submerged glacial moraines. Kittlitz's murrelets nest in rugged, upland areas, generally in early-successional habitats recently exposed by glacial recession or unvegetated habitats due to environmental conditions (alpine scree or barren habitat), frequently on remote, oceanic islands (Day et al. 1999, Kaler et al. 2009).

We constructed a bioenergetics model for breeding adult Kittlitz's murrelets to (1) estimate the energetic demands of reproduction and (2) test for the effects of commuting distance and prey quality (energy content) on the energy

budget of breeding Kittlitz's murrelets. We tested the following *a priori* hypotheses:

(1) *Commuting distance is less important to energy provisioned to the chick than prey quality, up to a certain threshold flight distance; (2) Availability of high-energy prey items for chick provisioning can compensate for lower chick provisioning rates, so that fledge date and mass at fledging are not affected***.**

The bioenergetics model estimates daily energetic demands for a breeding Kittlitz's murrelet under various conditions, incorporating total energy demands of flight, foraging, incubation, chick-provisioning, and time at-sea. We used sensitivity analysis to test the sensitivity of estimated adult energy expenditure rates to changes in model input parameters of interest and errors in estimated activity-specific energetic costs predicted from allometric equations.

MATERIALS AND METHODS

To provide input data for the bioenergetics model, we used a combination of data collected in the field and data from previously published studies. Data collection in the field was conducted as part of a larger study on the nesting and at-sea ecology of Kittlitz's murrelets in Icy Bay, Alaska. When empirical data were not available or obtainable for input parameters to the Kittlitz's murrelet bioenergetics model, we estimated input parameters using empirical data from similar species, adjusted allometrically for differences in body size.

Field Methods

Fieldwork was conducted in Icy Bay, Alaska, USA, during the 2008 and 2009 nesting seasons. Adult Kittlitz's murrelets were captured on the water at night using the night lighting method (Whitworth et al. 1997). Adults were captured either early in the nesting season during the incubation period (May 10 - June 2), or late in the nesting season during the chick-rearing period (July 15 to August 2). Body mass (± 1 g), wing chord (± 1 mm), and a blood sample (ca. 1 cm^3) for sexing were collected from each captured murrelet. To calculate commuting distances between nest sites and foraging areas, a subset of murrelets captured during incubation (n = 30 per year) were fitted with VHF radio transmitters and were relocated every 1-3 days using fixed wing aircraft or ground telemetry. Because murrelets were captured at night, when they generally do not feed (Jodice 1998; NRH, pers. obs.), total body mass measurements are assumed to be from birds with empty foreguts. Because we were not able to capture the same murrelets both early and late in the nesting season, or even in different years, we assessed changes in mass between the two stages of the nesting period and between the two years of the study at the population level only, as in Sealy (1975) and Hull et al. (2002).

The right wing of a subset of captured birds (n = 22) was measured directly for semi-wingspan length (spine to wing tip), and the outline of the outstretched

wing was traced onto heavyweight card stock in the field. Wingspan was calculated as double the measured distance from the spine to the tip of the outstretched wing (Pennycuick 2008). The area of one wing was calculated by dividing the weight of the cut out wing tracing by the weight of a 1-cm^2 piece of the same card stock (± 0.1 mg). Whole wing area, as defined in Pennycuick's (2008) flight model, includes the area of both wings plus the body section ("root box") between the wings. Therefore, the area of the single wing was doubled and added to the estimated root box area to calculate whole wing area (Pennycuick 2008).

Time-Activity Budgets

Time-activity budget data were collected on adult Kittlitz's murrelets during both the early nesting (May-June) and late nesting (July-August) periods using both direct observation and radio telemetry methods (e.g., Henkel et al. 2004). For direct observations of focal birds, we recorded diving, resting, preening, and wing flapping behaviors continuously for a minimum of 5 minutes. For radio-marked birds, we recorded diving and surface times only (Jodice and Collopy 1999). Dive times and time intervals spent at the surface were recorded for each focal bird for a minimum of 5 min, until the bird was lost from sight or the observer became too fatigued to continue. Preening and wing flapping constituted a small proportion of the overall time-activity budget (1.2% and <

1.0%, respectively) and, therefore, we did not consider these activities separately in our model.

Model Development

Energetic demand for an individual adult Kittlitz's murrelet was estimated using a combination of allometric equations for activity-specific energy expenditure rates and time-energy budget techniques, as described by Fort et al. (2010). The model was populated with values derived using a combination of empirical data and estimates from allometric equations based on behavioral, energetic, and physiological parameters for the species. The overall structure of the model follows the guidelines of Ricklefs (1983), using conceptual elements from Gaston (1985), Croll et al. (1991), and Kuletz (2002)(see below).

Model Parameters

Adult Time-Activity Budgets

Times spent at the nest during the early and late stages of the breeding season, denoted as T_{nest}, were based on the estimated time that breeding adult murrelets spent at their nest during the incubation period (24 – 48 hour incubation shifts, shared equally between both parents; Day et al. 1999; MLK, unpubl. data) or during nestling-rearing (Day et al. 1999; Kaler et al. 2009; MLK, unpubl. data). During the incubation period, nest attendance by breeding adults was assumed to

be 50% (continuous nest attendance shared equally with the mate), and the other 50% of available time was assumed to be spent away from the nest, either at-sea (T_{sea}) or commuting between nest site and the sea (T_{flight}). When delivering food (single prey items) to nestlings, breeding adults remain at the nest for 10 - 40 min (Kaler et al. 2009; MLK, unpubl. data). I assumed that, for the purposes of the bioenergetics model, the average time spent by an adult per nest visit during chick-rearing was 30 min.

T_{sea} was separated into time spent resting/loafing (T_{loaf}) and time spent foraging (T_{forage}). Foraging time included all activities comprising a foraging bout, including time spent diving and the time spent on the surface recovering between dives. The proportion of observed at-sea time spent loafing (T_{loaf}) vs. foraging (T_{forage}) was used to partition the daily time at sea into these two categories.

T_{flight} was estimated based on the sum of all flying time within a given 24-hour period. Time spent commuting between foraging areas and nest sites was calculated as the commuting distance (D_C) multiplied times the average commuting speed (80 km/h; Elliott et al. 2004; J. Cragg, pers. comm.). A range of values for D_C were calculated as the flyway distance between a nest site and commonly used foraging areas within the study area as determined using radio telemetry (mean = 35 km, range = 5 – 69 km).

Pelletier et al. (2008) suggested that wing-propelled diving birds with high wing-loading will minimize flight movements to compensate for the overall high

energy costs of flight. Accordingly, we assumed that nesting murrelets adjust for the high cost of flight by limiting movements beyond those required for commuting to and from their nest site. Murrelet flight movements may include movements between at-sea nocturnal resting areas and foraging areas, or between different foraging areas. These additional at-sea, non-commuting flight movements were assumed to consist of 20 min of additional flight time per day (Gaston 1985).

Adult and Nestling Energy Expenditure Rates

Activity-specific energetic costs were estimated based on the allometric equations of Birt-Friesen et al. (1989). Specifically, the allometric equation for average daily field metabolic rate (FMR) of seabirds in cold climates that use flapping flight was used to estimate daily energy expenditure of Kittlitz's murrelet:

$$\log y = 3.24\ (SE = 0.05) + 0.727\ (SE = 0.039) \log x,$$

where y = FMR (kJ/day), and x = average adult body mass (kg) (Birt-Friesen et al. 1989, eq. 6, p. 364).

In addition, metabolic rate at the nest (E_{nest}) was estimated by:

$$\log y = 1.45\ (SE = 0.06) + 0.737\ (SE = 0.074) \log x,$$

where y = E_{nest} (kJ/h), and x = average adult body mass (kg) (Birt-Friesen et al. 1989, eq. 4, p. 364). Metabolic rate when foraging (E_{forage}) was estimated by:

$$\log y = 1.86\ (SE = 0.11) + 0.748\ (SE = 0.132) \log x$$

where y = E_{forage} (kJ/h), and x = average adult body mass (kg) (Birt-Friesen et al. 1989, eq. 3, p. 363).

A foraging bout consisted of a series of dives (≥ 1) followed by short (≤ 90 s) surface-pause intervals. When at-sea and not engaged in a foraging bout (surface interval > 90 s, but generally longer), murrelets were assumed to be loafing on the surface of the water. The "loafing" activity category includes numerous activities that were either observed infrequently and comprised a very minor part of the time-activity budget (e.g., wing flapping, preening) or were difficult to observe and verify (e.g., foot-propelled swimming, digestion). Metabolic rate of alcids resting at sea (sea surface temperature [SST] = 10°C) has been shown to increase by roughly 50% over metabolic rate in air (Richman and Lovvorn 2011). Thus we assume metabolic rate for Kittlitz's murrelets resting on the surface of the water (average SST in Icy Bay is 6 – 8°C) is 50% greater than the metabolic rate at the nest.

The energy cost of flight (E_{flight}) was estimated using wing measurements (described above), adult body mass, and output of Pennycuick's (2008) Flight software. The average commuting flight speed recorded for both Kittlitz's and marbled murrelets is 80 km/h (Elliott et al. 2004; J. Cragg, pers. comm.). For commuting flights to provision nestlings, we assumed a 10-g fish (mean of fish sizes estimated from fish observed being held by adult Kittlitz's murrelets at sea prior to delivery to nestlings) held crosswise in the bill during the nest-bound

flight and adjusted the cost of flight accordingly. Flight altitude, an input variable in Pennycuick's model, was assumed to be 5 m above the water for flights at-sea (between foraging and resting areas; NRH, pers. obs). The elevation of known nest sites of Kittlitz's murrelets in Icy Bay ranged from 160 m to 2,550 m above sea level (Kissling et al. 2012). The majority of the flight time, however, is presumed to be close to sea level. For the purposes of the bioenergetics model, commuting flights to and from nest sites were assumed to be at 20 m above sea level, and increased flight costs to a nest site due to gain in altitude were compensated for by decreased flight costs during the seaward leg of the commute.

Average daily energy expenditure (ADEE) for breeding Kittlitz's murrelets was estimated based on the following equation:

$$ADEE = [T_{loaf} * E_{loaf}] + [T_{forage} * E_{forage}] + [T_{flight} * E_{flight}] + [T_{nest} * E_{nest}],$$

where ADEE is the sum of the time parameters (totaling 24 hrs) for each activity multiplied by the respective activity-specific metabolic rate.

For the purposes of the bioenergetics model, we assumed that the maximum sustained working capacity (MSWC) for Kittlitz's murrelets is four times basal metabolic rate (BMR; Drent and Daan 1980) and that breeding Kittlitz's murrelets would avoid ADEE that exceeded this MSWC for extended periods. For breeding adult Kittlitz's murrelets, we estimated MSWC separately for the early (incubation) and late (chick-rearing) stages of the breeding season,

based on average adult body mass during these two stages and the equation for BMR in seabirds from Bryant and Furness (1995):

$$BMR = 2.3 * (M_b)^{0.774},$$

where BMR is in kJ/d and M_b is adult body mass in grams.

Diet Composition and Assimilation Efficiency

Adult diet composition for the bioenergetics model was informed using results from Chapter 2. Based on stable isotope ratios in blood, the diet of adult Kittlitz's murrelets consists almost exclusively of zooplankton during early breeding (incubation period), and switches to predominantly forage fish during late breeding (chick-rearing period). Therefore, we assumed that murrelet diets were exclusively macrozooplankton during early breeding and exclusively forage fish during late breeding. Based on local availability of major types of forage fishes (NRH, pers. obs.), we assumed that during late breeding adult Kittlitz's murrelets consumed either capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), or juvenile Pacific herring (*Clupea pallasi*). We assigned values of energy content per prey item based on Davis et al. (1998) and Anthony et al. (2000).

To simplify the model, we selected commonly consumed prey types for each stage of the breeding period and based all calculations on mean estimates of prey item size and energy density to estimate average energy content per prey item

(Day et al. 1999; MLK, unpubl. data). Estimates of energy density, mass/length ratio, and assimilation efficiency for each prey type were taken from published studies (Jackson 1998, Anthony et al. 2000, Niizuma and Yamamura 2004). Information on nestling diet composition was gathered from published studies and from the current study (Day et al. 1999; Kaler et al 2009; MLK, unpubl. data). Prey types commonly delivered to nestlings included Pacific sand lance, capelin, juvenile Pacific herring, juvenile walleye pollock (*Theragra chalcogramma*), and surf smelt (*Hypomesus pretiosus*). These five prey types were categorized by quality (high, medium, and low), defined as energy content per prey item (mean energy density of prey type * mean fresh mass of prey type; see below).

Adult and Nestling Prey Requirements

Daily consumption rates of each prey type were estimated based on energy content of prey items and average daily energy consumption (ADEC). ADEC is the total amount of food energy that a breeding adult Kittlitz's murrelet must consume per day to balance energy expenditure. ADEC was estimated by dividing average daily energy expenditure (ADEE) by the metabolizable energy coefficient (MEC). The MEC during the early breeding season was assumed to be the assimilation efficiency on a diet of macrozooplankton (0.68; Jackson 1986, Kirkwood and Robertson 1997), and the MEC during the late breeding season was

assumed to be the assimilation efficiency on a diet of forage fish (0.80; Niizuma and Yamamura 2004).

We estimated energy consumption rate while foraging (ECR, kJ/h), based on ADEC and average time spent diving per day (T_{dive}):

$$ECR = ADEC/T_{dive},$$

assuming murrelets were in energy balance. We used ECR to estimate prey consumption rates for major prey categories (macrozooplankton and forage fish), assuming adult Kittlitz's murrelets were exclusively zooplanktivorous during the early breeding season and piscivorous during the late breeding season (see Chapter 2), and the average energy content per prey item for that prey category (see Table 3.5; Davis et al. 1998, Anthony et al. 2000).

To investigate how commuting distance and prey quality affect the energy budgets of adult Kittlitz's murrelets, we calculated ADEE for adult murrelets given different scenarios of total assimilable energy content of prey ("prey quality"; range: 2.8 – 5.8 kJ/g wet mass), and distance of the nest from the nearest foraging area (range: 5 – 69 km). Prey delivery rates to the nest were based on chick energy requirements, or the Peak daily assimilable energy requirement of nestlings (DED_{peak}), estimated using the equation of Visser (2002),

$$DED_{peak} = 14.06 * M_f^{0.848} * T_{nestling}$$

where M_f is chick body mass at fledging (and varies from 100 g [45% of adult mass] to 150 g [73% of adult mass; Nelson 1997, Kaler et al. 2009] and $T_{nestling}$ is

the length (in days) of the nestling period (mean nestling period is 25 days). We assumed that adults provisioned nestlings with prey at a rate that meets these daily energy requirements. Prey quality was parameterized as high, medium, or low for a 10-g prey item delivery, corresponding to average energy density of juvenile Pacific herring (6 kJ/g), capelin/smelt spp. (4.8 kJ/g), and juvenile walleye pollock (2.8 kJ/g; Anthony et al. 2000) at the size of prey items delivered to nestlings. We estimated ADEE for breeding Kittlitz's murrelets assuming individuals would not exceed MSWC for extended periods.

We used a sensitivity analysis procedure to assess the effects of variation in model input parameters to the estimates of FMR in breeding adult Kittlitz's murrelets. Mean estimates for each parameter were used to develop baseline values of FMR for a hypothetical Kittlitz's murrelet. Individual parameters were then varied ±20% of the mean (baseline), while holding all other model input parameters fixed. Percent change in FMR due to ±20% variation in each input parameter was calculated using this sensitivity analysis procedure.

Results

Mean total body mass of adult Kittlitz's murrelets was not significantly different between the early breeding season (females: 227 g, SD = 21.1, N = 24; males: 225 g, SD = 23.0, N = 22) and the late breeding season (females: 217 g, SD = 19.5, N = 21; males: 225 g, SD = 19, N = 20) in 2008 (t-test, P = 0.12). In 2009,

however, adult body mass was significantly different between early breeding (females: 258 g, SD = 22.3, N = 64; males: 244 g, SD = 24.8, N = 73) and late breeding (females: 215 g, SD = 23.0, N = 39); males: 219 g, SD = 16.9, N = 32; t-test, $P < 0.001$). In 2009, average mass of females was 17% less during the late breeding season and average mass of males was 10% less during the late breeding season (Figure 3.1). On average, adult Kittlitz's murrelets were heavier in the early stages of the breeding season in 2009 compared to 2008 (t-test, $P < 0.05$), but in the late stage of the breeding season mean body mass did not differ between the two study years (t-test, $P > 0.05$).

Based on the allometric equation of Bryant and Furness (1995), average BMR during the early breeding season was ~162 kJ/day (6.6 kJ/hr), depending on body mass. During the late breeding season, BMR was estimated at ~150 kJ/day (6.2 kJ/hr).

Adult wingspan and wing area differed between the sexes, with males (mean wingspan = 45.53 cm, SD = 1.14, N = 9) having slightly longer wings than females (mean wingspan = 44.03 cm, SD = 0.84, N = 13; t-test, $P < 0.001$; Table 3.2). Estimated flight costs in adult Kittlitz's murrelets varied between 61.5 kJ/hr (9.3 times BMR) and 81.1 kJ/day (13 times BMR), depending on body mass, sex, and stage of the breeding season (incubation vs. chick-rearing). Differences in estimated flight costs were primarily due to variation in (1) mean adult body mass (greater in both sexes during the early breeding season), (2) wingspan (greater in

males), and (3) stage of breeding (murrelets transporting fish to nestlings had higher flight costs).

At-sea Time-activity Budgets

Murrelets spent the majority of their at-sea time on the surface (88% during early breeding and 90% during late breeding) engaged in loafing (resting), which included preening (1.2% of time) and wing-flapping (< 1% time). Foraging (diving and intervals at the surface between dives that were ≤ 90 s) comprised 10% of total at-sea time during the early breeding season (incubation period) and 8% of total at-sea time during the late breeding season (chick-rearing period; Table 3.3). These values for time spent foraging are similar to those observed for marbled murrelets (mean proportion of time spent diving = 10-12%; Peery et al. 2009) and common murres (*Uria aalge*; 8-13%; Cairns et al. 1987). Average duration of foraging dives (early breeding season: 36 s, SD = 10, N = 132; late breeding season: 37 s, SD = 12, N = 87) and the proportion of at-sea time spent foraging vs. loafing were not significantly different between the early and late stages of the breeding period ($P < 0.1$; Table 3.3).

Energy Expenditure Rates

Average field metabolic rate (FMR) for a breeding adult Kittlitz's murrelet while incubating an egg at the nest during the early breeding season was estimated at 233

kJ/day (1.4 times BMR), and adult FMR when at sea between incubation shifts was estimated at 482 kJ/day (3 times BMR). Average daily FMR during the incubation period was estimated as 358 kJ/day (2.2 times BMR), assuming mean observed commuting distance of 35 km. The cumulative energy expended during an individual incubation/at-sea cycle was estimated to be ~715 kJ. During the chick-rearing period, average adult FMR was estimated at 580 kJ/day (3.6 times BMR) assuming mean flight distance (35 km) and moderate prey quality (4.8 kJ/g). For adult Kittlitz's murrelets commuting the longest distance between foraging area and nest site (68 km) and provisioning nestlings with low quality prey (2.8 kJ/g wet mass), FMR was estimated to reach as high as 1100 kJ/day (7 times BMR). By comparison, estimated FMR for a non-breeding Kittlitz's murrelet during the late breeding season was 347 kJ/day (2.2 times BMR).

Average FMR increased linearly with increasing commuting distance between foraging area and nest site and decreased consistently as prey quality increased (low, medium, high; Table 3.6). Daily food consumption requirements for breeding adults were estimated to range from 131 g/d to 208 g/d during the incubation period and from 117 g/d to 259 g/d during the chick-rearing period, depending on prey type (Table 3.5). Varying the average energy content of prey items resulted in changes in self-feeding rates (number of prey items consumed per day to balance energy expenditure) of up to 60% during incubation (when murrelets were presumed to feed on macrozooplankton) and up to 10% during the

chick-rearing stage (when murrelets were presumed to feed on forage fish). Nestling provisioning rates (kJ delivered per day) varied by up to 42% across the range in average energy content of prey items delivered to nestlings that was used in this study.

The theoretical MSWC for a 220-g Kittlitz's murrelet is about 650 kJ/d. Model estimates of FMR for breeding adult Kittlitz's murrelets during chick-rearing (580 kJ/day) were below MSWC for average observed commuting distances (35 km) and medium prey quality (4.8 kJ/g). FMR exceeded MSWC when commuting distance increased above ~31 km with low quality prey (2.8 kJ/g), ~53 km with medium quality prey (4.8 kJ/g) and ~64 km with high quality prey (5.8 kJ/g; Table 3.6). When commuting distance was 68 km, the longest distance observed, FMR exceeded MSWC regardless of prey quality.

Sensitivity Analysis

Estimates of FMR and percent change from the baseline estimate of FMR associated with consistently varying input parameters by ± 20% are presented in Tables 3.7a and 3.7b. A ± 20% change in the chick provisioning rate resulted in an estimated change in adult murrelet FMR of ± 8.1%. A 20% increase in energy density of prey fed to nestlings resulted in a 6.7% decrease in adult FMR, while a 20% reduction in prey energy density resulted in a 10.1% increase in adult FMR. A ± 20% change in the amount of time spent foraging resulted in a relatively small

change in FMR (< 0.5% change) because, based on time-activity data, foraging comprises a relatively small proportion of the time budget while at sea. When commuting distance was varied by ± 20%, the resulting estimate for FMR increased/decreased by ± 8.2%. A ± 20% change in the length of the nestling period resulted in a relatively small change in average daily FMR (2.4 – 3.2% change). A 20% increase in chick mass at fledging resulted in an increase in estimated adult FMR of 6.7%, whereas a 20% reduction in fledging mass resulted in a decrease in estimated adult FMR of 7.0%. Change in adult body mass by ± 20% affected FMR by roughly ± 7%, primarily because the energetic parameters are allometrically scaled based on body mass. For allometrically-estimated activity-specific metabolic rates, the effect on estimated FMR of varying each rate by ± 20% was proportional to the amount of time spent engaged in each specific activity and the energetic cost of that activity in the baseline model. Thus, varying by ± 20% the cost of flight (most energetically expensive activity category) and the energy expended while at sea (predominant activity in the time-activity budget) had the greatest proportional effect on estimated FMR (10.5% and 8.2%, respectively, Table 3.8b).

Discussion

Model Estimates

Our estimates of field metabolic rates for breeding Kittlitz's murrelets are higher than allometrically-derived estimates of FMR for other breeding birds. Using the allometric equation for seabird basal metabolic rate and the estimate of FMR as 3 times BMR (Bryant and Furness 1995) yields an estimated FMR of ~449 kJ/d for a 220-g murrelet. FMR using the allometric equation for FMR from Birt-Friesen et al (1989) is estimated as 578 kJ/day. Estimated FMR from an alcid-specific allometric equation (Hodum et al. 1998), based on empirical data from chick-rearing adults, was 558 kJ/d. The mean estimate of FMR for an adult Kittlitz's murrelet provisioning a nestling from the present study was 580 kJ/d. Our estimate of FMR was 23% greater than the estimate based on Bryant and Furness' (1995) allometric equation for seabirds, <1% greater than the estimate using the Birt-Friesen et al. (1989) equation for cold water seabirds with flapping flight, and 4% greater than the estimate based on Hodum et al.'s (1998) allometric equation for alcids.

High estimated FMR in Kittlitz's murrelets compared to the Atlantic seabirds used in the Bryant and Furness (1995) analysis may be due in part to the cold foraging and nesting habitats used by Kittlitz's murrelets. Elevated rates of energy expenditure, and higher ratios of FMR:BMR have been observed in seabirds existing at higher latitudes and in colder climates (Birt-Friesen et al. 1989). Comparatively high FMR in seabirds has also been associated with high wing-loading due to adaptations for wing-propelled pursuit-diving (Roby and

Ricklefs 1986). Alternatively, the BMR of Kittlitz's murrelets could be higher than predicted based on the Bryant and Furness (1995) allometric equation, and thus the ratio of FMR:BMR may be ≤ 4, consistent with that predicted by Drent and Daan (1980) and observed in some other breeding seabirds (Nagy 1987, Gabrielsen and Mehlum 1989).

During incubation, breeding murrelets and other pelagic seabirds incur an energy debt due to prolonged fasting during their incubation shift. To maintain energy balance over the incubation period, breeding adults must increase foraging effort when away from the nest. While at sea, breeding murrelets and other seabirds must acquire food energy at a higher rate than is necessary to meet their own energy demands (Ricklefs 1983), thereby allowing breeding adults to recover from energy deficits incurred during incubation shifts and to maintain energy balance while foraging for and provisioning nestlings. During incubation, energy expenditure rate while at sea was estimated to be 2.3 times the energy expenditure rate while incubating the egg. This difference is due to the increased energetic demands of pursuit-diving for food and thermoregulation while in cold water. Variation in thermoregulatory costs while at the nest due to variation in operative temperatures were not incorporated into this model, however, but may be highly variable depending on nest site characteristics, such as elevation, aspect, exposure, protection from weather, proximity to glacial ice, and insolation.

Prey Consumption

To meet daily energy demand during incubation, a breeding Kittlitz's murrelet would have to consume between 131 g and 208 g of macrozooplankton per day (2.9 kJ/g – 4.6 kJ/g; Davis et al. 1998; Table 3.5; see Chapter 2 for information on prey choice during this period). During chick-rearing, when Kittlitz's murrelets apparently switch from zooplanktivory to piscivory, estimates of prey consumption range from 117 g/day to 259 g/day, depending on whether they are foraging on juvenile Pacific herring (6.2 kJ/g) or juvenile walleye pollock (2.8 kJ/g; Anthony et al. 2000).

The rate of energy assimilation is a function of the food energy consumption rate and the assimilation efficiency of ingested food energy. Following Kirkwood's (1983) general model for rate of daily energy assimilation, DEA, a 220-g murrelet would be expected to have a maximum daily energy assimilation rate of approximately 576 kJ/d (DEA = 1713 $M_b^{0.72}$, where M_b = body mass in kg). This is roughly the same as the average estimated FMR for Kittlitz's murrelets during chick-rearing (580 kJ/d), but lower than model scenarios with low quality prey and long commuting distance, raising the possibility that FMR during chick-rearing may be limited by maximum assimilation rate and endogenous energy reserves. Kirkwood's (1983) allometric relationship is, however, based on a variety of birds on various diets and may not apply to piscivorous alcids. Nevertheless, this model does provide some evidence of

constraints on energy intake and expenditure in Kittlitz's murrelets. Assuming average assimilation efficiency of 0.68 for zooplankton (Jackson 1986, Kirkwood and Robertson 1997) and 0.80 for fish (Niizuma and Yamamura 2004), and an energy density of prey of between ca. 2 kJ/g (lowest energy density prey type, e.g., hyperiid amphipod; Davis et al. 1999) and ca. 5.8 kJ/g (highest energy density prey type, i.e., juvenile Pacific herring; Foy and Norcross 1999, Anthony et al. 2000), a murrelet can theoretically consume and utilize ca. 288 g of euphausiids, or 96 g of juvenile Pacific herring, 144 g of Pacific sand lance (4 kJ/g; Anthony et al. 2000), or 206 g of juvenile walleye pollock (2.8 kJ/g; Anthony et al. 2000) per day. Thus, during chick-rearing, Kittlitz's murrelets may be at or near their theoretical maximum sustained working capacity and expending more energy than can be consumed and assimilated to adequately balance their overall energy budget. However, murrelets may improve digestive efficiency through increased retention time (Hilton et al. 2000), but that would necessarily limit foraging time and food intake rate unless foraging efficiency is increased accordingly. Time-activity data suggest that Kittlitz's murrelets at-sea spend a large proportion of time (80% - 90%) loafing on the surface. This time for both resting and digestion may be an essential component of the overall time-activity budget.

Changes in Body Mass

Kittlitz's murrelets weighed more during the early part of the 2009 breeding season than in the early part of the 2008 breeding season, yet there was no between-year difference in adult body mass during the latter part of the breeding season. Moreno (1989) provided some possible explanations for seasonal mass loss in birds and outlined some adaptive strategies for why it may occur. The apparent loss of mass in both sexes of adult murrelets between the early and late stage of the breeding season in 2009 suggests either an adaptive or stress-induced physiological response to the cumulative energetic costs of murrelets commuting to and from nest sites, fasting during incubation bouts, and the increased foraging and flight effort required for provisioning a nestling. Norberg (1981) presented a hypothesis for an adaptive strategy that trades-off body mass, in the form of body fat reserves, for decreased metabolic costs for flight. For Kittlitz's murrelets during 2009, which, depending on sex, lost on average 10% (males) and 17% (females) of body mass between the early and late stages of the breeding season, potential energetic cost savings during flight varied between 9.2 kJ/d and 54 kJ/d, depending on the percentage of mass lost and amount of time spent flying per day (Table 3.7, Figure 3.2; Kvist et al. 2001, Pennycuick 2008), and assuming that flight speed did not vary with adult body mass. Elliott et al. (2004) found no difference in mean flight speed of marbled murrelets during the incubation and chick-rearing periods, and we assumed this applied to Kittlitz's murrelets as well.

Alternatively, greater average body mass observed in 2009 may be the result of more favorable pre-breeding foraging conditions and/or Kittlitz's murrelets storing energy (in the form of fat reserves) during the early breeding period as a buffer against the increased energy demands of reproduction. If we assume that the majority of body mass loss during the 2009 breeding season was due to the loss of fat reserves (Elliot et al. 2008), and the energy content of lipid is 39.3 kJ/g (Schmidt-Nielsen 1997), then the average mass loss of 10% [24.4 g] to 17% [43.4 g] is equivalent to 959 kJ to 1705 kJ of endogenous energy metabolized between early and late breeding. The amount of energy mobilized through the apparent metabolism of lipid is equivalent to 144% to 216% of estimated average daily energy expenditure (ADEE; 482 kJ/d) for a Kittlitz's murrelet during incubation. Since the apparent loss of mass during the breeding season was not observed in both 2008 and 2009 it seems unlikely to be an adaptive strategy for minimizing flight costs. However, these early season reserves may be a very important component of the overall energy budget of breeding murrelets during the incubation period, especially when considering longer than average incubation shifts and the associated fasting period when the adult is at the nest for an incubation shift lasting 24 – 48 hrs.

Time-Activity Budgets

Behavioral observations of Kittlitz's murrelets suggest that a large proportion of time at-sea is spent at the surface (88% - 90%), with proportionally little time spent foraging (8-10% of at-sea time-activity budget). This may mean that murrelets have flexibility in their time-activity budgets at sea. Conversely, murrelets may spend a large proportion of time at-sea resting, versus foraging or flying, to reduce overall energetic costs and to offset the high activity-specific energy expenditure rates during flight and diving (Pelletier et al. 2008).

An assumption of our model was that most of the empirical time-activity data were sampled from breeders. Approximately 70% of female murrelets captured in Icy Bay during May of 2008 and 2009 had elevated levels of vitellogenin and all had evidence of a brood patch (MLK, unpubl. data), indicating that a large proportion of the female population arrived on the breeding grounds physiologically prepared to breed (Vanderkist et al. 2000). This suggests that early in the breeding season, the time-activity budgets are from a sample of individuals that were either breeders or prospective breeders. Based on a radio-tagged subsample of these birds, less than 15% went on to successfully initiate breeding (MLK, unpubl. data). Therefore, during the early breeding season the proportion of breeders may have been considerably higher than non-breeders. Later in the breeding season the proportion of non-breeders and failed breeders increases, possibly violating the assumptions of the model. However, Kuletz (2005) determined that dive behavior of self-feeding and chick-rearing murrelets

were similar, suggesting that our assumption is supported with respect to dive times, but not necessarily time spent foraging (for self and nestling).

Sensitivity Analysis

Changes to the provisioning rate of chicks had the greatest proportional impact on estimates of FMR in chick-rearing Kittlitz's murrelets. In the model, provisioning rate was a function of energy content of prey items and energy demand of the nestling. Thus, for a fixed nestling energy demand an adult murrelet can minimize energy expenditure by increasing the energy content of chick meals, either by increasing prey size or increasing prey energy density, or a combination of the two. Alternatively, by extending the nestling period (thereby slowing nestling growth) adult Kittlitz's murrelets provisioning nestlings can lower their estimated FMR, at the cost of increasing the total cumulative energy cost of breeding for the adult. Chick provisioning rates per adult as low as 0 fish per day and as high as 10 fish per day have been observed (Kaler et al. 2009; MLK and NRH, unpubl. data), but not for extended periods. This equates to an estimated short-term FMR of 3.1 times BMR (no deliveries) and 9.5 times BMR (10 deliveries), more than double the hypothetical MSWC (Drent and Daan 1980). Thus, it appears that Kittlitz's murrelets are capable of temporarily increasing energy expenditure to meet the energetic demands of nestlings, as has been observed in other seabirds (Birt-Friesen 1989, Fyhn et al. 2001). These results

suggest that a decrease in energy content of prey delivered to a nestling, from a 10-g juvenile Pacific herring (60 kJ) to a 10-g juvenile walleye pollock (28 kJ), and subsequent increase in average nestling provisioning rate (from 1.7 to 3.7 fish per day) to maintain nestling energy intake rate results in a 31% increase in adult FMR. An increase in FMR of this magnitude would exceed the MSWC threshold and could potentially affect individual health.

Sensitivity analysis indicated that a 20% change in commuting distance resulted in an 8% change in FMR. Estimated FMR for a Kittlitz's murrelet commuting with a 48-kJ prey load (one-way transport of a 10-g capelin at 4.8 kJ/g) and commuting 35 km (average observed commuting distance) is 580 kJ/day, whereas estimated FMR for the same murrelet commuting 68 km (maximum commuting distance observed) is 821 kJ/day, a 42% increase in energy expenditure. To account for the higher cost of commuting further while maintaining energy provisioning rates to nestlings, Kittlitz's murrelets can increase the energy content of prey loads delivered to nestlings by selecting prey with greater energy density (e.g., from a capelin at 4.8 kJ/g to a Pacific herring at 5.8 kJ/g), thereby improving the efficiency of energy provisioning to the nest and decreasing their daily energy demands by 14% (821 kJ/day to 708 kJ/day). However, the lower FMR estimate is still greater than the MSWC threshold and may result in negative implications for individual fitness. Thus, Kittlitz's

murrelets can potentially adjust to variation in commuting distance by increasing the energy content of prey delivered to the nest up to a certain threshold.

Conclusions

The reproductive ecology of Kittlitz's murrelets is energetically-demanding and breeding adults must operate close to or above expected thresholds for maximum prolonged energy expenditure rates (Birt-Friesen et al. 1989, Adams et al. 1991, Piersma 2002), especially during the chick-rearing period. Estimates of FMR for breeding adult Kittlitz's murrelets increased above the hypothetical threshold of MSWC when average commuting distance to the nest was greater than 27 km and while provisioning low-quality prey (2.8 kJ/g), 46 km while provisioning medium-quality prey (4.8 kJ/g), or 56 km while provisioning high-quality prey (5.8 kJ/g). Estimated maximum rates of energy assimilation for Kittlitz's murrelets, based on allometric equations for birds in general, predict that energy balance can only be achieved for FMRs up to the average estimated FMR based on our bioenergetics model. For scenarios where FMR is higher than average (e.g., commuting distances > 35 km and prey energy density < 4.8 kJ/g), Kittlitz's murrelets may not be able to maintain energy balance due to constraints on their capacity to assimilate energy. In response to energy deficits during the breeding season, Kittlitz's murrelets may lose mass as the breeding season progresses, but only if they have been able to deposit fat reserves in the lead-up to

incubation. Overall, output from the bioenergetics model suggests that Kittlitz's murrelets can adjust to higher commuting costs between foraging areas and nest sites by selecting higher quality prey up to a certain threshold, above which would require increasing FMR to levels that likely reduce subsequent adult survival and negatively affect lifetime reproductive success.

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Figure 3.1. Seasonal change in total body mass for female (solid, red) and male (open, black) Kittlitz's murrelets in Icy Bay, Alaska during the 2008 and 2009 breeding seasons.

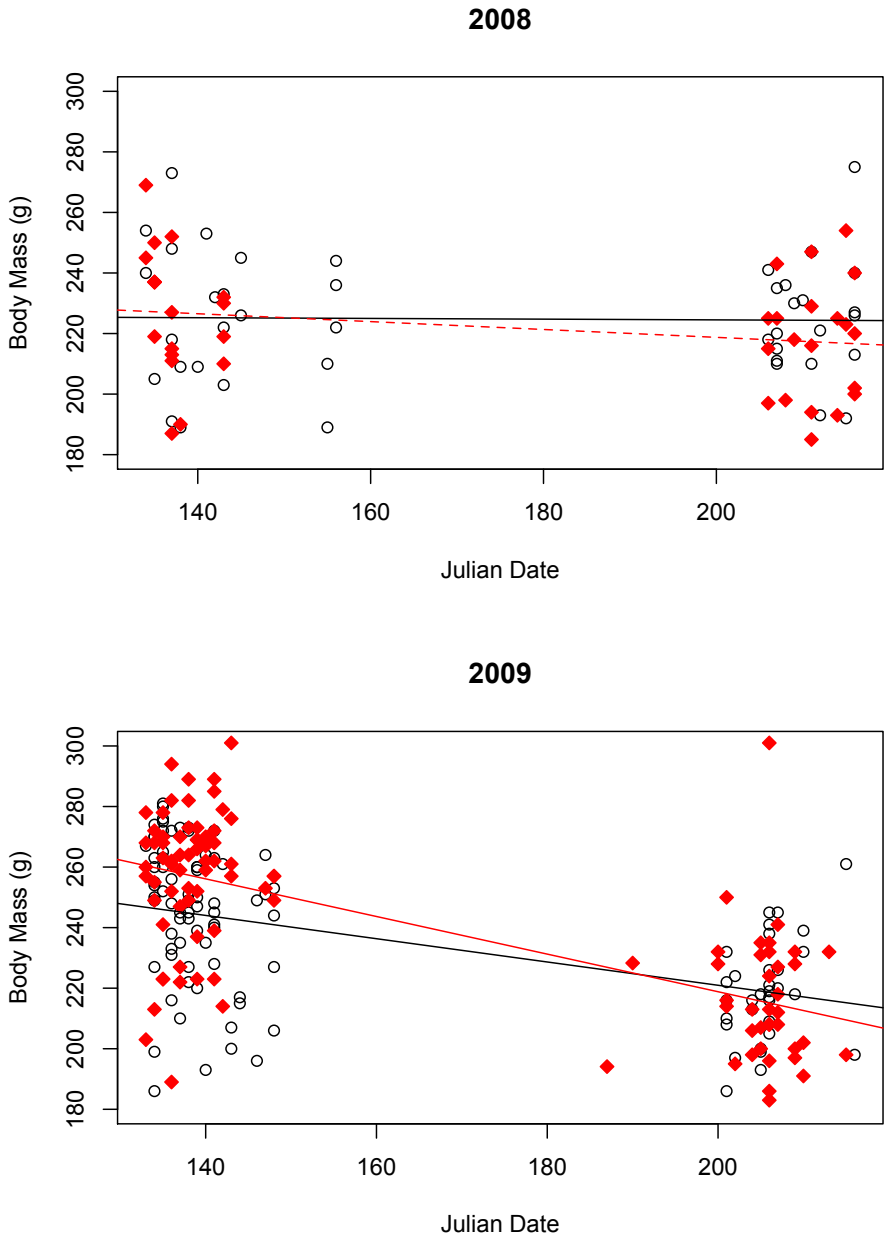


Figure 3.2. Results of sensitivity analysis for model input parameters and activity-specific energy expenditure rates (costs) for the bioenergetics model of adult Kittlitz's murrelets (*Brachyramphus brevirostris*) during the chick-rearing period. The model was run with mean observed or estimated values for each parameter to calculate a baseline value for field metabolic rate (FMR). The sensitivity of FMR to variation in the input variables for the model was tested by individually adjusting each mean parameter estimate by +/- 20% while holding all other parameters at the mean (baseline) level. Percent change in estimated FMR is plotted for each parameter of interest.

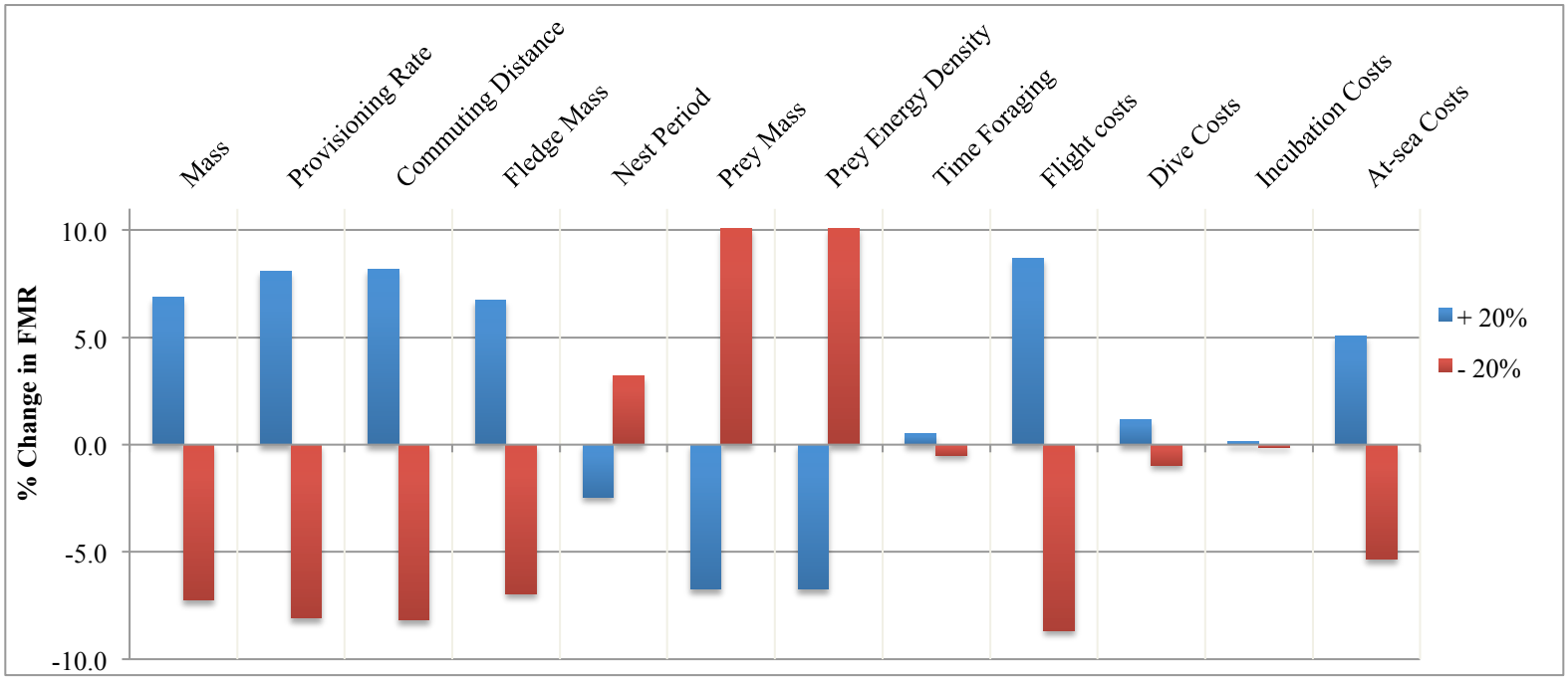


Table 3.1. Time-activity budget and energetic parameter estimates used in the bioenergetics model for breeding adult Kittlitz's murrelets. Time-activity budgets were calculated from empirical data on Kittlitz's murrelet behavior during early breeding (incubation) and late breeding (chick-rearing) periods. Energetic parameters were estimated using allometric equations for high latitude seabirds (Bryant and Furness 1995) or seabirds from cold climates that use predominantly flapping flight (Birt-Friesen et al. 1989).

		CODE	EARLY	LATE	REFERENCE
TIME ACTIVITY BUDGET (% of 24-hr period)					
AT NEST		T_{nest}	50	3.8 – 5.1	this study
TOTAL FLYING		T_{flight}	1.3 – 4.5	4.7 - 17.8	this study
FLYING (NEST TO SEA)		$T_{commute}$	1.0 – 4.2	4.4 - 17.5	this study
FLYING AT SEA		T_{travel}	0.3	0.3	this study
RESTING AT SEA		T_{loaf}	42.3 - 43.8	61.6 - 74.7	this study
FORAGING AT SEA		T_{forage}	4.3 - 4.4	9.2 - 11.2	this study
ENERGETICS		**EARLY**	**xBMR**	**LATE**	**xBMR**	
BASAL METABOLIC RATE (BMR; kJ/hr)	**BMR**	6.6	1.0	6.2	1.0	Bryant and Furness 1995
AT NEST (kJ/hr)	$\mathbf{E_{nest}}$	9.7	1.5	9.2	1.5	Birt-Friesen et al. 1989
FLYING (kJ/hr)	$\mathbf{E_{flight}}$	76.2	11.6	66.1	10.6	Birt-Friesen et al. 1989
AT SEA (kJ/hr)	$\mathbf{E_{atsea}}$	14.5	2.2	13.9	2.2	Richman and Lovvorn 2011
FORAGING (kJ/hr)	$\mathbf{E_{forage}}$	24.5	3.7	23.3	3.7	Birt-Friesen et al. 1989

Table 3.2. Wing metrics and estimated flight costs at a flight velocity of 80 km/h for Kittlitz's murrelets during the early breeding (incubation) and late breeding (chick-rearing) seasons while carrying a 10-g fish. Flight energetics were modeled using Pennycuick's (2008) flight energetics models.

		MASS	WINGSPAN	WING AREA	FLIGHT POWER	BMR*	FLIGHT COST	MULTIPLE OF BMR	MASS-SPECIFIC WORK AT 80 km/hr
		kg	*m*	m^2	*W*	*kJ/hr*	*kJ/hr*	*xBMR*	*kJ/kg*
EARLY	Female	0.247	0.4403	0.0203	22.5	6.8	81.1	11.9	31.2
	Male	0.241	0.4553	0.0211	19.6	6.7	70.5	10.5	28.6
LATE	Female	0.217	0.4403	0.0203	18.4	6.2	66.2	10.7	29.8
	Male	0.221	0.4553	0.0211	17.1	6.3	61.5	9.8	27.7
WITH 10-g FISH	Female	0.227	0.4403	0.0203	19.8	6.2	71.2	11.5	30.4
	Male	0.231	0.4553	0.0211	18.4	6.3	66.2	10.5	28.2

*BMR calculated using the allometric equation in Bryant and Furness 1995: BMR = 2.3 $M^{.774}$, where M = mass (g).

Table 3.3. Proportion of time at sea spent loafing (on the water but not foraging), foraging (diving and rest time between dives within the same foraging bout), preening, and wing-flapping, and mean (SD) duration of dives during the early breeding (May-June) and late breeding (July-August) seasons.

	LOAFING	FORAGING	PREEN*	WING FLAP*	AVERAGE (sd) DIVE DURATION (s)
EARLY	88.34%	10.43%	1.13%	0.10%	36 (10)
LATE	89.93%	8.01%	1.32%	0.73%	37 (12)

*Preening and wing-flapping comprised a very small proportion of the overall time-activity budget and so were combined with time spent loafing for estimating field metabolic rates.

Table 3.4. Mean daily estimates of time allocated to specific activities during the early breeding (incubation) and late breeding (chick-rearing) seasons (% of 24-hr day) for Kittlitz's murrelets in Icy Bay, Alaska. Mean estimates are calculated using the average observed commuting distance and range (in parentheses) is calculated using the observed range of commuting distances.

	AT NEST	FLYING	FORAGING	AT SEA
INCUBATION	0.50*	0.03 (0.02 – 0.09)	0.05 (0.09 – 0.10)	0.42 (0.82 – 0.88)
CHICK-REARING	0.02 (0.01 – 0.03)	0.21 (0.04 – 0.65)	0.06 (0.03 – 0.08)	0.71 (0.29 – 0.87)

*24-hr incubation shift averaged over 2 days

Table 3.5. Estimated daily food consumption (g/day) by Kittlitz's murrelets during the early and late breeding season while feeding on different prey types. Forage fish prey types are grouped into categories of low[1], medium[2], and high[3], and quality based on average energy density (kJ/g wet mass)[4].

		ZOOPLANKTON			**FORAGE FISH**		
	ADEE[5](kJ/d)	AMPHIPOD *2.9 kJ/g*	EUPHAUSIID *4.1 kJ/g*	COPEPOD *4.6 kJ/g*	LOW[1] *2.8 kJ/g*	MEDIUM[2] *4.8 kJ/g*	HIGH[3] *5.8 kJ/g*
EARLY	482	244 g/day	172 g/day	154 g/day	NA[6]	NA[6]	NA[6]
LATE	580	NA[6]	NA[6]	NA[6]	252 g/day	147 g/day	114 g/day

[1]Low: juvenile walleye pollock
[2]Medium: capelin, Pacific sand lance, surf smelt
[3] High: juvenile Pacific herring
[4]Prey energy density values from Anthony et al. 2000 and Davis et al. 1998
[5] Calculated using bioenergetics model
[6]NA denotes prey types not consumed during each period based on stable isotope analysis. See Chapter 2.

Table 3.6. Maximum average commuting distance for Kittlitz's murrelet provisioning nestling while maintaining Field Metabolic Rate (FMR, kJ/day)) below Maximum Sustained Working Capacity (FMR ~ 650 kJ/day). Calculations were made under different scenarios of prey quality (average total energy density per prey item delivered: low [walleye pollock] = 2.8 kJ/g, medium [capelin] = 4.8 kJ/g, high [Pacific herring] = 6.0 kJ/g) for a 10-g prey item and fledging mass from 100 – 150 grams. Nestling period was held constant at 25 days.

			COMMUTING DISTANCE		
ADULT MASS	**FLEDGE MASS**	**$DMEP_{peak}$**	*Pollock (2.8 kJ/g)*	*Capelin (4.8 kJ/g)*	*Pacific Herring (5.8 kJ/g)*
g	*g*	*kJ/day*	33	57	69
220	100	233.0	31	53	64
220	110	252.6	28	49	59
220	120	271.9	27	46	56
220	130	291.0	25	43	52
220	140	309.9	23	41	49
220	150	328.6	23	41	49

[1]Daily Metabolizable Energy Provisioned (DMEP, for seabirds) was estimated using nestling daily energy demand from Visser (2002).

Table 3.7a. Results of a sensitivity analysis for specific parameters of the bioenergetics model for adult Kittlitz's murrelets (*Brachyramphus brevirostris*) during the chick-rearing period. The model was run with mean observed or estimated values for each parameter to calculate a baseline value for field metabolic rate (FMR). The sensitivity of the model was tested by individually adjusting each mean parameter estimate by +/- 20% while holding all other parameters at the mean (baseline) level. The newly calculated estimate of FMR and the % change in FMR from the baseline estimate are provided.

	MASS	**PROVISIONING RATE**	**COMMUTING DISTANCE**	**FLEDGING MASS**	**NESTLING PERIOD**	**PREY MASS**	**PREY ENERGY DENSITY**	**TIME FORA-GING**
	g	*fish/adult/day*	*km*	*g*	*days*	*g*	*kJ/g*	*hr/day*
MEAN	220.0	3	35.0	110.0	25.0	10.0	4.8	1.5
BASELINE FMR	580.1	580.1	580.1	580.1	580.1	580.1	580.1	580.1
+20%	264.0	3.6	42.0	132.0	30.0	12.0	5.8	1.8
FMR	619.9	626.9	627.4	619.2	565.9	541	541	583.0
% CHANGE	**6.9**	**8.1**	**8.2**	**6.7**	**-2.4**	**-6.7**	**-6.7**	**0.5**
-20%	176.0	2.4	28.0	88.0	20.0	8.0	3.8	1.2
FMR	538.1	533.2	532.7	539.7	598.6	638.6	638.6	577.3
% CHANGE	**-7.2**	**-8.1**	**-8.2**	**-7.0**	**3.2**	**10.1**	**10.1**	**-0.5**

Table 3.7b. Results of a sensitivity analysis for activity-specific rates of energy expenditure for chick-rearing Kittlitz's murrelets (*Brachyramphus brevirostris*). The model was run with mean estimated values for each parameter to calculate a baseline value for murrelet field metabolic rate (FMR; see methods for allometric equations). The sensitivity of the model was tested by individually adjusting each mean parameter estimate by +/- 20%, while holding all other parameters at the mean (baseline) level. The newly calculated FMR estimate and the % change in FMR from the baseline estimate are provided.

	FLIGHT *kJ/hr*	**DIVE** *kJ/hr*	**INCUBATION** *kJ/hr*	**AT-SEA** *kJ/hr*
MEAN	66	25	9.7	14.8
BASELINE FMR	580.1	580.1	580.1	580.1
+20%	79.2	30.0	11.6	17.26
FMR	640.8	587	580.9	627.7
% CHANGE	**10.5**	**1.2**	**0.1**	**8.2**
-20%	52.8	20	7.76	11.84
FMR	519.3	573.1	579.2	532.7
% CHANGE	**-10.5**	**-1.2**	**-0.1**	**-8.2**

CHAPTER 4

SYNOPSIS AND CONCLUSIONS

Nicholas R. Hatch

Summary

This study is the first extensive investigation of Kittlitz's murrelet foraging ecology using stable isotope analysis and the first quantitative assessment of the metabolic costs of reproduction in this species. While the two core chapters of my thesis are fundamentally different in character, the overall results strongly suggest that Kittlitz's murrelets occupy a narrow ecological niche. In Chapter 2 we learned from stable isotopes in feathers and blood that Kittlitz's murrelets exhibit seasonally distinct foraging habits, in particular a full trophic level difference between diets during the vernal pre-alternate molt and the autumnal pre-basic molt. During the breeding season murrelets switch from consuming primarily low trophic level prey (macrozooplankton) to consuming higher trophic level prey (forage fishes). This shift in diet coincides with the onset of chick provisioning demands during the nesting period, when adult murrelets must locate, capture, and deliver forage fish to their single nestling at nest sites that can be a considerable distance from foraging areas. In Chapter 3, we investigated how variability in both commuting distance (distance between nest site and foraging area) and prey quality (energy content of single prey items delivered to nestlings) affects the overall energy expenditure rate of a breeding Kittlitz's murrelet. During the incubation period, each breeding Kittlitz's murrelet spends about half its time fasting while performing incubation duties. Under some conditions, Kittlitz's murrelets may lose mass during the breeding season, suggesting

that breeding adults may rely in part on stored energy (if they have it) to meet requirements for energy expenditure. During chick-rearing, the field metabolic rate (FMR) of Kittlitz's murrelets may exceed the theoretical limits of sustained metabolic output under scenarios of commuting distance between foraging areas and nest site and prey energy content that are observed in the wild.

The results of both chapters combined suggest that Kittlitz's murrelets nesting in the area of Icy Bay, Alaska may have such high energy requirements for reproduction that variation in the quality and availability of forage fish during chick-rearing can result in an energetic bottleneck that constrains overall productivity. Breeding adult Kittlitz's murrelets can compensate for longer commuting distances and lower chick meal delivery rates by selecting prey with higher energy content, up to a certain level of commuting effort. A decrease in availability of high-quality forage fish during the chick provisioning stage could, however, increase FMR of breeding adults above a threshold that, if sustained, could lead to loss of fitness.

There is evidence that numbers of Kittlitz's murrelets are in decline in some core population areas (Kuletz et al. 2011, Piatt et al. 2011). The magnitude and extent of these apparent declines are unknown (Kirchoff 2011), as is the period over which any decline may have occurred. Stable isotope signatures of Kittlitz's murrelets over the past century (1907-2009; Chapter 2) suggest that the trophic level of the diet has not changed dramatically in southeastern Alaska during this period. Nevertheless,

$\delta^{13}C$ became progressively depleted over this time period. Whether the significant trend toward more depleted $\delta^{13}C$ in Kittlitz's murrelet feathers reflects a change in diet composition or merely a change in the isotopic composition of the prey base is not clear and it will require further investigation to resolve this question. Similar trends in isotope ratios have been observed in other marine taxa from the Gulf of Alaska and Bering Sea regions (Schell 2000). Schell (2000) attributed the trend in $\delta^{13}C$ of whale baleen from the Bering Sea to an overall decrease in primary productivity. This explanation, however, was contested by Cullen et al. (2000), who suggested that the Seuss effect, or the change in the ratio of carbon isotopes in the atmosphere and oceans due to the combustion of fossil fuels, provided a more parsimonious explanation for the observed trend. Further investigation of the trends in baseline isotope profiles in the marine environment is needed to provide more insight into these trends and how they may relate to the foraging habits of marine consumers like the Kittlitz's murrelet.

It has been suggested that *Brachyramphus* murrelets have evolved life history traits of low reproductive output and high adult survival, and may rely on occasional favorable breeding seasons to produce large cohorts (M. Kissling, pers. comm.). Results of modeling the energetics of breeding Kittlitz's murrelets (Chapter 3) suggest that breeding may be a period of nutritional stress due to extended time spent fasting during incubation shifts and the overall high energetic demands of commuting during

chick-rearing. In the lead-up to the breeding season, Kittlitz's murrelets forage on low trophic level prey, presumably taking advantage of spring blooms of herbivorous macrozooplankton in the Gulf of Alaska (Coyle and Pinchuck 2005). A delay or mismatch in the spring bloom of zooplankton may disrupt the timing of vitally important energy storage in Kittlitz's murrelets during this pre-breeding period when murrelets may need to gain additional mass, which may provide a buffer for poor foraging conditions during incubation and/or high metabolic costs during chick-rearing.

Kittlitz's murrelets are central place foragers during the breeding season (Orians and Pearson 1979). As such, they are restricted to foraging within an energetically feasible distance from their nest site. As foraging distance increases, commuting costs increase as a function of the energetic efficiency of flight and flight speed. The tradeoff for Kittlitz's murrelets between procuring quality prey, both for self and for provisioning the nestling, and restricting energy expenditure below a level that may severely compromise survival and overall fitness may be an important determinant of reproductive success. Reproductive output for individual murrelets is apparently quite low (Day and Nigro 2004, Kaler et al. 2009, USFWS 2010), even compared to other alcids, and therefore murrelets must exhibit high adult survival in order to replace themselves during their lifetime and maintain stable populations. There is evidence that only a small proportion (< 10%) of the population attempts to

breed in most years (M. Kissling, unpubl. data), suggesting that adult murrelets may frequently skip years between nesting attempts and only attempt to reproduce when conditions are highly conducive to successful nesting.

Future Research

Our understanding of the seasonal variability in the foraging habits of Kittlitz's murrelets could be enhanced with more sampling from the non-breeding period, particularly the winter and early spring months. This information could be acquired through blood sampling of Kittlitz's murrelets captured at sea. Finding Kittlitz's murrelets during the winter may not be easy, but with new data from satellite telemetry it may soon be possible to find aggregations of over-wintering Kittlitz's murrelets.

To improve dietary inferences and to allow the use of mixing model techniques to quantify diet composition, it is imperative that proper diet/tissue fractionation rates are calculated for this species. Diet/tissue fractionation rates have been experimentally calculated for similar species, such as the common murre (*Uria aalge*; Becker et al. 2007), but have never been calculated for any of the *Brachyramphus* murrelets. While others have used estimates from similar species for isotope-diet mixing models (Becker & Beissinger 2006, Norris et al. 2007), the assumptions in

doing so are not trivial (Bond & Diamond 2010), and to fail to meet these assumptions can lead to erroneous results.

The results of Chapter 3 could be greatly improved with empirical measurements of field metabolic rates and basal metabolic rates of *Brachyramphus* murrelets. I was not able to measure metabolic rates of Kittlitz's murrelets as part of this study, instead relying on predictions of allometric equations and measurements from similar or taxonomically-related species. The doubly labeled water method requires recapturing the same individual a short time (24-48 hr) after initial capture. This would be unlikely to succeed with Kittlitz's murrelet. However, respirometry of a resting murrelet may be possible if captured under the right conditions. Additional flight modeling may also provide novel information that could improve our understanding of fast flying seabirds such as the *Brachyramphus* murrelets. Even without these improvements the bioenergetics model as presented in Chapter 3 can be used as a base for testing other hypotheses related to Kittlitz's murrelets during the breeding season. While acknowledging the assumptions inherent to this type of modeling, it may be possible to estimate energetic costs of various changes to either time-activity or energy budgets caused by environmental change (e.g., climate change), disturbance, or anthropogenic alteration of key habitats.

The isotope data presented in this thesis suggest that Kittlitz's murrelets consume high trophic level prey during the post-breeding, pre-basic molt. The $\delta^{15}N$

values for post-breeding are higher than what is found in prey from the breeding area, Icy Bay, Alaska, suggesting that these birds molted their flight feathers in an area that is isotopically quite different from Icy Bay. Recent data from satellite-tagged Kittlitz's murrelets from the same Icy Bay population suggest that murrelets make long-distance migratory movements post-breeding (M. Kissling, unpubl. data). These movements included rapid flights up the coast to Prince William Sound, west to the Alaska Peninsula, and as far north as the Bering Sea. Collecting prey samples from these areas was beyond the scope of this project; however, there are some published stable isotope data from these areas that can provide a frame of reference. Kurle et al. (2011) reported higher $\delta^{15}N$ in some fish muscle samples from the Bering Sea as compared to the same type (species, age, size, season) of fish from the Gulf of Alaska, suggesting a higher baseline trophic level for forage fish from the Bering Sea ecosystem. Additionally, there is evidence that $\delta^{13}C$ of marine mammal tissues in the Bering Sea is more depleted than in the Gulf of Alaska (Hirons et al. 1998, Kurle & Gudmundson 2007). By coupling satellite telemetry data and isotope data it may be possible to track not only individual murrelets, but groups or subpopulations of murrelets by assigning them to isotopically distinct post-breeding molting areas (Oppel & Powell 2008).

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