Examining hair growth rates and dietary patterns of wild and captive bears

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Abstract

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The feeding ecology of wildlife has important implications for individual health, population productivity, community structure, and ecosystem functioning. For bears of the family Ursidae, food resources and feeding behavior primarily impact population dynamics via effects on cub production and survival. Much of what is known about the feeding ecology of bears is based on analyses of various tissues collected from capture-based research efforts, harvested animals, or non-invasive approaches. The use of multiple chemical tracer methods provides an informative view of the diet, as each tissue spans a unique timeline. However, inference about diet from hair has been limited by a lack of quantitative data on the timing of the molt and hair growth rates. Addressing physiological assumptions is essential to gain insights into the feeding patterns in wild bear populations in dynamic ecosystems.

Climate change is shifting the phenology, availability, and selection of food resources for bears across multiple ecosystems. Because polar bears (*Ursus maritimus*) specialize in both food and habitat type, they are particularly vulnerable to environmental change. Detailed studies of polar bear foraging are necessary for a comparative and predictive understanding of how diets may change with a loss of sea ice habitat and increased use of coastal habitats. One such documented coastal habitat is freshwater glacier ice, which provides year-round access to prey for Baffin Bay polar bears, although the feeding habits of polar bears using glacier ice relative to those following the retreating ice and/or seasonally moving onshore are not known.

This dissertation comprehensively investigates the interpretation of dietary data derived from hair samples and the drivers of diet variability in polar bears, with the overarching goal of contributing to an improved understanding of the feeding ecology of bears. First, methods were developed to document hair growth in three species of captive bears. The methods of hair dye and ^{13}C- and ^{15}N-labeled glycine identified periods of hair growth and detected individual and seasonal variations in hair growth rates, with their effectiveness not being dependent on the bear species. Second, the timing and rate of hair growth were quantified in captive polar bears across an annual cycle, incorporating variables of body location and season. Hair growth was detected at similar rates throughout spring, summer, and fall, while there was slower growth in winter, consistent with the anticipated patterns of an annual molt. Third, dietary patterns among wild polar bears of different sexes, ages, and movement patterns were evaluated in relation to sea ice metrics using stable isotopes and total mercury concentrations in hair. Baffin Bay polar bears showed limited variation in their feeding habits, as indicated by stable isotope values and total mercury concentrations, despite differences in inter-annual sea ice conditions and individual space-use strategies. Fourth, patterns of diet composition were evaluated among Baffin Bay polar

bears with distinct coastal and offshore space-use strategies using relative abundances of fatty acid signatures in fat samples, a tissue representing a different time period (winter-fall) than hair (spring-summer). While demographic and short-term temporal variation was minimal, fatty acid signatures and diet estimates clearly differed between coastal polar bears using glacier fronts and offshore bears using pack ice habitat. Collectively, results from these chapters bridge experimental and applied settings, improve interpretations of bear hair samples, and provide insight into the factors driving diet variability in wild polar bears.

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DEDICATION

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Chapter 1. INTRODUCTION

1.1 APPROACHES TO STUDYING BEAR DIET

Feeding ecology in wildlife is directly linked to individual health, population productivity, distribution patterns, community structure, and ecosystem functioning (Altmann et al. 1993, Oro et al. 2004, Dobson 2009, Nielsen et al. 2010, Ripple et al. 2014). In bear species of the family Ursidae, survival and reproduction are dependent on food resources and foraging behavior (Schwartz & Franzmann 1991, Noyce & Garshelis 1994, Derocher & Stirling 1995, Hilderbrand et al. 1999, Hertel et al. 2018). Climate change is shifting the phenology, availability, and selection of food resources for bears across multiple ecosystems (Deacy et al. 2017, Laidre et al. 2018b, Kurth et al. 2024). Changes in food resources, fasting patterns, and habitat use can increase the potential for human-bear interactions and conflicts (Atwood et al. 2016b). Understanding how diet variability relates to fasting, habitat use, and ultimately human-wildlife conflicts is necessary to manage and conserve bear species effectively.

Bear diet has been quantified through various methods, including direct observation, scat analysis, and chemical analysis of tissues (Ramsay & Hobson 1991, Derocher et al. 2002, Thiemann et al. 2008, Cherry et al. 2011, Gormezano & Rockwell 2013, McKinney et al. 2013, Rogers et al. 2015, Jaouen et al. 2016, Tartu et al. 2016). Tissue chemical analyses provide ecological information without requiring direct, continuous observation, which is often difficult for large, elusive, species in remote environments (Budge et al. 2006, Newsome et al. 2010). Much of what we know about the feeding ecology of bears is based on analyses of various tissues collected through capture-based research efforts, from harvested animals, or non-invasive approaches such as hair snags. Use of multiple chemical tracers and methods provides an

informative view of the diet, as each tissue spans a unique timeline and represents a distinct metabolic pathway (Cherry *et al.*, 2011; Bowen and Iverson, 2013).

Fatty acid signature analysis is one method that can be used to explore broad dietary patterns, as well as provide a quantitative estimate of the species composition of the diet (Tucker et al. 2008). Adipose samples provide indicators of health and ecology during the timeframe just prior to collection because fat has a high biochemical turnover rate compared to hair (Kurle & Worthy 2002). The resulting diet estimates are from fat stores that were likely accumulated in the preceding weeks to months (Iverson et al. 2004, Budge et al. 2006, Nordstrom et al. 2008, Thiemann et al. 2008, 2022). Quantitative fatty acid signature analysis (QFASA) estimates diet composition of a predator by modeling a combination of different proportions of prey species to best match the observed predator fatty acid signature after accounting for fatty acid specific patterns of metabolism (Iverson et al. 2004). There have been significant advances in the analysis of fatty acids to better address assumptions (Bromaghin et al. 2015a c, 2017).

Hair is a particularly useful tissue because it can be collected via multiple approaches and provides insight into bear diets (Rogers et al. 2015, 2020, Rode et al. 2016, Mowat et al. 2017, Boucher et al. 2019b, Johnson et al. 2019), stress levels (Macbeth et al. 2010, 2012, Cattet et al. 2014, Bechshoft et al. 2015, Weisser et al. 2016), individual identification via genetics (Dreher et al. 2007, Proctor et al. 2010, Wirsing et al. 2020), and exposure to contaminants (Born et al. 1991, Dietz et al. 2006, St. Louis et al. 2011, Bechshoft et al. 2015, 2016). Hair samples are metabolically inert and, therefore, provide information about bears during the time period in which the hair is grown (Tucker et al. 2008). However, one of the primary current limitations to using hair is a lack of data on the timing and rate of fur growth throughout and following the annual molt. By identifying the timeframe represented by hair samples, researchers can enhance

the interpretation of seasonal dietary patterns, hormonal fluctuations, and other key indicators of polar bear health.

1.2 ADDRESSING ASSUMPTIONS: MEASURING BEAR HAIR GROWTH RATES

North American bear species have variable access to food seasonally (Stirling & McEwan 1975, Belant et al. 2006) and are thought to undergo an annual molt between May and October (Obbard 1987, Jacoby et al. 1999, Schwartz et al. 2003). Although hair growth rates have been estimated for grizzly bears (*Ursus arctos horribilis*) and polar bears (*Ursus maritimus*), these studies have been limited to estimating a single rate for the entire hair growth period (e.g., grizzly bears in British Columbia, Mowat et al. 2017), used shaved patches which could have resulted in compensatory growth (e.g., Argyris 1968), or were restricted to only a seasonal period (e.g., Felicetti et al. 2004, Erlenbach 2020; Hein et al. 2021). There have been no hair growth rates estimated for black bears (*Ursus americanus*), and no studies have investigated seasonal variation in growth rate via methods that avoid shaving.

The process of hair growth and replacement includes molt and new hair growth, with shedding of old fur occurring before, during, or following new hair growth (Ling 1970, Fraser et al. 2013, Rolfes et al. 2021). Environmental factors (e.g., photoperiod, temperature, and snow cover) cue the increased production of hormones that stimulate new hair growth (Zimova et al. 2018, Déry et al. 2019, O'Brien et al. 2020). Other factors that affect intra- and inter-specific variation in hair growth and molt timing include age class, sex, reproductive status, body mass and condition, and access to food resources (Zimova et al. 2018, Déry et al. 2019). Despite the importance of hair growth for understanding life history, the drivers and phenology of the mammalian molt are not well understood within and among many species, including bears (Beltran et al. 2018, Zimova et al. 2020).

Bears in zoos provide an excellent opportunity to document hair growth patterns while addressing a critical need to better understand the ecology and health of wild bears. Studying captive animals to better understand wild populations has become increasingly popular, although this field has a rich history of providing foundational knowledge of animal biology and ecology. Zoos began to incorporate research into mission statements and organized programs with personnel in the 1980s and 90s, following the extinction crisis and passing of the US Endangered Species Act (Kaufman et al. 2019). Although there are many limitations to the inferences that can be made based on differences between captive and wild bears, captive polar bears still have intrinsic physiological processes that will reflect bears in the wild. Importantly, repeated access to captive bears can allow for assessment of the variability of hair growth rates relative to factors such as season and body region. Addressing physiological assumptions is essential to gain insights into the feeding patterns in wild bear populations in dynamic ecosystems.

1.3 FEEDING ECOLOGY IN WILD BEARS: A FOCUS ON POLAR BEARS

Polar bears are particularly vulnerable to climate change because they specialize in both prey and habitat type (Davies et al. 2004, Kovacs & Lydersen 2008). There are 20 subpopulations of polar bears across the Arctic with varying population statuses, some of which are entirely data deficient. Subpopulations are defined by mark-recapture, satellite telemetry, population genetics, and traditional ecological knowledge (Obbard et al. 2010). Variation in polar bear responses to reduced sea ice among subpopulations is associated with sea ice ecoregion type, status of regional prey populations, and ecosystem health/productivity (Regehr et al. 2010, Rode et al. 2014, 2018, Pilfold et al. 2015, Whiteman et al. 2015, Hamilton et al. 2017). Polar bears in different subpopulations, or even in different habitats within a subpopulation (i.e., coastal versus offshore), may show sea ice-associated dietary shifts (McKinney et al. 2017a).

Polar bears are specialist top predators that rely on a lipid-rich diet to satisfy their nutritional needs (Stirling & Archibald 1977, Rode et al. 2021, Stricker et al. 2022). Polar bears require large amounts of fat in their diets, with their primary prey consisting of ringed (*Pusa hispida*) and bearded (*Erignathus barbatus*) seals, and occasionally belugas (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), and walrus (*Odobenus rosmarus*) (Calvert & Stirling 1990, Smith & Sjare 1990, Stirling & Oritsland 1995). Ringed seals are often hunted at their clawed-in-ice breathing holes or clawed-in-snow birth lairs, with a higher proportion of pups killed in spring during times of high seal productivity (Smith 1973, Stirling & Archibald 1977). Larger and heavier prey, such as bearded seals, are more often preyed upon by male polar bears (Derocher & Stirling 1990, Cherry et al. 2011). Polar bears eat the fat from their seal prey, often leaving the meat (Stirling & McEwan 1975). Polar bears are specialized and adapted to a lipid-rich prey, limiting the potential for a large dietary shift (Rode et al. 2022). Terrestrial food sources have been deemed insufficient to offset the loss of ice-based predation on marine lipids required by polar bears for survival (Derocher et al. 1993, Rode et al. 2015a). Polar bears rely on their store of adipose tissues during times of low food availability and fasting (Ramsay & Stirling 1988). Ice seals, the primary prey of polar bears, may become less abundant with reduced area of ice for pupping (Stenson & Hammill 2014). Decreased sea ice reduces polar bears' access to their ice-associated prey because bears rely on sea ice as a hunting platform (Stirling & Derocher 1993, Moore & Huntington 2008, Galicia et al. 2016). Declines in available ice and increased fragmentation may lead to increased energy demands from a higher requirement for mobility in polar bears and therefore may explain observed body condition declines (Pagano et al. 2018).

Deteriorating habitat is causing significant biological changes in the Baffin Bay (BB) subpopulation, which is shared between Canada and Greenland. Although the observed population trend is uncertain (SWG [Scientific Working Group to the Canada-Greenland Joint Commission on Polar Bear] 2016), body condition and reproduction declined between the 1990s and 2000s as shown through morphometric measurements, aerial observations, and traditional ecological knowledge (Dowsley & Wenzel 2008, Rode et al. 2012, SWG 2016, Laidre et al. 2020). Baffin Bay is one of five polar bear subpopulations within the seasonal sea ice ecoregion and the region is therefore ice-free in summer (Amstrup et al. 2008, Laidre et al. 2013, 2018a b). The rapid decrease of Arctic sea ice has resulted in longer open water seasons, with earlier onset of break-up and later dates of freeze-up (Overland & Wang 2013, Barnhart et al. 2016, Stern & Laidre 2016). Polar bears in BB use large proportions of accessible habitat while moving across the pack ice, and the date of arrival to and departure from Baffin Island closely correlates with sea ice retreat and advance (Laidre et al. 2013, 2020, SWG 2016). BB Bears that make long-distance movements across the pack ice ('offshore bears') spend their summer on land (Baffin Island) without access to marine prey resources and are likely to fast for three or more months (Ferguson et al. 1997, Laidre et al. 2020a). Another subset of bears, resident at glacier fronts in NW Greenland year-round ('coastal bears'), have been observed with satellite telemetry in recent years and documented using traditional ecological knowledge (Born et al. 2011, SWG 2016, Laidre et al. 2020). The use of glacier fronts by BB polar bears during the open water season may become more common due to the need for year-round access to a hunting platform as loss of sea ice continues (Laidre et al. 2020a). Polar bears in BB have a diverse diet, confirmed using a fatty acid mixing model to include ringed seals, bearded seals, harp seals (*Pagophilus groenlandicus*), harbor seals (*Phoca vitulina*), and belugas (Galicia et al. 2015). However, this

study was limited to data collected from subsistence-hunted bears and did not include samples from females with cubs or resident coastal BB females. Coastal and offshore movement patterns are found in other polar bear subpopulations and previous studies have investigated polar bear dietary and contaminant patterns related to space-use (Rogers et al. 2015, Boucher et al. 2019a, Blévin et al. 2020), but none to date have focused on an ecoregion of seasonal sea ice or the BB subpopulation. Understanding the intersection of sea-ice metrics, movement patterns, and resource use for a subpopulation that undergoes a completely ice-free season is increasingly important as sea ice continues to decline throughout the Arctic.

Detailed studies of polar bear foraging are necessary for comparative and predictive understanding of how diets may change with a loss of sea ice habitat and increased use of coastal habitats. Using isotopic tracers and mercury concentrations allows an investigation of feeding habits and general trophic position. Carbon stable isotope ratios ($^{13}C/^{12}C$) are representative of different feeding habitats (i.e., offshore vs. coastal), whereas nitrogen stable isotope ratios ($^{15}N/^{14}N$) and total mercury concentrations are tracers of trophic position (Fisk et al. 2002, Galloway et al. 2015). Sulfur stable isotope ratios ($^{34}S/^{32}S$) are especially effective at distinguishing between terrestrial and open-ocean feeding (Barros et al. 2010, Matthews & Ferguson 2015, Szpak & Buckley 2020). Stable isotopes can also trace diet through the food web, identifying carbon sources from pelagic and sympagic primary producers that eventually reach top predators (Hobson et al. 2002, Horton et al. 2009). Sulfur isotopes are also used across benthic-pelagic gradients, and combining carbon and sulfur signals is the most effective combination at distinguishing between primary producer groups (Peterson et al. 1985, Connolly et al. 2004). Stable isotopes analysis has been the primary tool to examine dietary patterns related to distinct coastal and offshore movement patterns within polar bear subpopulations

(Rogers et al. 2015, Boucher et al. 2019a, Blévin et al. 2020, Stern et al. 2021), but multiple methods are recommended to ensure reliable diet information (Bowen and Iverson, 2013).

Combining fatty acid analyses with stable isotopes analyses allows more detailed information on diet and the pathways and energy transfer among organisms (Tucker et al. 2008, Wang et al. 2016). Fatty acids can be used to compare feeding patterns based on relative proportions of fatty acid signatures and diet estimates generated by QFASA. The use of fatty acid signatures has been employed to infer feeding patterns in other marine mammals, seabirds, and fish (Smith et al. 1996, Dahl et al. 2003, Cooper et al. 2009, Kelley et al. 2010, McMeans et al. 2012, Choy et al. 2020). Fatty acid analysis using QFASA has estimated the diet composition of other populations of polar bears, such as those in East Greenland and the Barents Sea (McKinney et al. 2013, 2017a). Neither fatty acid signatures nor QFASA has been applied to comparing the diets of coastal and offshore polar bears.

1.4 DISSERTATION OVERVIEW AND RESEARCH OBJECTIVES

My dissertation focuses on addressing the assumptions that underlie the interpretation of dietary data derived from hair samples and investigating the drivers of diet variability in polar bears, with the overarching objective of contributing to an improved understanding of polar bear feeding ecology in a rapidly changing Arctic ecosystem. My dissertation begins by concentrating on the physiology of individual bears and how information at this level can be extrapolated to inform applied research. In my second chapter, I develop methods to document hair growth in bears. I build on this for my third chapter, where I design a study to quantify the timing and rate of hair growth in zoo polar bears. I then apply the use of dietary tracers from two distinct tissues to elucidate the feeding habits of the wild subpopulation of BB polar bears. In my fourth chapter, I use stable isotopes and mercury in hair as tracers to detect dietary patterns across different

sex/age classes and movement patterns of polar bears in the spring – summer. Finally, in my fifth chapter, I compare the diet composition of wild polar bears with distinct coastal and offshore space-use strategies using fatty acid signatures in fat samples.

In Chapter 2, my collaborators and I developed experimental methods to measure hair growth rates in black, grizzly, and polar bears. Through a collaboration with three zoos, we had continued access to individual bears over time, allowing for a sampling frequency that is not feasible with wild bears. We evaluated two methods: 1) applying a small patch of hair dye (or bleach) on the rump or foreleg, and 2) feeding an isotopically labeled amino acid (glycine) capsule that 'marks' time at a particular location as it is incorporated within the hair. Both methods identified periods of hair growth and detected individual and seasonal variation in hair growth rates. The effectiveness of the method was not dependent on the bear species. Our findings establish two effective methods to measure seasonal hair growth rates, and we estimated hair growth rates for three North American bear species.

In Chapter 3, my collaborators and I quantified the timing and rate of hair growth in captive polar bears across an annual cycle, incorporating variables of body location and season. We estimated the seasonal hair growth of eight polar bears in four zoos by analyzing guard hairs collected over a 6- to 18-month period using previously validated methods of hair dye and ^{13}C- and ^{15}N-labeled glycine, developed in Chapter 2. Hair growth was detected in each of the four seasons, with comparable hair growth rates across spring, summer, and fall. Winter hair growth rates were slower compared to other seasons, consistent with expected growth patterns associated with an annual molt. We also detected differences in the rate of hair growth between body regions. This research lays the groundwork for incorporating seasonality into wild-collected hair samples

to allow a fine-scale analysis component across many disciplines in polar bear research, management, and conservation.

In Chapter 4, peer-reviewed and published in *Marine Ecology Progress Series* (Stern et al. 2021), my collaborators and I evaluated feeding patterns using stable isotopes and mercury in hair as tracers in wild polar bears with distinct coastal and offshore space-use strategies. Additionally, we evaluated broad dietary patterns amongst bears of varying sex and age, and across seasons (spring – summer). Despite wide fluctuations in inter-annual sea ice conditions and differences in space-use strategies among individuals, stable isotope values and total mercury concentrations suggested limited variation in feeding habits among BB polar bears. Total mercury concentrations were related to age class, and nearly half exceeded the suggested threshold for neurological effects in polar bears at 5.4 μg g^{-1}DW. We detected no differences between coastal and offshore adult female polar bears in hair sample carbon, nitrogen, and sulfur stable isotope values and total mercury concentrations. However, we found seasonal variation in $\delta^{13}C$ and $\delta^{34}S$ across both space-use strategies, with $\delta^{34}S$ suggesting that all BB polar bears may prey on a higher proportion of benthic-feeding bearded seals in late summer relative to spring. The specialized BB polar bear diet suggests limited feeding plasticity under ongoing climate warming.

In Chapter 5, peer-reviewed and published in *Ecosphere* (Stern et al. 2024a), my collaborators and I evaluated patterns of diet composition among wild polar bears of varying movement patterns, sex, and age using fatty acid signatures in fat samples, a tissue representing a different time period (winter—fall) than hair (spring—summer). We found, using QFASA-generated diet estimates, that ringed and bearded seals are the primary and secondary prey of BB polar bears for all sex/age classes and sampling years, except for a single anomalous year in

2009. While demographic and short-term temporal variation was minimal, fatty acid signatures and QFASA-generated diet estimates clearly differed between coastal polar bears using glacier fronts and offshore bears using pack ice habitat. The combined use of FA signatures and QFASA-generated estimates emphasized the relative importance of space-use strategy as compared to demographic and temporal variation in influencing BB polar bear feeding patterns. As space-use strategies change due to the continued loss of sea ice habitat, our results suggest important implications for polar bear feeding patterns.

My dissertation chapters collectively provide a comprehensive investigation into using tissue samples to understand the feeding ecology of bears. Chapters 2 and 3 establish seasonal hair growth rates for polar bears, which is crucial for accurately interpreting data obtained from hair samples collected in the wild. The importance of this finding is further supported in Chapter 4, which demonstrates that habitat tracers, specifically carbon and sulfur stable isotopes, vary between the base and tip hair segments and thus fluctuate over the timescale proportional to the tissue growth rate. In Chapter 5, the analysis of fatty acid signatures revealed a difference in diet between coastal and offshore space-use strategies, a distinction not observed in the timescale represented by hair. This dissertation bridges experimental and applied settings, enhances the ability to make informed interpretations of bear hair samples, and offers insight into the factors driving diet variability in wild polar bears.

Chapter 2. HAIR GROWTH ESTIMATION IN NORTH AMERICAN URSIDS

2.1 ABSTRACT

The feeding ecology of wildlife populations has important implications for individual health, population productivity, and distribution patterns. For bears, food resources and feeding behavior primarily affect population dynamics via effects on cub production and survival. Much of what is known about the feeding ecology of bears is based on analyses of various tissues collected from capture-based research efforts, harvested animals, or non-invasive approaches. However, inference about diet from hair has been limited by a lack of quantitative data on the timing of the molt and hair growth rates. We conducted a study to design methods to quantify hair growth rates of three species in the family Ursidae (n = 1 polar bear, *Ursus maritimus*; n = 3 black bears, *Ursus americanus*; n = 3 grizzly bears, *Ursus arctos horribilis*) through a collaboration with zoos between 2019 and 2020. We identified and implemented visual and biochemical approaches, proven safe for humans and other animals, to quantify the rate and timing of hair growth. These methods relied on voluntary bear behaviors that were trained using positive reinforcement. We specifically evaluated two methods: 1) applying a small patch of hair dye (or bleach) on the rump or foreleg, and 2) feeding an isotopically labeled amino acid (glycine) capsule that 'marks' time at a particular location as it is incorporated within the hair. We then collected hair at regular intervals (every 1-2 weeks) for five months from locations on the bear consistent with commonly sampled collection points in wild-caught bears. Both methods identified periods of hair growth and detected individual and seasonal variation in hair growth rates. The effectiveness of the method was not dependent on the bear species. This study provides the first step for developing a

foundation for incorporating seasonality in the wild-collected hair samples by assessing growth over an annual cycle.

2.2 INTRODUCTION

Feeding ecology in wildlife is directly linked to individual health, population productivity, and species distribution patterns (Altmann et al. 1993, Oro et al. 2004, Nielsen et al. 2010). Large mobile consumers such as bears are dependent on food resources for their survival and reproduction, underscoring the importance of feeding behavior (Schwartz & Franzmann 1991, Noyce & Garshelis 1994, Derocher & Stirling 1995, Hilderbrand et al. 1999, Hertel et al. 2018). The diet composition of bears can be highly variable, and food is often a major limiting resource (Stirling & Øritsland 1995, Schwartz et al. 2003, Mitchell & Powell 2007, Rogers et al. 2015). Climate change is shifting the phenology, availability, and selection of food resources for bears across multiple ecosystems (Deacy et al. 2017, Laidre et al. 2018b, Kurth et al. 2024). Changes in food resources, fasting patterns, and habitat use can increase the potential for human-bear interactions and conflicts (Atwood et al. 2016b). Understanding the diet variability of bears is necessary for effective management and conservation.

Bear diets have been quantified through various methods, including observation, scat analysis, and measurement of molecular tracers in tissue (Ramsay & Hobson 1991, Derocher et al. 2002, Thiemann et al. 2008, Cherry et al. 2011, Gormezano & Rockwell 2013, McKinney et al. 2013, Rogers et al. 2015, Jaouen et al. 2016, Tartu et al. 2016). Tissue analyses are commonly used for diet estimation because they do not require direct, continuous observation, which is often difficult for elusive mobile species in remote environments (Budge et al. 2006, Newsome et al. 2010). Meanwhile, scat analysis can provide insight into the foods being consumed by an individual, but not the dietary proportions of food items or over timescales longer than hours to

days (Nielsen et al. 2018, Hein et al. 2020). Much of what we know about the feeding ecology of bears is based on analysis of tissues collected from live-captured individuals, harvested animals, or non-invasive approaches such as hair snags (Hobson et al. 2000, Thiemann 2008, McKinney et al. 2017b, Haroldson et al. 2020, Ro et al. 2020, Stern et al. 2021).

Hair is a useful tissue because it can be collected via multiple approaches, including some that are minimally invasive, and provides insight into bear diets (Rogers et al. 2015, 2020, Rode et al. 2016, Mowat et al. 2017, Boucher et al. 2019b, Johnson et al. 2019), stress levels (Macbeth et al. 2010, 2012, Cattet et al. 2014, Bechshoft et al. 2015, Weisser et al. 2016), exposure to contaminants (Born et al. 1991, Dietz et al. 2006, St. Louis et al. 2011, Bechshoft et al. 2015, 2016), and permits individual identification via genetics (Dreher et al. 2007, Proctor et al. 2010, Wirsing et al. 2020). Hair samples are metabolically inert and, therefore, provide information about bears during the period in which the hair is grown (Tucker et al. 2008). However, one of the primary limitations to using hair to infer information on bear ecology is a lack of data on the timing and rate of fur growth throughout and following the molting period. Although studies have estimated hair growth for some bear species, methods have varied and seasonal variation in the rate of growth and the degree to which hair growth continues year-round remains unclear (Felicetti et al. 2004, Mowat et al. 2017, Erlenbach 2020, Hein et al. 2021).

North American bear species have variable access to food seasonally (Stirling & McEwan 1975, Belant et al. 2006), leading to varying dietary insights over the hair growth period. These bears are thought to undergo an annual molt between May and October (Obbard 1987, Jacoby et al. 1999, Schwartz et al. 2003). Bears have two layers of hair, guard hair and underfur, which can be distinguished by physical characteristics (Obbard 1987). While hair growth rates have been estimated for grizzly bears (*Ursus arctos horribilis*) and polar bears (*Ursus maritimus*), these

studies have been limited to estimating a single rate for the entire growth period, using shaved patches that may have resulted in compensatory growth (Argyris 1968), not distinguishing between underfur and guard hair, or restricting the analysis to seasonal period (Felicetti et al. 2004, Mowat et al. 2017, Erlenbach 2020, Hein et al. 2021). There have been no hair growth rates estimated for black bears (*Ursus americanus*), and no studies have investigated seasonal variation in growth rate via methods that avoid shaving.

The process of hair growth and replacement includes molt and new growth, with shedding of old fur occurring before, during, or following new hair growth (Ling 1970, Fraser et al. 2013, Rolfes et al. 2021). Environmental factors (e.g., photoperiod, temperature, and snow cover) cue the increased production of hormones that stimulate new hair growth (Zimova et al. 2018, Déry et al. 2019, O'Brien et al. 2020). Other factors that affect intra- and inter-specific variation in hair growth and molt timing include age class, sex, reproductive status, body mass and condition, and access to food resources (Zimova et al. 2018, Déry et al. 2019). Despite the importance of hair growth for understanding life history, the drivers and phenology of the mammalian molt are not well understood within and among many species, including bears (Beltran et al. 2018, Zimova et al. 2020).

Bears in captive settings such as zoos provide the opportunity to document hair growth patterns and improve methods that use hair to better understand the ecology and health of wild bears. Here, we develop and compare two methods for measuring guard hair growth in captive polar bears, black bears, and grizzly bears, both based on applying a marker to the hair and then monitoring the movement of the marker along the hair shaft over time: 1) a visual marker of hair dye or bleach and 2) a molecular marker of isotopically labeled, ingestible glycine that is incorporated within the hair as it is metabolized by the bear. The choice to use hair dye or bleach

was implemented as a simple strategy that could be used to measure hair growth without requiring additional analyses. Hair bleach has previously been used in captive bears to identify shedding periods (Jimbo et al. 2020) and is used for marking bears to avoid resampling (Pagano et al. 2014). Isotopically labeled glycine has been used to measure vibrissae growth rates in both wild and captive settings (Hirons et al. 2001, Tyrrell et al. 2013, Aurioles-Gamboa et al. 2019). In this method, the labeled glycine acts as a static marker of time that is apparent in the tissue's carbon ($\delta^{13}C$) or nitrogen ($\delta^{15}N$) isotopic composition if the tissue is actively growing during the incorporation period. Thus, we also investigated incorporation times of C and N to identify the time lag between ingestion and routing into hair.

Our primary objective was to assess the efficacy of hair dye or bleach and labeled-glycine methods for estimating seasonal hair growth rates, as well as the logistical feasibility for such estimation in captive polar and temperate bear species. Bears are large predators, and access to individuals is limited, even within captive environments. The implementation of any method involving zoo bears necessitates extensive planning and comprehensive positive reinforcement training. Evaluating a method's logistical feasibility accounted for ease of implementation, cost, and the expertise required for analysis. The simultaneous employment of two independent methods applied to the same individuals allowed for direct comparison. Our secondary objective was to estimate hair growth rates for three species of bears (*U. americanus, U. arctos horribilis, and U. maritimus*). Through the development of methods to measure seasonal hair growth rates, we gain the ability to accurately measure aspects of bear ecology during times of the year in which environmental conditions may be limiting. This is an important tool to better understand the effects of climate warming and habitat change on polar, black, and grizzly bears, including the physiological and nutritional implications.

2.3 METHODS

We fed bears capsules with glycine enriched in ^{13}C or ^{15}N to "mark" the hair at a known time point and applied a small patch of hair dye/bleach to the rump or foreleg of the bear to identify the starting date for measuring hair growth. We then collected hair from the dye/bleach patch at regular intervals, measured the advancement of the dye/bleach mark, and measured the bulk $^{13}C/^{12}C$ and $^{15}N/^{14}N$. The rump and foreleg were chosen for their parallels with standard protocols of hair collection from free-ranging bears and because these were body regions that could be safely sampled by zookeepers on a regular basis using positive reinforcement without sedation. The sampling location for each bear was determined and limited by the trained behaviors and facility set-up. Plucking hair rather than cutting or shaving has been shown to minimize sample loss (Schwertl et al. 2003), and avoids potential effects on measuring hair growth that could result from compensatory growth due to shaving (Argyris 1968). Hair dye and bleach estimated hair growth between the time of application and the time that hair was collected, whereas the glycine isotopic marker estimated hair growth between the time the marker was fed and the time that hair was collected. The visual and chemical hair marking protocols were timed to allow the estimation of potentially variable hair growth rates throughout different stages of the molt.

The methods used in this study required participating facilities to have accessibility to bears trained to allow the application of hair dye or bleach and the subsequent hair sampling without sedation, as well as the availability of staff time for sampling. Sample sizes for hair collection included three male black bears at Oregon Zoo [Portland, OR, USA], one male polar bear at Point Defiance Zoo & Aquarium [Tacoma, WA, USA], and three male grizzly bears at Detroit Zoo [Royal Oak, MI, USA]. Hair samples were collected during 5-month sampling periods to

test if our methods were able to identify periods of growth and detect seasonal and individual variation in growth rates. The timing of sampling periods for each species varied due to logistical limitations; hair growth patterns were monitored from February to June (2019) for one polar bear, June to October (2019) for three black bears, and April to August (2020) for three grizzlies. Whole blood and serum were collected to gain an understanding of the incorporation time and availability of glycine to be incorporated into the hair. Whole blood and serum collections were possible with one male black bear at Oregon Zoo, one male polar bear at Point Defiance Zoo & Aquarium, and one female polar bear at San Diego Zoo [San Diego, CA, USA] trained for voluntary blood draws without sedation. However, the female polar bear at San Diego Zoo did not participate in hair collection and provided only serum for this study. Whole blood and serum samples were collected prior to the glycine dose to provide an isotopic baseline and for 2 – 3 months following the glycine dose to aid in determining how quickly labeled isotope levels decrease. The U.S. Fish and Wildlife Service authorized the sample collection, which adhered to protocols approved by the U.S. Geological Survey's Institutional Animal Care and Use Committee (USGS IACUC-2017-09).

2.3.1 *Hair dye or bleach application*

Hair dye or bleach was painted onto small patches of hair down to the skin in areas that would be subsequently sampled on the polar bears *(n* = 1), black bears (*n* = 3), and brown bears (*n* = 3). The small patch of hair dye on a polar bear or bleach on black or brown bears was intended to create a color contrast that would allow visual tracking of hair growth rate. Non-toxic human-grade IGORA Royal and Clairol brand hair dyes and bleach were applied to the bear's rump or foreleg through openings in a mesh door, fence, or crate within the habitat's training

area. Bleach or hair dye was re-applied after 1 – 5 months at the same location when the coloration began to fade or following a substantial shedding event.

Hair dye was prepared and mixed onsite just prior to application. Schwarzkopf Professional IGORA Royal Natural Shades (1-1, black violet, and 1-0, black neutral) was mixed with IGORA Royal Oil 20-volume Developer at a 1:1 ratio. Ardell Gray Magic Color Additive was added to the dye mix to help hair color penetrate deeper into the cortex. The bear voluntarily allowed the hair dye to be applied as close to the skin as possible using the flat applicator brush included with the dye, an auto parts cleaning brush with stiff bristles, or a syringe. If the mixture was too thick for the syringe, rubbing alcohol was added to help the dye flow more freely. After application, the dye set for 30-45 minutes and was subsequently rinsed with water.

Bleach was prepared using a 1:2 ratio of bleach powder to developer. Both IGORA Royal and Clairol brands of bleach were used with the 40-volume developer. The mixture of powder and developer was mixed with a whisk until no powder was visible; powder remaining in the mixture indicates that the bleach was not fully activated. The bleach was applied immediately after mixing for maximum effectiveness. Much like the hair dye, the bleach was applied using a flat applicator brush, an auto parts cleaning brush, a syringe, the zookeeper's hands through protected contact, or a comb. After application, it set for a minimum of 45 minutes and was reapplied throughout to retain the solution's moisture. Following the setting period, bear hair was rinsed with water multiple times and cleansed with baby shampoo.

2.3.2 *Isotopically labeled consumable capsule preparation and dosing*

Glycine is an amino acid found naturally in proteins and is often taken as a human nutrition supplement (Soh et al. 2023). Isotopically labeled glycine has been widely used in human and animal studies, including those measuring vibrissae growth (Heine et al. 1983, Boutton 1991,

Parhofer et al. 1991, Hirons et al. 2001, Pauli et al. 2010, de Godoy et al. 2018, Aurioles-Gamboa et al. 2019). We used glycine that was isotopically labeled either on the carbon atom in the carboxyl group (1-^{13}C; 99 atom percent) or the nitrogen atom in the amine group (^{15}N; 98 atom percent) from Cambridge Isotope Labs (Andover, Massachusetts). Atom percent is a proportional measure of the heavy isotope relative to the light isotope of that particular element at the label site (i.e., carboxyl group or amine group). Both isotopically labeled glycine powders were microbiological and pyrogen tested. Black bears (n = 3) and polar bears (n = 2) were provided isotopically labeled glycine powder enclosed in gelatin capsules (hereafter referred to as a "dose"), and the capsules were embedded in a food reward. Grizzly bears were not dosed with isotopically labeled glycine due to logistical constraints. The capsules were embedded in food the bears would be motivated to eat (meatballs for polar bears, fruit for black bears). Concentrations of isotopically labeled glycine (5 mg/kg) were similar to those used in previous studies to achieve an enriched δ^{13}C or δ^{15}N distinct from natural values in the vibrissae of elephant seals (*Mirounga leonine*), harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*) (Hirons et al. 2001, Aurioles-Gamboa et al. 2019).

Dosing with the labeled glycine capsule occurred before or during the hypothesized active hair growth period – late winter/early spring for polar bears and early summer for black bears (Kolenosky 1987, Obbard 1987, Jacoby et al. 1999). The male polar bear participating in hair collection was dosed with a ^{15}N-labeled glycine capsule and a ^{13}C-labeled glycine capsule approximately 2.5 months (77 days) apart. We staggered the dosing of the ^{13}C- and ^{15}N-labeled glycine to have two distinct, non-overlapping markers, ensuring they would be incorporated at different times throughout the hair growth period. The female polar bear participating in serum collection to measure incorporation time was dosed with a ^{15}N-labeled glycine capsule. The three

black bears were dosed once, simultaneously, with both ^{13}C- and ^{15}N-labeled glycine and were not re-dosed because zookeeper observations of the shaved patches on their paws indicated that their hair-growing season had concluded 2.5 months after the initial dose. The simultaneous dosing of ^{13}C- and ^{15}N-labeled glycine allowed us to evaluate the lag between consumption and incorporation in blood and, subsequently, in hair for ^{13}C and ^{15}N.

2.3.3 *Sample collection and lab analysis*

Hair was collected on an approximate weekly or bi-weekly schedule from the same, marked region on the bear's body using pliers, hemostats, or forceps to pluck a minimum of 10 whole guard hairs, including the intact bulb, with the bear's voluntary cooperation. Samples were inspected in the laboratory, and the distance from the hair root to the base of the dye/bleach was measured to the nearest millimeter (mm) for ≥8 hairs and then averaged. The measured hairs were then prepared for isotope analysis. Hairs were rinsed twice with 2:1 chloroform:methanol and once with distilled water, oven-dried at 50° C for 24 hours, subsectioned with a razor blade into 5 - 10 mm segments, and loaded into tin capsules. Approximately 200−600 μg of the 5 - 10 mm sectioned hairs were weighed and packed for analysis. In order to meet the minimum weight requirement, we sectioned at least 8 hairs.

Whole blood and serum for stable isotope analysis were collected from the bear's paw through protected contact, and with the bear's voluntary participation. At San Diego Zoo, a 2 mL sample of serum was collected 7 times from the female polar bear during the dosing period: 6 days prior to ingestion of the capsule, 2 days following ingestion of the capsule, and on days 8, 15, 23, 35, and 52. At Point Defiance Zoo & Aquarium, whole blood was collected from the male polar bear 7 times over two dosing periods – 3 days prior to ingestion of the ^{15}N-labeled

capsule and 5 and 8 days after, and on days 2,4, 7, and 8 after ingestion of the ^{13}C-labeled capsule. At Oregon Zoo, whole blood was collected 6 times during the dosing period: prior to ingestion of the capsule (day 0) and on days 8, 29, 50, 71, and 85. There was not enough whole blood at Point Defiance Zoo & Aquarium or Oregon Zoo to spin down to 2mL of serum. Blood samples were shipped frozen (i.e., on dry ice) for analysis and were freeze-dried upon arrival.

Stable isotopes of hair and blood were measured using continuous flow isotope ratio mass spectrometry at the U.S. Geological Survey Geology, Geophysics, and Geochemistry Stable Isotope Laboratory, Denver, CO, USA. The standard deviations for replicate analyses of reference materials (USGS 40, -4.52‰ and -26.39‰ for $\delta^{15}N$ and $\delta^{13}C$ respectively; USGS 41a, 36.55‰ and 47.55‰; internal nylon standard, -1.3‰ and -26.7‰) averaged less than 0.2‰ for $\delta^{15}N$ and $\delta^{13}C$, and the mean absolute difference from certified values was 0.01‰ for δ15 N and 0.004‰ for $\delta^{13}C$. Replicates of serum and whole blood samples differed by means of 0.05 ‰ for $\delta^{15}N$ and 0.1‰ for $\delta^{13}C$. Because of the pooled nature of the hair samples, it was not possible to replicate analyses on the same hairs. Thus, hair sample replicates were from the same sampling date but were comprised of different sub-samples, differing by means of 2.13‰ for $\delta^{15}N$ and 0.34‰ for $\delta^{13}C$.

2.3.4 *Estimation of hair growth rate and timing*

Hair growth rates were calculated by determining the slope of the relationship between new growth (in mm) and the time interval (days). Due to the varying intervals between collection dates, we report hair growth rates in the unit of the slope (mm day^{-1}). For dye/bleach methods, the length of the undyed or unbleached hair was plotted against the number of days after the dye or bleach application that the sample was collected, and a linear regression model was fit to the

data. For ^{15}N- and ^{13}C-labeled glycine, we identified the 5 or 10-mm segment of the hair that contained the peak $\delta^{15}N$ and $\delta^{13}C$ values. We required that the peak $\delta^{15}N$ and $\delta^{13}C$ values were above the mean plus three times the standard deviation of baseline values to avoid mislabeling of a peak due to natural variation. Baseline means and standard deviations were calculated from unlabeled hair segments (Table S2.1). The midpoint length of the segment containing the peak (in mm) was plotted against the sampling date, and a linear model was fitted if there were at least three measurements within a time period. We fit generalized linear models (GLMs) for individual bears and generalized linear mixed models (GLMMs) for multiple bears of the same species to estimate an overall rate with "individual" as a random effect. All models had a response variable of growth (in mm) and a single fixed effect of time (in days). For the models that required a random effect, we used the 'lme4' package to fit a GLMM (Bates et al. 2015). For individual bear models, we used the 'stats' package to fit a GLM (R Core Team 2017). Analysis of Covariance (ANCOVA) was used to compare slope values among methods using a significance level alpha of 0.05. All statistical tests and models were run using R v.4.0.3 (R Core Team 2017).

To investigate the timing of hair growth within the 5-month study period for each species, we evaluated whether the first and last samples collected from each individual showed active growth. Active growth for the first sample was defined as a non-zero value for the undyed or bleached portion of the hair or the presence of peak $\delta^{15}N$ or $\delta^{13}C$ values. For the last sample in a time period, hair was considered to be actively growing if the value for the undyed or bleached portion of the hair or the midpoint of a segment containing peak $\delta^{15}N$ or $\delta^{13}C$ values was greater than the previous sample.

2.3.5 *Incorporation time calculations*

We estimated the incorporation time of ^{15}N and ^{13}C in hair, serum, and whole blood. For inert tissues such as hair, incorporation represents the time required for ^{15}N- and ^{13}C-labeled glycine to mix among body pools of nitrogen and carbon after ingestion and incorporate into newly synthesized hair (Rode et al. 2016). Incorporation in serum and whole blood represents the circulation of the enriched nitrogen and carbon pools, where whole blood incorporation depends on the synthesis of red blood cells. We calculated the level of enrichment after incorporation by subtracting a baseline value from the peak $\delta^{15}N$ or $\delta^{13}C$ values. The baseline values for hair were the same as those used in identifying peaks for the hair growth rate calculations. The baseline $\delta^{15}N$ values for serum and whole blood were determined from samples collected 6 days prior to dosing (10.3‰) and on the day of dosing (8.9‰), respectively. For serum and whole blood, levels of enrichment in relation to the baseline are reported for the sample date following the peak measurement and final collection date of the sampling period to serve as a qualitative indicator of circulation time. Incorporation time was not compared across tissue types as the sampling intervals were different.

2.4 RESULTS

2.4.1 *Method feasibility and implementation*

Ease of implementation, cost, and expertise needed for analysis were considered when evaluating a method's logistical feasibility. Both methods required repeated hair pulls to obtain samples. Hair pull attempts were not always successful, specifically with the polar bear during the April breeding season. We pulled a total of 42 hair samples from the polar bear, 77 hair samples from the three black bears, and 110 hair samples from the three grizzly bears. These

samples included duplicate pulls from the same sampling day and pulls below the minimum required number of guard hairs with intact roots. We measured or analyzed 15 hair samples from the polar bear, 32 hair samples from the three black bears, and 29 hair samples from the three grizzly bears. Implementing the dye/bleach method was more difficult than feeding a labeled-glycine dose because the application required continuous cooperation from the bear. The labeled-glycine method requires a larger financial investment, both for the glycine and the analysis cost, compared to the hair dye/bleach method. The sample preparation and analysis for the labeled glycine requires expertise and specialized equipment, whereas the hair dye/bleach method does not. The methods share a common source of error in that a length variable needed to be estimated, either through averaged measurements with the dye/bleach method or by using midpoints of fixed segment lengths with the labeled glycine method. Both methods were feasible within the parameters of this study and allowed the estimation of hair growth rates and timing.

The hair dye/bleach application and labeled-glycine feeding were done at the beginning of the 5-month study period for each species (Table 2.1). Hair dye/bleach was re-applied if there was a major shedding event or the dye/bleach faded (Table 2.1). Tuff and Takoda, both black bears, shed their bleached hairs at different points in the study, while Blizzard, a polar bear, had a faded dye spot near the end of the study. The three grizzly bears had bleach applied to their other foreleg to have a second, more visible mark. Blizzard required a second dose of labeled glycine to ensure growing hairs were marked (Table 2.1). Hair growth was measured for the polar bear during two time periods: February - March and April – June (Figure 2.1, Table 2.2). Hair growth was measured during the June – July period and August - October period for black bears (Table 2.3). For the three grizzly bears, the left foreleg bleach application allowed the estimation of a hair growth rate for all bears between April and May, whereas the right foreleg

application allowed for a rate estimate for May (n = 2 bears, 4-5 samples per bear) and June – August (n = 2 bears, 3 samples per bear) (Table 2.4).

2.4.2 *Incorporation times and enrichment of ^{13}C and ^{15}N*

The enriched glycine label circulated in the blood and was subsequently incorporated into the hair at detectable magnitudes soon after dosing (Figure 2.2). In the serum of a female polar bear (305 kg), ^{15}N enrichment peaked within 2 days after dosing, by 24.9‰ over baseline, at the first sampling event post-dosing. This enrichment fell to 11‰ on day 15 and 2.8‰ on day 52 post-dosing. The whole blood of a male polar bear (446 kg) was enriched in ^{15}N by 3.1‰ on day 5 and by 5‰ on day 8 post-dosing; no increase in $\delta^{13}C$ was observed within the first 8 days. In whole blood of one male black bear (197 kg – Takoda), $\delta^{13}C$ did not enrich within 85 days, and $\delta^{15}N$ enriched by 4.2‰ after 8 days, by 3.8‰ on day 29, and 2.7‰ on day 85 post-dosing. The incorporation time in hair for a male polar bear (446 kg) was shorter for ^{15}N than for ^{13}C (7 vs. 13 days), although the values peaked in a similar time frame (14 vs. 13 days). Hair was enriched by 24.9‰ in $\delta^{15}N$ and by 0.8‰ in $\delta^{13}C$ at the peak value. Both ^{15}N and ^{13}C were incorporated into the hair of the three male black bears by the first sampling event post-dosing at 4 (193 kg – Tuff), 7 (197 kg – Takoda), and 8 (218 kg – Cubby) days. The three black bears, in order of increasing weight and sampling date, were enriched by 54.7‰, 44.2‰, and 19.3‰ in $\delta^{15}N$, and by 4.9‰, 3.9‰, and 1.1‰ in $\delta^{13}C$ at peak values.

The $\delta^{15}N$ peak values in hair growth calculations averaged 35.6 ± 3.3‰ in February – March for polar bears (baseline value of 12.9 ‰), and 53.8 ± 8.3‰ in June – July and 34.7 ± 4.6‰ in August – October for black bears (baseline average of 9.6 ± 0.3‰). The $\delta^{13}C$ peak values averaged -14.9 ± 0.4‰ in April - June for polar bears (baseline average of -16.0 ± 0.2‰), and -

14.3 ± 0.8‰ in June – July and -16.2 ± 0.4‰ in August – October for black bears (baseline average of -18.4 ± 0.1‰). The $\delta^{15}N$ peak and $\delta^{13}C$ peak values were most enriched for the black bear with the lowest body weight, and most depleted for the bear with the highest body weight.

2.4.3 *Precision of hair growth timing and rate estimation*

Hair growth timing was detectable and consistent between the labeled glycine and dye/bleach methods. According to both methods, hair was actively growing at the time of the first collection dates for the polar bear and black bears (Table 2.1). Both methods showed that the polar bear and one black bear had active growth through the last collection date, whereas two black bears had no growth after September (Table 2.1). The bleach method showed variability in growth time frames between April and August. Of the two bears sampled through August, one bear had growth ending in July and the other through August (Table 2.1).

Polar bear hair growth rates were significantly different from zero for both methods and all time periods ($p < 0.05$; Table 2), except the dye-based rate for April – May ($p = 0.06$; Table 2.2). In black bears, hair growth rates measured in June and July were significantly different from zero ($p < 0.01$; Table 2.3), whereas rates measured in August - October were not significantly different from zero ($p > 0.05$; Table 2.3). For grizzly bears, the bleach hair growth rates significantly differed from zero for one individual in May – April and all individuals in May ($p < 0.05$; Table 2.4). Both the hair dye/bleach and labeled-glycine methods produced similar rate estimates, with no significant differences between ^{15}N-labeled glycine, ^{13}C-labeled glycine, and hair dye/bleach methodologies within the April – June period for the polar bear and the June – July and August – October periods for black bears. There was one significant difference between

dye and ^{15}N-labeled glycine in February – March for polar bears, where the growth rate estimated from hair dye was lower than the rate estimated by ^{15}N-labeled glycine ($p < 0.05$).

The hair dye/bleach and labeled-glycine methods detected individual and seasonal variation in hair growth rates. For species with multiple individuals, we estimated an average rate and quantified the contribution to the variance of individual bear as a random effect using GLMMs. The GLMMs estimated average hair growth rates for black bears (Table 2.3) and grizzly bears (Table 2.4). The average black bear hair growth rates estimated in June - July were significantly higher than those measured in August – October ($p < 0.05$). The variance of the random effect of individual bear was smaller than the residual variation of the GLMM for both species (black bears: $s^2_{Individual} = 34.40$; $s^2_{residual} = 81.26$; grizzly bears: $s^2_{Individual} = 70.9$; $s^2_{residual} = 193.9$).

2.5 DISCUSSION

Both hair dye/bleach and labeled-glycine methods were useful in tracking individual and seasonal variation in hair growth timing and rate for three different species of Ursidae. Although the hair dye/bleach method was more difficult to implement, it had lower costs and required less analysis expertise than the labeled-glycine method. The labeled-glycine method also required validating circulation and incorporation time. Enrichment in ^{15}N in polar bear serum peaked within 2 days post-dosing, confirming that the labeled nitrogen was rapidly available for incorporation into the hair. The label reached similar peak enrichment in hair and serum, 24.9‰ above baseline. Both ^{15}N and ^{13}C reached peak enrichment in the hair within 2 weeks of dosing, which ensured a minimal lag in detecting hair growth. The magnitude of ^{15}N enrichment was much larger than ^{13}C which may be due to differences in the relative quantities of the element in

the animal's body composition (Hirons et al. 2001) or the flexible routing of dietary carbon to other metabolic pathways, such as lipid synthesis (Newsome et al. 2014, Stricker et al. 2022).

The daily hair growth rates estimated by hair dye or bleach and isotopically labeled glycine methods were comparable for polar and black bears, with only one significant difference when compared within a season. This suggests that the effectiveness does not depend on the bear species. The model fit (estimated by R^2_{adj}) was similar across methods, with a few exceptions. Hair growth measurements taken in June followed a fresh application of dye at the beginning of the month, which may have reduced variability and error in measurements. The labeled-glycine method also required a second dose for polar bears to ensure a marker was available for incorporation throughout the hair growth period; otherwise, growth rates would only be monitored for a single season. Some growth rates from both methods were estimated to be negative, which suggests a growth rate of zero with error. Further research could inform the effectiveness of a method during slow and rapid hair growth periods.

All bears in this study had a hair growth period that lasted for a minimum of two months. We observed hair growth in the polar bear as early as February, in contradiction to the most commonly hypothesized hair growth window between May and August (Kolenosky 1987). We had the advantage of a larger sample size for black and grizzly bears, and were able to document individual variation in hair growth timing. Erlenbach (2020) also observed variability in hair growth timing among captive male grizzly bears. Individual variability in timing influences conclusions in free-ranging bears; Macbeth et al. (2010) attribute the observed variability of wild grizzly bear hair cortisol concentration to differences in the hair growth timing and pattern of individuals.

Our findings suggest that the average guard hair growth rates ranged between 0.34 – 0.84 mm day^{-1} for the polar bear, 0.10 – 0.67 mm day^{-1} for black bears, and 0.53 - 1.05 mm day^{-1} for grizzly bears. Polar bear hair growth rates in the present study were similar to those estimated by Hein et al. (2021). Hein et al. (2021) estimated hair growth rates of 0.76 mm day^{-1} in June/early July, compared to our dye-based estimate of 0.84 ± 0.06 mm day^{-1} in June. It is important to note that Hein et al. (2021) sampled from the neck region and did not distinguish between underfur and guard hair, whereas our study sampled from the rump and included exclusively guard hairs. The peak grizzly bear hair growth rate in May (1.05 mm day^{-1}) was similar to those estimated by previous studies (Felicetti et al. 2004, Mowat et al. 2017, Erlenbach 2020). In captive grizzly bears in May - October, hair growth rates were previously calculated using shaved patches on the back (Felicetti et al. 2004) or shoulder (Erlenbach 2020). According to Mowat et al. (2017), the guard hair growth rates of wild grizzly bears range between 2 - 3 cm/month, or 0.67 – 1 mm day^{-1} (assuming a 30-day month). These hairs were collected from a barbed wire trap, so the body region collection is unknown. Previous studies of bears have shown that hair samples from different regions of the body produce variable results for steroid hormone levels (Macbeth et al. 2010, Hein et al. 2021). Future studies should investigate variation in hair growth across body regions within a species.

Studies measuring hair growth rates should consider factors that are thought to influence molt, such as sex, age, reproductive class, latitude, and food availability (Schwartz et al. 2003, Macbeth et al. 2010). The variability in these characteristics was limited due to the nature of our methods-development study. All hair growth estimates in this study were based on samples from adult males, and the sampling zoos' latitudes overlap with the natural and historical range for black and grizzly bears, but not for polar bears. We were unable to replicate the seasonal food

availability of wild bears, and food deprivation or hibernation could affect hair growth during the winter months. However, the sampling months in this study are concentrated in spring through fall. Captivity provides continued access to sample an individual over time, allowing for a sampling frequency that is unfeasible with wild bears. Until a hair growth study with wild bears is logistically and financially feasible, developing methods to measure hair growth rates in captive bears is an important first step.

The hair dye or bleach and isotopically labeled glycine methods were comparable for polar and black bears. Although there was no alternative method for comparison, the bleach method effectively documented hair growth in grizzly bears. The length of the hair growth period varied among individuals and bear species, which affected the estimated hair growth rate. Our findings establish two effective methods to measure seasonal hair growth rates, and we estimated hair growth rates for three North American bear species. This study provides the first quantitative data describing hair growth in black bears and demonstrates a strong seasonality in the growth. Further investigation on the timing and rate of hair growth over an annual cycle will be important for incorporating seasonality in the interpretation of ecological data from wild-collected hair samples.

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2.8 FIGURES

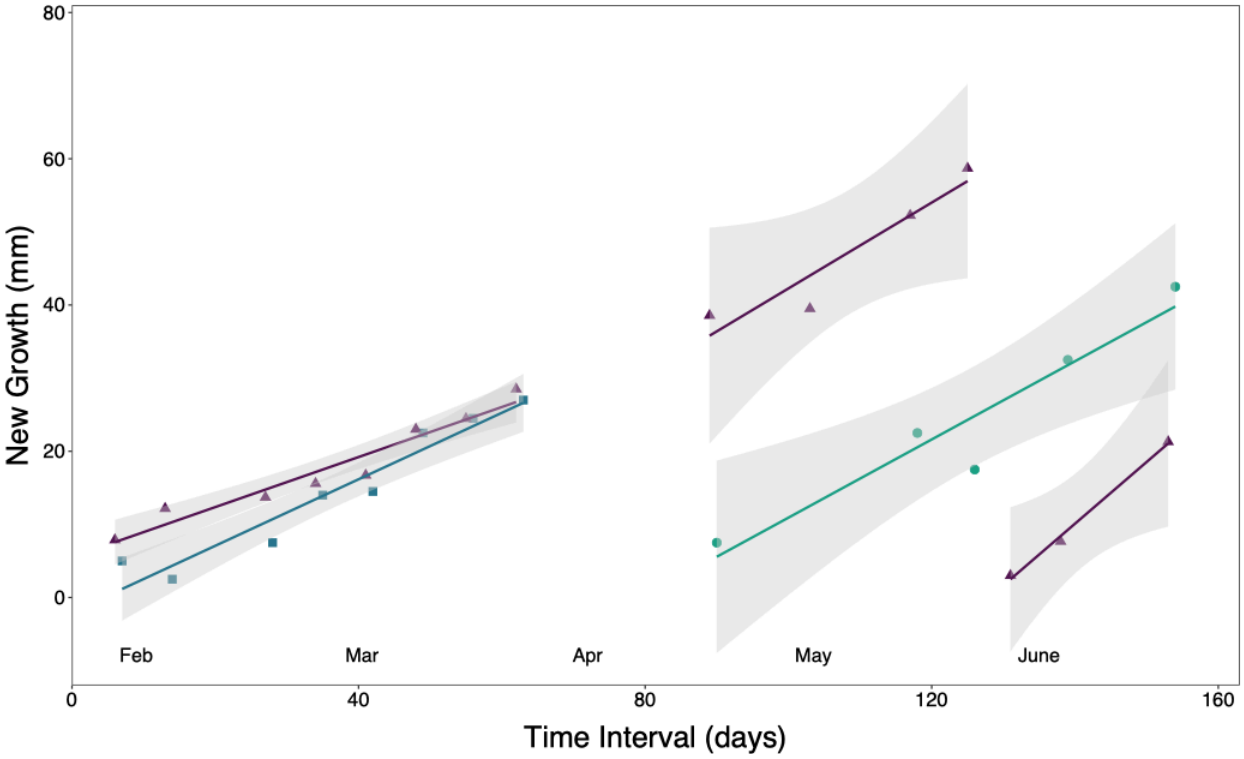

Figure 2.1 Linear regression models of new growth (in millimeters) versus the day of the study for a male polar bear at the Point Defiance Zoo & Aquarium for all hair-marking methods (dye, ^{15}N-labeled glycine, and ^{13}C-labeled glycine). Markings were applied on Day 0 (^{15}N-labled glycine), Days 1 and 132 (dye), and Day 77 (^{13}C-labeled glycine). Dye is represented by purple triangles, ^{15}N-labeled glycine is represented by blue squares, and ^{13}C-labeled glycine is represented by green circles.

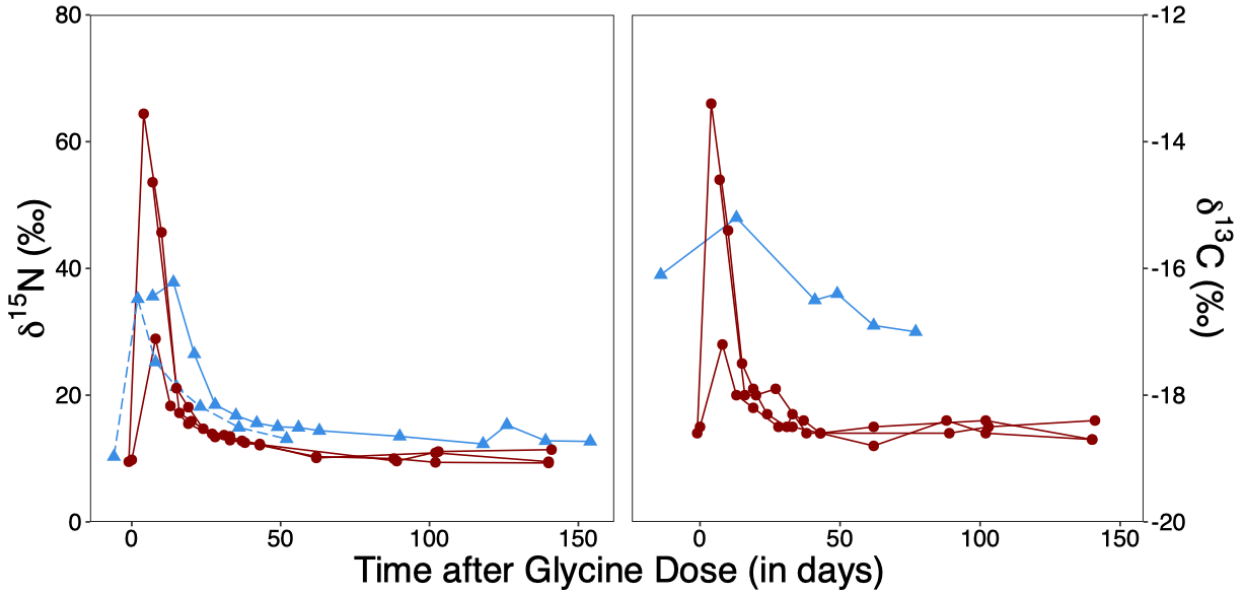

Figure 2.2 Incorporation of enriched glycine label in polar and black bear hair and polar bear serum over time. The panels show changes in $\delta^{15}N$ (left) and $\delta^{13}C$ (right) values, plotted against the sampling date (days after dosing). Blue triangles represent polar bear samples, with hair shown by solid lines and serum by a dashed line. Red circles represent black bear hair samples, indicated by solid lines.

2.9 TABLES

Table 2.1 Schedule of hair dye/bleach applications, isotopically labeled glycine doses, and hair collection for three bear species. Hair dye application is represented by "D", bleach application is represented by "B", ^{13}C-labeled glycine dose is represented by "C", and ^{15}N-labeled glycine dose is represented by "N". The 5-month study period for each species is shaded in blue, with individual hair growth windows shaded in grey. Months without usable samples are indicated by "*ns*", signifying the absence of samples rather than a shortened hair growth period.

	2019											
	J	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
Polar bear												
Blizzard	**N D**			**C**		**D**						
Black bears												
Cubby						**N C B**						
Takoda						**N C B**			**B**			
Tuff						**N C B**	**B**					
	2020											
	J	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
Grizzly bears												
Boo			**B**		**B**			*ns*				
Mike			**B**		**B**							
Thor			**B**		**B**							

Table 2.2 Hair growth rates ± standard error (mm day^{-1}) of a male polar bear at Point Defiance Zoo & Aquarium for all marking methods (hair dye, ^{15}N-labeled glycine, and ^{13}C-labeled glycine) in a) February - March and b) April – June. Hair samples were collected from the rump. In parentheses, the adjusted R^2 and the number of sampling events (n) are reported. If a rate is significantly different from zero, the number of asterisks indicates the level of significance; there is one asterisk if $p < 0.05$, two asterisks if $p < 0.01$, and three asterisks if $p < 0.001$.

a) **February - March**

Hair dye	*^{15}N-labeled glycine*
0.34 ± 0.04 *** (R^2_{adj} = 0.93, n = 8)	0.45 ± 0.05 *** (R^2_{adj} = 0.92, n = 8)

b) **April - June**

Hair dye	*^{13}C-labeled glycine*
April – May: 0.59 ± 0.14 (R^2_{adj} = 0.84, n = 4) *June:* 0.84 ± 0.06 * (R^2_{adj} = 0.99, n = 3)	*April – June:* 0.53 ± 0.10 * (R^2_{adj} = 0.87, n = 5)

Table 2.3 Hair growth rates ± standard error (mm day^{-1}) of three male black bears at Oregon Zoo for all marking methods (bleach, ^{15}N-labeled glycine, and ^{13}C-labeled glycine) in a) June – July and b) August – October. Hair samples were collected from the rump of the three bears. In parentheses, the adjusted R^2 and the number of sampling events (n) are reported. If a rate is significantly different from zero, the number of asterisks indicates the level of significance; there is one asterisk if $p < 0.05$, two asterisks if $p < 0.01$, and three asterisks if $p < 0.001$. The average hair growth ± the standard error (mm day^{-1}) estimated by the generalized linear mixed model is reported in the final row.

a) **June - July**

	Bleach	*^{15}N-labeled glycine*	*^{13}C-labeled glycine*
Cubby	0.60 ± 0.13 ** (R^2_{adj} = 0.76, n = 7)	0.55 ± 0.06 ** (R^2_{adj} = 0.94, n = 6)	0.55 ± 0.06 ** (R^2_{adj} = 0.94, n = 6)
Takoda	0.64 ± 0.05 *** (R^2_{adj} = 0.97, n = 6)	0.67 ± 0.06 ** (R^2_{adj} = 0.97, n = 5)	0.67 ± 0.06 ** (R^2_{adj} = 0.97, n = 5)
Tuff	0.80 ± 0.08 *** (R^2_{adj} = 0.92, n = 9)	0.61 ± 0.07 *** (R^2_{adj} = 0.91, n = 9)	0.56 ± 0.06 *** (R^2_{adj} = 0.92, n = 9)
Average	0.67 ± 0.21	0.58 ± 0.22	0.56 ± 0.22

b) **August - October**

	Bleach	*^{15}N-labeled glycine*	*^{13}C-labeled glycine*
Cubby	0.15 ± 0.11 (R^2_{adj} = 0.23, n = 4)	0.22 ± 0.16 (R^2_{adj} = 0.25, n = 4)	0.22 ± 0.16 (R^2_{adj} = 0.25, n = 4)
Takoda	-0.01 ± 0.05 (R^2_{adj} = -0.87, n = 3)	-0.30 ± 0.30 (R^2_{adj} = 0.003, n = 3)	-0.30 ± 0.30 (R^2_{adj} = 0.003, n = 3)
Tuff	0.49 ± 0.22 (R^2_{adj} = 0.66, n = 3)	0.16 ± 0.13 (R^2_{adj} = 0.18, n = 3)	0.16 ± 0.09 (R^2_{adj} = 0.38, n = 3)
Average	0.14 ± 0.10	0.10 ± 0.17	0.10 ± 0.17

Table 2.4 Hair growth rates ± the standard error (mm day^{-1}) of three male grizzly bears at Detroit Zoo using the bleach method. Bleach growth rates from April – May samples were calculated from samples plucked from the left foreleg, whereas growth rates from May and June - August were sampled from the right foreleg. In parentheses, the adjusted R^2 and the number of sampling events (n) are reported. If a rate is significantly different from zero, the number of asterisks indicates the level of significance; there is one asterisk if $p < 0.05$, two asterisks if $p < 0.01$, and three asterisks if $p < 0.001$. The average hair growth ± the standard error (mm day^{-1}) estimated by the generalized linear mixed model is reported in the final row.

	April - May	**May**	**June - August**
Boo	1.08 ± 0.14 * (R^2_{adj} = 0.95, n = 4)	N/A	N/A
Mike	0.08 ± 0.15 (R^2_{adj} = -0.54 , n = 3)	1.08 ± 0.14 * (R^2_{adj} = 0.95, n = 4)	0.79 ± 0.39 (R^2_{adj} = 0.62, n = 3)
Thor	0.78 ± 0.27 (R^2_{adj} = 0.71, n = 4)	1.02 ± 0.21 * (R^2_{adj} = 0.84, n = 5)	0.27 ± 0.70 (R^2_{adj} = -0.74, n = 3)
Average	0.68 ± 0.23	1.05 ± 0.64	0.53 ± 0.39

2.10 SUPPLEMENTAL MATERIALS

Table S2.1 Baseline $\delta^{15}N$ and $\delta^{13}C$ values with standard deviations for unlabeled segments of hairs. The number of segments is denoted in parentheses. Samples from Tuff and Cubby were taken from hair samples with no enrichment in any segment. For Takoda, the 5 segments furthest from the labeled root sample were used as a baseline. For Blizzard's $\delta^{15}N$, the segment furthest from the labeled root was used, whereas all segments for the $\delta^{13}C$ were before dosing.

	Polar bear	***Black Bears***		
	Blizzard	*Cubby*	*Takoda*	*Tuff*
$\delta^{15}N$	12.9 ± NA (n = 1)	9.6 ± 0.2 (n = 5)	9.4 ± 0.4 (n = 5)	9.7 ± 0.3 (n = 5)
$\delta^{13}C$	-16.0 ± 0.2 (n = 26)	-18.3 ± 0.2 (n =5)	-18.5 ± 0.1 (n =5)	-18.3 ± 0.2 (n =5)

Chapter 3. QUANTIFYING THE TIMING AND RATE OF HAIR GROWTH IN POLAR BEARS

3.1 ABSTRACT

Polar bears are experiencing rapid loss of Arctic sea ice habitat and associated declines in body condition, survival, and abundance. Polar bear research often occurs during a short field season in the spring or fall, during which a suite of samples (*e.g.*, blood, fat, hair) is collected from immobilized bears that are physically captured. Hair is a useful tissue because it reflects polar bear diet, stress levels, and contaminant exposure, and can be collected without immobliziation using hair snares. Unlike other tissues that indicate health and ecology just prior to collection, hair reflects ecological conditions during the period of growth. To date, inference from hair is limited by a lack of information on polar bear hair growth timing and rates throughout the molt. Here, we estimated seasonal growth rates from guard hairs collected over a 6- to 18-month period from eight captive polar bears (4 males, 4 females) in four zoos using previously validated methods of hair dye and ^{13}C- and ^{15}N-labeled glycine. Hair growth was detected in all seasons, with comparable hair growth rates across spring, summer, and fall, while growth rates slowed during winter. This result was consistent with expected growth patterns in wild bears associated with an annual molt. This work enhances our ability to study polar bear health and ecology throughout the year using hair samples collected in the wild.

3.2 INTRODUCTION

Polar bears (*Ursus maritimus*) are experiencing rapid loss of their sea ice habitat throughout much of their range (Derocher et al. 2004, Regehr et al. 2016). Loss of sea ice has been associated

with declines in bear body condition, survival, and population size (Stirling et al. 1999, Regehr et al. 2007, Rode et al. 2010, Bromaghin et al. 2015b, Lunn et al. 2016). Improvements in short- and long-term projections of the effects of sea ice loss on polar bears are critical for making management decisions, which require a better understanding of mechanistic relationships between environmental threats and polar bear health. To date, much of what is known about polar bears has been derived from capture-based sampling and deployment of satellite collars. However, increasing variability in Arctic sea ice and the remote areas in which polar bears inhabit have further constrained the sampling of bears via capture-based approaches. As a result, minimally invasive sampling approaches, such as hair snares and biopsy darting, have become increasingly important for studying and monitoring polar bear ecology and health. There is a need to improve the utility of samples that can be collected via minimally invasive and capture-based research, such as hair.

Hair is a useful tissue because it can be used to estimate prey and nutrient contributions to polar bear diets (Rogers et al. 2015, Rode et al. 2022, Stricker et al. 2022), stress levels (Macbeth et al. 2012, Bechshoft et al. 2015, Weisser et al. 2016), and contaminant exposure (Born et al. 1991, Dietz et al. 2006, St. Louis et al. 2011, Bechshoft et al. 2015, 2016) and can be collected via multiple approaches, including some that are minimally invasive. Much of what we know about the feeding ecology of bears is based on analysis of hair, which can be collected from live-captured individuals, harvested animals, or hair snags in areas where polar bears come onshore. One of the primary limitations to using hair is a lack of data on the timing and rate of hair growth throughout the year and following the annual molt. Uncertainty in the timeframe represented by hair has limited our understanding of polar bear health and ecology. The ability to study polar bear ecology

throughout the year, particularly during seasons in which conditions restrict fieldwork, is important to better understand the implications of habitat change.

Polar bear hair is thought to grow determinately during the gradual molting period, presumed to occur between April and August (Kolenosky 1987, Born et al. 1991, St. Louis et al. 2011, Stern et al. 2021). This molting period is thought to conclude before winter when, unlike other bear species, only pregnant polar bears den (Ramsay & Stirling 1988). All other sex and age classes remain active and continue to either hunt prey on available sea ice or reduce their activity. The use of biochemical and visual markers (*i.e.*, isotopically labeled glycine and hair dye) with bears enables the monitoring of hair growth (Stern et al. 2024b) while avoiding any compensatory increase in growth that might occur as a result of shaving. These methods were shown to be effective in tracking individual and seasonal variation in hair growth timing and rate for three species of bears, including polar bears (Stern et al. 2024b). Accompanying the need to understand polar bear hair growth patterns throughout the year, the spatial orientation and progression of hair growth and molting across the body can be variable (Ling 1970) and are not well-documented for bears. To date, hair growth of a single adult male polar bear has been estimated by shaving, but only for the months of June-August (Hein et al. 2021). Hein et al. (2021) collected from the neck region and did not distinguish between underfur and guard hair, whereas Stern *et al.*, (2024b) collected from the rump and exclusively sampled guard hairs. To improve the interpretation of polar bear ecology and health from studies that use hair, information is needed on variability in the rate and timing of polar bear guard hair growth throughout the year and across different body regions.

An inability to sample individual wild polar bears over time precludes estimating hair growth throughout the year. Polar bears in zoos, alternatively, provide the opportunity to track hair growth

patterns over multiple seasons across multiple individuals. In this study, we build on the work of Stern *et al.*, (2024b) to use hair dye and ^{13}C- and ^{15}N-labeled glycine to estimate hair growth rates throughout the year in zoo polar bears. Our primary objective was to compare the timing and rate of polar bear hair growth across all seasons. We also sought to identify differences in seasonal hair growth rates between body regions. This work creates a foundation for incorporating seasonality in the wild-collected hair samples to allow a fine-scale analysis component across many disciplines in polar bear research, management, and conservation.

3.3 METHODS

We monitored hair growth of eight individual polar bears over three years at four facilities in North America (Table S1). This included foreleg hair samples from two adult males (Baffin, York) and shoulder hair samples from one adult female (Star) over 14 months at Assiniboine Park Zoo [Winnipeg, MB, CAN], foreleg hair samples from one adult male (Nuka) and two adult females (Anana, Suka) over 6 months at Detroit Zoo [Royal Oak, MI, USA], rump hair samples from one adult male (Blizzard) over 18 months at Point Defiance Zoo & Aquarium [Tacoma, WA, USA], and rump hair samples from one adult female (Tatqiq) over 13 months at San Diego Zoo [San Diego, CA, USA]. The duration for sample collection was a minimum of 12 months at all facilities apart from the Detroit Zoo (6 months only). The rump and foreleg were chosen as sampling sites for their parallels with standard protocols of hair collection from free-ranging polar bears and because the body regions could be safely sampled by zookeepers on a regular basis using positive reinforcement training without sedation. The shoulder was sampled for the female at Assiniboine Park Zoo because it was the only trained sampling location at the time. Three bears were born in captivity (Anana, Nuka, and Suka) and five were born in the wild; four

were rescued near Churchill, Manitoba (Blizzard, Baffin, Star, and York) and one was rescued in Utqiagvik, Alaska (Tatqiq).

Detailed methods for monitoring hair growth followed those identified in Stern *et al.*, (2024b). In brief, we fed captive polar bears (n = 8) capsules with glycine enriched in ^{13}C or ^{15}N and applied a small patch of hair dye to the rump, shoulder, or foreleg of the bear to identify the starting date for measuring hair growth. We then collected hair from the dye patch at regular intervals, measured the advancement of the dye mark, and measured the $\delta^{13}C$ and $\delta^{15}N$ isotopic compositions along the shaft of the guard hairs. We measured the total length of the hair because the application of growth rates requires an understanding of how hair lengths differ between body regions and across seasons. Visual and chemical hair marking was timed to allow the estimation of hair growth rates at different stages of the molt and across multiple seasons. Non-toxic human-grade IGORA Royal (Schwartzkopf Professional, Dusseldorf, Germany) and Clairol (Wella Company, Geneva, Switzerland) brand black or brown hair dye was applied onto small patches of hair down to the skin in areas that would be subsequently sampled. Dye was applied using positive reinforcement training on non-sedated bears through openings in a mesh door, fence, or crate within the habitat's training area. Hair dye was re-applied after 1 – 5 months at the same location when the coloration began to fade or following a substantial shedding event (Table S1).

We used glycine that was isotopically labeled either on the carbon atom in the carboxyl group (1-^{13}C; 99 atom percent) or the nitrogen atom in the amine group (^{15}N; 98 atom percent) from Cambridge Isotope Labs (Andover, Massachusetts) for facilities in the United States or Sigma-Aldrich (Saint Louis, Missouri) for the facility in Canada. Polar bears were provided isotopically labeled glycine powder enclosed in gelatin capsules (hereafter referred to as a

"dose"), and the capsules were embedded in a food reward. Isotopically labeled glycine was fed at concentrations (5 mg/kg) that achieved enrichment (^{13}C and ^{15}N) distinct from natural values in the vibrissae of pinnipeds (Hirons et al. 2001, Aurioles-Gamboa et al. 2019) and validated with bears in Stern *et al.*, (2024b). We staggered the dosing of the ^{13}C- and ^{15}N-labeled glycine to have two non-overlapping markers that would incorporate throughout the hair growth period (Table S1). Additional information on the methodology is detailed in Stern *et al.*, (2024b).

Hair was collected weekly or bi-weekly from the same region on the bear's body using pliers, hemostats, or forceps to pluck a minimum of 10 whole guard hairs that included the intact root. For each sample, the total length and the distance from the hair root to the base of the dye were measured for at least 8 hairs to match the number of hairs required for isotopic analysis, and then averaged. The measured hairs were then prepared for isotope analysis. Hairs were rinsed twice with 2:1 chloroform:methanol and once with distilled water, oven-dried at 50° C for 24 hours, subsectioned with a razor blade into 5-10 mm sections, and loaded into tin capsules. Approximately 200−600 μg of the 5-10 mm sectioned hairs were weighed and packed for analysis. To meet the minimum weight requirement for the mass spectrometer, we sectioned at least 8 hairs.

Stable isotopes of hair were measured using continuous flow isotope ratio mass spectrometry at the U.S. Geological Survey (USGS) Geology, Geophysics, and Geochemistry Stable Isotope Laboratory, Denver, CO, USA and the University of Windsor's Trophic Ecology Laboratory, Windsor, ON, CAN. For all standards run at the USGS lab (USGS 40, USGS 41a, and an internal nylon standard), the standard deviation of replicate analyses measured ≤ 0.2‰ for $\delta^{15}N$ and $\delta^{13}C$, and the mean absolute difference from certified values was 0.1‰ for δ15 N and $\delta^{13}C$. For all standards run at the Trophic Ecology lab (USGS 40, NIST1577c, Urea IVA33802174,

and an internal tilapia muscle standard), the standard deviation of replicate analyses measured ≤ 0.4‰ for $\delta^{15}N$ and 0.2‰ for $\delta^{13}C$, and the mean absolute difference from certified values was -0.1‰ for $\delta^{15}N$ and 0.3‰ for $\delta^{13}C$. To ensure comparability between labs, we submitted samples of salmon tissue, a reference material from the University of Washington IsoLab (Seattle, WA, USA). The reference material averages from both labs differed by 0.14 ‰ for $\delta^{15}N$ and 0.04 ‰ for $\delta^{13}C$. Because of the pooled nature of the hair samples, it was not possible to replicate analyses on the same hairs. Thus, hair sample replicates were from the same sampling date but were comprised of different sub-samples, differing by means of 1.95 ‰ for $\delta^{15}N$ and 0.26 ‰ for $\delta^{13}C$.

We evaluated whether the first and last samples collected from each individual within each season showed active growth. We defined seasons as spring (March – May), summer (June – August), fall (September – November), and winter (December – February). Active growth for the first sample in a season was defined as a non-zero value for the new hair growth after the dye application or the presence of a peak in $\delta^{15}N$ or $\delta^{13}C$ values. For the final sample in a season, hair was considered to be actively growing if the dye or isotopic mark had progressed further along the hair shaft compared to the previous sample. If there was only one sample in a season, the sample was either considered to be the first sample if collected within the first month of the season or the last sample if it was pulled in the last month of the season.

Hair growth rates were calculated by determining the slope of the relationship between new growth (in millimeters) and the time interval (days). For dye methods, the length of the new hair growth after the dye application was plotted against the number of days after the dye application that the sample was collected, and a linear regression model was fit using the 'stats' package (R Core Team 2017). For ^{15}N- and ^{13}C-labeled glycine, we identified the 5 or 10-mm segment of the

hair that contained the peak $\delta^{15}N$ and $\delta^{13}C$ values. We identified the peak $\delta^{15}N$ and $\delta^{13}C$ values as those that were both the highest value in the segment series and above the mean of the baseline values plus three times their standard deviation to avoid mislabeling of a peak due to natural variation. Baseline means and standard deviations were calculated from hair collected before dosing, samples with no discernable apex or fluctuation in enrichment across all segments, or segments furthest from the segment containing a clearly identifiable enriched peak (Table S2). We plotted the midpoint length of the segment containing the peak (in mm) against the sampling date and fit a linear model if there were at least two measurements within a season (R Core Team 2017). We could not calculate a seasonal rate for the dye and labeled-glycine methods under the following conditions: if only one sample was collected within the season, the bear was not yet dosed, behavioral constraints limited sampling, the labeled glycine was not detected, or the label was not identifiable to a dosing event (Table S3).

We used a two-factor ANOVA followed by Tukey's Honestly Significant Difference (HSD) test to detect effects of the methods used (^{15}N-labeled glycine, ^{13}C-labeled glycine, or dye) within a season. If no significant differences between methods within each season were detected, we averaged across all methods for each bear in each season to avoid pseudoreplication. In the cases where there were multiple rates for the same bear and method, either because of multiple years of sampling or multiple doses within the same period, we included these rates in the average. Outliers were identified within each season and body region (if $n > 1$) as values greater than or equal to 1.5 times the interquartile range below the third quartile or above the first quartile. Following the removal of outliers, a two-factor ANOVA was used to detect differences in averaged hair growth rate between body regions and seasons. Further differences among body regions and seasons were examined using Tukey's HSD test. The average length of hair samples

was summarized for each body region and season, and a two-factor ANOVA was followed by Tukey's HSD test to examine differences between body regions and seasons. For each two-factor ANOVA, the interaction between predictors was examined and removed from the final model if non-significant. We used a significance level of $\alpha = 0.05$ for all comparisons. All statistical tests and models were run using R v.4.0.3 (R Core Team 2017).

3.4 RESULTS

3.4.1 *Timing of hair growth*

Hair was actively growing at the first collection date for all 8 polar bears in spring (March-early May), 7 of 8 polar bears in summer (June-July), 6 of 7 polar bears in fall (September), and 2 of 4 polar bears in winter (December). The bears that did not show active hair growth at the first collection date either started growing later in the season (Star had growth in mid-June, and Tatqiq in October) or showed no hair growth during the entire season (Star and Blizzard in winter). Hair growth continued through the last collection date for 7 of 8 polar bears in spring (late May), 7 of 8 polar bears in summer (August), 6 of 6 polar bears in fall (October - November), and 4 of 5 polar bears in winter (February). The bears without active growth at the final collection date in spring and summer had growth that stopped mid-season: Nuka had active growth until mid-May, and Blizzard had active growth until late July. Star did not have growth throughout the full winter season.

The methods used in this study (labeled glycine and hair dye) showed similar active growth for all seasons except fall. In the fall, results from the methods differed at the first collection date for 2 of 7 bears: hair dye detected growth that was not evident with ^{15}N-labeled glycine for one bear, whereas for the other bear, ^{15}N-labeled glycine detected growth that dye did not. Similarly, at the final sample collection date in the fall, results from the methods differed for 4 of 6 bears,

where the dye method detected hair growth for three bears that was not evident with ^{15}N-labeled glycine, while the opposite was true for the fourth bear.

For bears sampled during the same season for two or more years (n = 2), there were differences in hair growth timing between years. In winter, Blizzard exhibited hair growth in February 2019, but not in February 2020 or 2021. Both dye and ^{15}N-labeled glycine detected hair growth throughout February 2019, whereas no growth was detected by either method in December 2019, January 2020, and February 2020. Blizzard was opportunistically sampled on the rump during a physical exam on 30 March 2021. According to the dye on the collected hair, no growth occurred between 23 July 2020 and 30 March 2021. Star exhibited no hair growth during late spring in 2021, but early spring growth in 2022. Hair dye detected no growth between April and May 2021, whereas the dye detected growth in early to late March 2022.

3.4.2 *Rate of hair growth*

We initially estimated 71 seasonal hair growth rates from the 8 polar bears using hair dye (n = 32), ^{15}N-labeled glycine (n = 27), and ^{13}C-labeled glycine (n = 12) (Table S3). There were 8 negative values, and these were excluded from further analysis. For the remaining positive values, there were no significant differences in hair growth between methods within each season ($p_{adj} > 0.50$). Averaging methodologies for each bear, we estimated 25 seasonal hair growth rates (Table 1) on the foreleg (n = 15), rump (n = 6), and shoulder (n = 4). We identified Nuka's hair growth rate in spring to be an outlier, as the growth rate was equal to the lower threshold for outliers, and thus excluded this rate from further analysis. No other outliers were identified across all body regions and seasons.

Our results suggest the seasonal average hair growth rates range between 0.21 to 0.89 mm day^{-1} for the foreleg, 0.14 to 0.58 mm day^{-1} for the rump, and 0.00 to 0.69 mm day^{-1} for the

shoulder. The mean hair growth rate on the foreleg was 0.81 mm day^{-1} in spring, 0.78 mm day^{-1} in summer, 0.74 mm day^{-1} in fall, and 0.40 mm day^{-1} in winter (Figure 1). The mean hair growth rate for the rump was 0.58 mm day^{-1} in summer, 0.57 mm day^{-1} in spring, 0.43 mm day^{-1} in fall, and 0.14 mm day^{-1} in winter (Figure 1). The mean hair growth rate for the shoulder was 0.69 mm day^{-1} in spring, 0.44 mm day^{-1} in summer, 0.18 mm day^{-1} in fall, and 0.00 mm day^{-1} in winter (Figure 1). Average seasonal hair growth rates were significantly different across body regions ($p = 0.001$). The foreleg exhibited higher rates in comparison to the rump ($p_{adj} = 0.03$) and the shoulder ($p_{adj} = 0.003$). There were no significant differences in growth rates between the shoulder and rump ($p_{adj} = 0.60$). There were significant differences in hair growth across seasons ($p = 0.004$) and no significant interaction between body region and season ($p = 0.90$). Winter hair growth rates were slower compared to spring ($p_{adj} = 0.003$) and summer ($p_{adj} = 0.008$) rates, but not fall ($p_{adj} = 0.09$). There were no significant differences in spring hair growth rates compared to rates in summer ($p_{adj} = 0.93$) or fall ($p_{adj} = 0.44$), and no significant difference between summer and fall hair growth rates ($p_{adj} = 0.73$).

3.4.3 *Variation in hair length across body regions and seasons*

The average hair lengths ranged from 4.2 – 15.7 cm for the foreleg, 1.2 – 10.3 cm for the rump, and 2.7 – 5.9 cm for the shoulder (Table S4). Average hair sample lengths were significantly different across body regions ($p < 0.0001$). The foreleg hair was longer than the rump ($p_{adj} < 0.0001$) and shoulder ($p_{adj} = < 0.0001$) hairs. There were no significant differences in hair lengths between the shoulder and rump ($p_{adj} = 0.11$). There were significant differences in hair length across seasons ($p < 0.0001$). Summer and fall hair sample lengths were not significantly different ($p_{adj} = 0.93$), and these seasons had the longest hair samples compared to all other seasons ($p_{adj} < 0.004$). When examined within each body region, summer foreleg and

rump hair samples were significantly longer compared to hair samples in spring (foreleg: p_{adj} = 0.01, rump: p_{adj} = 0.01), but not in fall (foreleg: p_{adj} = 0.99, rump: p_{adj} = 0.99). Hair was significantly longer in summer than in winter on the foreleg (p_{adj} = 0.01), but not on the rump (p_{adj} = 0.09). There were no differences in shoulder hair length between any of the seasons (p_{adj} = 1.0).

3.5 DISCUSSION

We measured the rates and timing of hair growth for eight zoo polar bears during all four seasons to provide the first comprehensive hair growth study for this species. Hair on the foreleg, rump, and shoulder grew at comparable rates across spring, summer, and fall. However, hair growth rates were slower in winter, consistent with expected growth patterns associated with an annual molt. Hair growth rate and length depended on the body region, with higher rates and longer hairs on the foreleg compared to the rump and shoulder. Differences in hair growth and length between body regions are important considerations when interpreting data from wild samples. Collectively, these findings provide a more precise understanding of seasonality in polar bear hair growth that can be used to improve inference on dietary patterns, hormonal fluctuations, and other indicators of polar bear health.

The average hair length did not differ between summer and fall, nor did hair growth rates differ between spring, summer, and fall. Our result that hair continued to grow between spring and fall is consistent with a previous study that demonstrated that wild polar bears may continue hair growth until October (Rogers *et al.*, 2015) and assumptions about hair growth in previous studies that used polar bear hair (Boucher *et al.*, 2019b; Stricker *et al.*, 2022). Using the average length in summer/fall (foreleg: 104 mm; rump: 73.5 mm; shoulder: 44 mm; Table S4) divided by

the average growth rate in spring – fall (foreleg: 0.72 mm day^{-1}; rump: 0.55 mm day^{-1}; shoulder: 0.44 mm day^{-1}; Table 1), we estimate that hair samples collected in late summer/fall represent approximately 144 days, 134 days, and 100 days prior to collection on the foreleg, rump, and shoulder respectively.

In our study, the summer/fall hair samples were the longest, while the shorter winter and spring samples reflect the new hairs grown in the same year of collection. The length of the summer/fall hair samples likely resembles the prior year's growth, which is assumed to be reflected in hair samples collected from free-ranging polar bears in spring. The time period represented in a spring hair sample can be estimated based on the average hair length in summer/fall (foreleg: 104 mm; rump: 73.5 mm value; shoulder: 44 mm; Table S4) divided by the average growth rate across all four seasons (foreleg: 0.68 mm day^{-1}; rump: 0.48 mm day^{-1}; shoulder: 0.33 mm day^{-1}; Table 1), or by average growth rate for spring - fall, assuming negligible growth during winter (foreleg: 0.72 mm day^{-1}; rump: 0.55 mm day^{-1}; shoulder: 0.44 mm day^{-1}; Table 1) which results in hair samples collected in spring representing approximately the 144 - 153 days prior to collection on the foreleg, 134 - 153 days prior to collection on the rump, and 100 - 133 days prior to collection on the shoulder.

Foreleg hair was longer and grew faster than rump and shoulder hair, highlighting the importance of considering sampling location when interpreting data from wild samples. Foreleg hair length is a sexually dimorphic trait and is age-related in male polar bears (Derocher et al. 2005). Derocher et al. (2005) suggest the foreleg guard hairs may be maintained for more than one year, given their age-related length. The sexually dimorphic nature of this body region may affect the timing and rate of hair growth, although our study shows conflicting patterns of growth among males with no age-related patterns. One 15-year-old male (Nuka, an intact male) had very

slow growth in spring (0.06 mm day^{-1}) and elevated rates in summer (1.02 mm day^{-1}) and fall (0.75 mm day^{-1}). One 4-year-old male (Baffin) and another 6-year-old male (York) had growth in spring, but one had a reduced winter growth rate (0.21 mm day^{-1}), whereas the other demonstrated consistent hair growth across all four seasons (0.54 – 0.59 mm day^{-1}). The consistent growth rate on the latter individual's foreleg throughout all seasons is contrary to assumptions that growth would be reduced outside of the primary molt (Rode et al. 2022). If this pattern is confirmed with more individuals in future studies, segmental analysis of hair could provide insight into polar bear ecology year-round. It is important to note we were unable to replicate the prey or seasonal food availability of wild bears and that low prey availability could affect hair growth in wild polar bears. Further, individual variation in the timing of hair growth has been documented in captive and wild studies of grizzly bears (Macbeth et al. 2010, Erlenbach 2020) and may be influenced by factors such as sex, age, reproductive class, latitude, and food availability (Schwartz et al. 2003, Macbeth et al. 2010).

Polar bears are large predators, and access to individuals is limited, even within captive environments. Implementing methods and collecting samples necessitates extensive planning and comprehensive positive reinforcement training. In this study, we confirm that hair dye and labeled-glycine methods yielded similar results for the timing and rate of seasonal hair growth. Our systematic experimental approach to monitoring hair growth identified that hair growth occurred year-round for most bears, with significantly lower rates during the winter months, and that hair growth rates differ between body regions. These findings allow for a more precise estimation of the timeframe represented by hair samples. Future studies that utilize captive polar bears could improve on our study by coinciding the dose and dye dates with the start of a defined season to increase the sample size of seasonal hair growth rates. Further research to identify

drivers of variation in hair growth rates and timing, particularly among individuals, would also aid in interpreting data from hair. These approaches would help further our understanding of the timing and rate of polar bear hair growth throughout the year, which is crucial for accurately interpreting data obtained from hair samples collected in the wild.

3.6 ACKNOWLEDGMENTS

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3.8 FIGURES

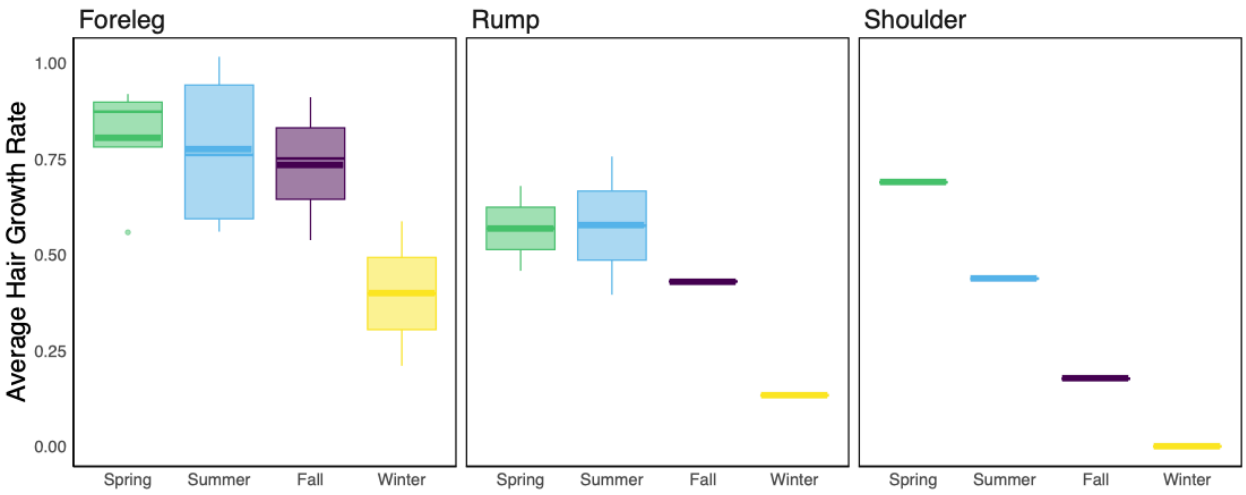

Figure 3.1 Boxplots of the seasonal hair growth rates (mm day^{-1}) on the foreleg (left panel; n = 5 bears), rump (middle panel; n = 2 bears), and shoulder (right panel; n = 1 bear) of polar bears. The mean hair growth rate (mm day^{-1}) is represented by a thick line, and the median is represented by a thin line. Spring (March – May) values are plotted in green, summer (June – August) in blue, fall (September – November) in purple, and winter (December – February) in yellow.

3.9 TABLES

Table 3.1 Averaged hair growth rates (mm day^{-1}) of polar bears for all seasons. Hair samples were collected from the foreleg, shoulder, or rump of the bears; the collection location is denoted in parentheses under each bear's name. The number of hair growth rates contributing to the average (n) are reported.

	Spring	**Summer**	**Fall**	**Winter**
Anana (*Foreleg*)	0.86 (n = 1)	0.94 (n = 4)	NA	NA
Baffin (*Foreleg*)	0.56 (n = 5)	0.56 (n = 3)	0.54 (n = 3)	0.59 (n = 1)
Blizzard *(Rump)*	0.46 (n = 6)	0.40 (n = 2)	NA	0.14 (n = 3)
Nuka (*Foreleg*)	0.06 (n = 1)	1.02 (n = 2)	0.75 (n = 2)	NA
Star (*Shoulder*)	0.69 (n = 1)	0.44 (n = 1)	0.18 (n = 2)	0.00 (n = 1)
Suka (*Foreleg*)	0.89 (n = 1)	0.60 (n = 4)	NA	NA
Tatqiq *(Rump)*	0.68 (n = 3)	0.76 (n = 3)	0.43 (n = 2)	NA
York (*Foreleg*)	0.92 (n = 5)	0.76 (n = 3)	0.91 (n = 2)	0.21 (n = 1)

3.10 SUPPLEMENTAL MATERIALS

Table S3.1 Schedule of hair dye applications and consumption of isotopically labeled glycine doses. Hair dye application is represented by "D", ^{13}C-labeled glycine is represented by "C", and ^{15}N-labeled glycine is represented by "N". The length of each facility's participation in the study is shaded in blue.

	2019												2020											
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Detroit Zoo																								
Anana																**N D**	**C D**	**N**	**D**		**D**			
Nuka																**D**	**C D**	**N D**			**D**			
Suka																**N**	**C D**	**N**	**D**		**D**			
Point Defiance Zoo & Aquarium																								
Blizzard	**N D**			**C**		**D**				**D**			**N D**		**C**	**N D**	**C**	**N**						
San Diego Zoo																								
Tatqiq											**N D**			**C D**		**N**	**C**	**N D**						

	2021												2022											
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Assiniboine Park Zoo																								
Baffin		**N**	**C D**	**N**	**C**	**N**				**N D**														
Star		**N**	**C**	**N D**	**C**	**N**		**D**		**N**														
York		**N**	**C D**	**N D**	**C**	**N**				**N D**														

Table S3.2 Baseline $\delta^{15}N$ and $\delta^{13}C$ values (‰ relative to air and V-PDB, respectively; ± one standard deviation) for unlabeled segments of hairs. The number of segments is denoted in parentheses.

	$\delta^{15}N$	$\delta^{13}C$
Anana (*Foreleg*)	11.4 ± 0.6 $(n = 13)_3$	-16.7 ± 0.2 $(n = 8)_3$
Baffin (*Foreleg*)	11.4 ± 0.1 $(n = 9)_3$	-21.5 ± 0.3 $(n = 12)_2$
Blizzard *(Rump)*	12.9 ± 0.4 $(n = 11)_2$	-16.6 ± 0.1 $(n = 6)_3$
Nuka (*Foreleg*)	14.6 ± 0.9 $(n = 91)_1$	-15.1 ± 0.4 $(n = 14)_1$
Star (*Shoulder*)	11.2 ± 0.2 $(n = 7)_2$	-21.3 ± 0.2 $(n = 14)_2$
Suka (*Foreleg*)	14.0 ± 0.2 $(n = 11)_3$	-15.7 ± 0.4 $(n = 14)_1$
Tatqiq *(Rump)*	9.0 ± 0.4 $(n = 7)_2$	-16.3 ± 0.1 $(n = 8)_3$
York (*Foreleg*)	14.9 ± 0.9 $(n = 9)_3$	-21.3 ± 0.2 $(n = 7)_3$

NOTE: Baseline samples included hair 1) collected before dosing, 2) samples with no discernable apex or fluctuation in enrichment across all segments, or 3) segments furthest from the segment containing a clearly identifiable enriched peak.

Table S3.3 Hair growth rates ± the standard error (mm day^{-1}) of polar bears for all methods (dye, ^{15}N-labeled glycine, and ^{13}C-labeled glycine) for spring (A), summer (B), fall (C), and winter (D). Hair samples were collected from the foreleg, shoulder, or rump of the bears; the collection location is denoted in parentheses under each bear's name. In parentheses, the adjusted R^2 and the number of sampling events (n) are reported. Negative values are reported in red. If there are more than 2 observations and the rate is significantly different than zero, the number of asterisks indicates the significance level; there is one asterisk if $p < 0.05$, two asterisks if $p < 0.01$, and three asterisks if $p < 0.001$.

A) **Spring** (March - May)

	Dye	**^{15}N-labeled glycine**	**^{13}C-labeled glycine**
Anana (*Foreleg*)	NA_1	0.86 ± NA (R^2_{adj} = NA, n = 2)	NA_1
Baffin (*Foreleg*)	*2021:* 0.25 ± 0.21 (R^2_{adj} = 0.18, n = 3) *2022:* 0.87 ± NA (R^2_{adj} = NA, n = 2)	0.62 ± 0.08 * (R^2_{adj} = 0.95, n = 4)	0.71 ± NA (R^2_{adj} = NA, n = 2)
Blizzard *(Rump)*	*2019:* 0.44 ± 0.03 * (R^2_{adj} = 0.97, n = 9) *2020:* 0.42 ± NA (R^2_{adj} = NA, n = 2)	*2019:* 0.51 ± 0.09 ** (R^2_{adj} = 0.90, n = 5) *2020:* 0.48 ± NA (R^2_{adj} = NA, n = 2)	*2019:* 0.35 ± 21 (R^2_{adj} = 0.46, n = 3) *2020:* 0.56 ± 0.03 * (R^2_{adj} = 0.99, n = 3)
Nuka (*Foreleg*)	0.06 ± 0.53 (R^2_{adj} = -0.97, n = 3)	NA_2	NA_4
Star (*Shoulder*)	*2021:* -0.03 ± 0.14 (R^2_{adj} = -0.92, n = 3) *2022:* 0.69 ± NA (R^2_{adj} = NA, n = 2)	NA_4	NA_4
Suka (*Foreleg*)	NA_1	0.89 ± NA (R^2_{adj} = NA, n = 2)	NA_4
Tatqiq *(Rump)*	0.62 ± 0.01 ** (R^2_{adj} = 1, n = 3)	0.83 ± NA (R^2_{adj} = NA, n = 2)	0.59 ± NA (R^2_{adj} = NA, n = 2)
York (*Foreleg*)	*2021:* 0.63 ± 0.30 (R^2_{adj} = 0.63, n = 3) *2022:* 1.51 ± NA (R^2_{adj} = NA, n = 2)	*Dose 1:* 0.71 ± 0.09 * (R^2_{adj} = 0.96, n = 4) *Dose 2:* 0.84 ± 0.03 * (R^2_{adj} = 1, n = 3)	0.93 ± 0.09 (R^2_{adj} = 0.98, n = 3)

NOTE: We could not calculate a seasonal rate for a method if 1) only one sample was collected within the season, 2) the bear was not yet dosed, 3) sampling was not possible due to behavioral constraints, 4) the labeled glycine was not detected, or 5) the label was not identifiable to a dosing event.

B) **Summer** (June – August)

	Dye	**^{15}N-labeled glycine**	**^{13}C-labeled glycine**
Anana (*Foreleg*)	0.98 ± NA (R^2_{adj} = NA, n = 2)	*Dose 1:* 0.95 ± 0.10 (R^2_{adj} = 0.99, n = 3) *Dose 2:* 0.90 ± 0.02 * (R^2_{adj} = 1, n = 3)	0.94 ± NA (R^2_{adj} = NA, n = 2)
Baffin (*Foreleg*)	0.35 ± 0.21 (R^2_{adj} = 0.28, n = 6)	0.62 ± 0.06 (R^2_{adj} = 0.98, n = 3)	0.71 ± 0.06 ** (R^2_{adj} = 0.98, n = 4)
Blizzard *(Rump)*	*2019:* 0.49 ± 0.13 * (R^2_{adj} = 0.73, n = 5) *2020:* -0.27 ± NA (R^2_{adj} = NA, n = 2)	*2019:* NA_1 *2020:* NA_5	*2019:* 0.35 ± 0.10 (R^2_{adj} = 0.80, n = 4) *2020:* -0.36 ± NA (R^2_{adj} = NA, n = 2)
Nuka (*Foreleg*)	1.04 ± 0.15 * (R^2_{adj} = 0.94, n = 4)	1.0 ± 0.00 *** (R^2_{adj} = 1, n = 3)	NA_4
Star (*Shoulder*)	0.44 ± 0.10 ** (R^2_{adj} = 0.77, n = 7)	NA_4	NA_4
Suka (*Foreleg*)	*Dye 2:* 0.10 ± NA (R^2_{adj} = NA, n = 2) *Dye 3:* 0.42 ± NA (R^2_{adj} = NA, n = 2)	*Dose 1:* 0.89 ± 0.17 * (R^2_{adj} = 0.90, n = 4) *Dose 2:* 0.97 ± 0.07 ** (R^2_{adj} = 0.98, n = 4)	NA_4
Tatqiq *(Rump)*	0.44 ± 0.20 (R^2_{adj} = 0.65, n = 3)	0.99 ± 0.05 * (R^2_{adj} = 0.99, n = 3)	0.84 ± 0.02 * (R^2_{adj} = 1, n = 3)
York (*Foreleg*)	0.69 ± 0.18 * (R^2_{adj} = 0.71, n = 7)	0.78 ± 0.05 ** (R^2_{adj} = 0.99, n = 4)	0.81 ± 0.02 *** (R^2_{adj} = 1, n = 4)

NOTE: We could not calculate a seasonal rate for a method if 1) only one sample was collected within the season, 2) the bear was not yet dosed, 3) sampling was not possible due to behavioral constraints, 4) the labeled glycine was not detected, or 5) the label was not identifiable to a dosing event.

C) **Fall** (September – November)

	Dye	**^{15}N-labeled glycine**	**^{13}C-labeled glycine**
Anana (*Foreleg*)	NA_1	NA_1	NA_1
Baffin (*Foreleg*)	*Dye 1:* -0.03 ± 0.57 (R^2_{adj} = -0.50, n = 4) *Dye 2:* 0.13 ± 0.53 (R^2_{adj} = -0.88, n = 3)	*Dose 3:* 1.15 ± NA (R^2_{adj} = NA, n = 2) *Dose 4:* 0.33 ± NA (R^2_{adj} = NA, n = 2)	NA_4
Blizzard *(Rump)*	NA_1	-0.36 ± NA (R^2_{adj} = NA, n = 2)	-0.21 ± NA (R^2_{adj} = NA, n = 2)
Nuka (*Foreleg*)	0.48 ± NA (R^2_{adj} = NA, n = 2)	1.03 ± NA (R^2_{adj} = NA, n = 2)	NA_4
Star (*Shoulder*)	0.13 ± 0.06 (R^2_{adj} = 0.34, n = 7)	0.23 ± 0.07 (R^2_{adj} = 0.82, n = 3)	NA_4
Suka (*Foreleg*)	NA_1	NA_1	NA_1
Tatqiq *(Rump)*	0.33 ± 0.28 (R^2_{adj} = 0.15, n = 3)	0.53 ± 0.17 (R^2_{adj} = 0.81, n = 3)	NA_4
York (*Foreleg*)	*Dye 2:* -0.80 ± 0.08 ** (R^2_{adj} = 0.97, n = 4) *Dye 3:* 1.37 ± NA (R^2_{adj} = NA, n = 2)	0.46 ± NA (R^2_{adj} = NA, n = 2)	NA_4

NOTE: We could not calculate a seasonal rate for a method if 1) only one sample was collected within the season, 2) the bear was not yet dosed, 3) sampling was not possible due to behavioral constraints, 4) the labeled glycine was not detected, or 5) the label was not identifiable to a dosing event.

D) **Winter** (December – February)

	Dye	**^{15}N-labeled glycine**	**^{13}C-labeled glycine**
Anana (*Foreleg*)	NA_3	NA_3	NA_3
Baffin (*Foreleg*)	0.59 ± 0.12 ** (R^2_{adj} = 0.81, n = 6)	NA_4	NA_4
Blizzard *(Rump)*	*2019:* 0.25 ± 0.12 (R^2_{adj} = 0.61, n = 3) *2020:* 0.00 ± NA (R^2_{adj} = NA, n = 2)	*2019:* 0.15 ± 0.18 (R^2_{adj} = -0.14, n = 3) *2020:* -0.33 ± 0.29 (R^2_{adj} = 0.14, n = 3)	NA_4
Nuka (*Foreleg*)	NA_3	NA_3	NA_3
Star (*Shoulder*)	0.00 ± 0.09 (R^2_{adj} = -0.25, n = 6)	0.00 ± 0.20 (R^2_{adj} = -1.00, n = 3)	NA_4
Suka (*Foreleg*)	NA_3	NA_3	NA_3
Tatqiq *(Rump)*	NA_1	$NA_{1,4}$	NA_1
York (*Foreleg*)	0.21 ± 0.15 (R^2_{adj} = 0.17, n = 6)	$NA_{4,5}$	NA_4

NOTE: We could not calculate a seasonal rate for a method if 1) only one sample was collected within the season, 2) the bear was not yet dosed, 3) sampling was not possible due to behavioral constraints, 4) the labeled glycine was not detected, or 5) the label was not identifiable to a dosing event.

Table S3.4 Averaged total hair length ± one standard deviation (in cm) of polar bear hair samples for all body regions and seasons. The minimum and maximum sample hair lengths (in cm) are included, with the sample size in parentheses.

	Spring	**Summer**	**Fall**	**Winter**
Foreleg	8.4 ± 2.7 5.6 – 15.7 (n = 20)	10.7 ± 1.6 7.2 – 14.5 (n = 25)	10.0 ± 2.9 4.2 – 14.9 (n = 17)	8.0 ± 2.9 5.0 – 14.3 (n = 12)
Rump	4.3 ± 1.7 1.6 – 6.5 (n = 16)	7.0 ± 1.4 5.2 – 9.6 (n = 11)	7.9 ± 2.0 5.3 – 10.3 (n = 6)	3.9 ± 2.5 1.2 – 6.7 (n = 7)
Shoulder	5.0 ± 0.9 3.6 – 5.9 (n = 5)	4.2 ± 1.2 2.7 – 5.7 (n = 7)	4.6 ± 0.4 4.0 – 5.1 (n = 7)	4.1 ± 0.3 3.7 – 4.4 (n = 6)

Chapter 4. FEEDING HABITS OF BAFFIN BAY POLAR BEARS *URSUS MARITIMUS*: INSIGHT FROM STABLE ISOTOPES AND TOTAL MERCURY IN HAIR

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4.1 ABSTRACT

Loss of sea ice brought on by climate change affects polar bear (*Ursus maritimus*) access to prey. Here we investigated variation in feeding habits of the Baffin Bay (BB) polar bear subpopulation in relation to sea ice, habitat use, season, and demography using hair carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) stable isotope values and total mercury (THg) concentrations as ecological tracers. We analyzed hair samples from BB polar bears (n = 131) of all age and sex classes live-captured in West Greenland during the spring of 2009-2013. BB polar bears occupied a narrow isotopic space, suggesting limited variation in carbon sources and trophic position within the subpopulation. THg concentrations (5.1 ± 0.2, 0.3 - 12.5 μg g^{-1} dw) were related to age class and nearly half exceeded the known threshold for neurological effects in polar bears at 5.4 μg g^{-1} dw. Although distinct coastal and offshore space-use strategies have been reported for BB polar bears, our results suggest that both strategies lead to similar carbon sources and trophic positions. We found seasonal variation in $\delta^{13}C$ and $\delta^{34}S$ across both space-use strategies, with $\delta^{34}S$ suggesting that all BB polar bears may predate on a higher proportion of the benthic-feeding bearded seal (*Erignathus barbatus)* in late summer relative to spring. Despite

wide fluctuations in inter-annual sea ice conditions and differences in space-use strategies among individuals, stable isotope values and THg concentrations suggested limited variation in feeding habits among BB polar bears. The variation of habitat tracers ($\delta^{13}C$ and $\delta^{34}S$) was related to season, whereas trophic tracer ($\delta^{15}N$ and THg) variation was driven by demographic group. The specialized BB polar bear diet suggests limited feeding plasticity under continued climate warming.

4.2 INTRODUCTION

Arctic food webs have shown to be less stable and resilient to climate change compared to those at lower latitudes (McCann et al. 2005, McMeans et al. 2015). In these food webs, apex predators are important for top-down ecosystem regulation of prey density (Horswill et al. 2016, Florko et al. 2020). Polar bears (*Ursus maritimus*) are specialized top predators that rely on a lipid-rich diet to sustain high energy intake obtained from ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) in particular (Stirling & Archibald 1977, Galicia et al. 2015). The rapid decrease of Arctic sea ice has resulted in longer open water seasons, with earlier onset of break-up and later dates of freeze-up (Overland & Wang 2013, Stern & Laidre 2016). Decreased sea ice reduces polar bears' access to their ice-associated marine mammal prey (Moore & Huntington 2008). As a result, polar bears experience longer fasting periods which lead to increased energetic stress, reduced body weight and reproductive success with lower juvenile survival rates (Rode et al. 2014, Laidre et al. 2020a). The response of a polar bear subpopulation to climate change varies with local sea ice regimes, status of regional prey populations, and ecosystem productivity (Regehr et al. 2010, Rode et al. 2014, 2018, Pilfold et al. 2015, Whiteman et al. 2015, Laidre et al. 2020b). Polar bears in different subpopulations, and

even in different habitats within a subpopulation, may show sea ice-associated dietary shifts (McKinney et al. 2013). Studies of polar bear foraging are therefore necessary for understanding of how diets may change with loss of sea ice habitat and increased use of coastal habitats.

Stable isotopes integrate and record dietary patterns over a timescale proportional to tissue growth rate (Bowen et al. 2013). Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes have been used to show individual variation in polar bear diet and trophic level related to age and contaminant load (Ramsay & Hobson 1991, Polischuk et al. 2001, Bentzen et al. 2007, Horton et al. 2009). Values of $\delta^{15}N$ are primarily tracers of trophic position and $\delta^{13}C$ are used to trace carbon sources from pelagic and sympagic primary producers that eventually reach top predators (Hobson et al. 2002, Horton et al. 2009). Sulfur isotopes ($\delta^{34}S$) are especially effective at distinguishing between terrestrial and open ocean feeding (Barros et al. 2010, Matthews & Ferguson 2015, Szpak & Buckley 2020). Combining $\delta^{13}C$ and $\delta^{34}S$ signals is the most effective for distinguishing between primary producers (Peterson et al. 1985, Connolly et al. 2004). Total mercury (THg) concentrations are informative for monitoring health in relation to biological effects thresholds and can also provide an additional metric to quantify polar bear foraging ecology (Dietz et al. 2011, 2013, McKinney et al. 2017b, Yurkowski et al. 2020). Together, the use of a combination of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ (CNS) stable isotopes and THg facilitates insight into polar bear subpopulation feeding habits, trophic position and potential health threats.

Baffin Bay (BB) is one of five polar bear subpopulations within the seasonal sea ice ecoregion, which is characterized by having an ice-covered winter and an almost ice-free summer (Amstrup et al. 2008, Laidre et al. 2013, 2018a b). Polar bears in BB use large proportions of accessible habitat while moving across the pack ice, and the dates of arrival to and departure from Baffin Island are closely correlated with sea ice retreat and advance (Laidre et al.

2013, 2020, SWG [Scientific Working Group to the Canada-Greenland Joint Commission on Polar Bear] 2016). BB bears that make long-distance movements across the pack ice ('offshore bears') spend their summer on land (Baffin Island) without access to marine prey resources and are likely to fast for three or more months (Laidre et al. 2020a). Another subset of BB bears has been observed with satellite telemetry in recent years and documented using traditional ecological knowledge to be resident at glacier fronts ('coastal bears') in Northwest Greenland year-round (Born et al. 2011, SWG 2016, Laidre et al. 2020a). The use of glacier fronts by some BB polar bears during the open water season may become more common due to the abundance of ringed seals in Melville Bay (*e.g.,* Born et al. 1999, Laidre et al. 2020a) and the need for year-round access to a hunting platform as loss of sea ice continues (Ferguson et al. 2001, Laidre et al. 2020a). Previous studies have investigated polar bear dietary and contaminant patterns related to distinct coastal and offshore movement patterns (Rogers et al. 2015, Boucher et al. 2019a, Blévin et al. 2020), but none to date have focused on an ecoregion of seasonal sea ice or the BB subpopulation in particular. Understanding the intersection of sea ice dynamics, movement patterns, and resource use for subpopulations experiencing a completely ice-free season is increasingly important as sea ice continues to decline throughout the Arctic. In this study, we assess the feeding habits of BB polar bears from 2009 to 2013 using hair CNS stable isotope values and THg concentrations as ecological tracers. First, we evaluate whether intra-population variation in stable isotope values and THg concentrations are associated with population demographics and sea ice metrics. Second, using tracer measurements in segmented guard hair of a subset of adult females, we compare how these tracers vary with seasons and coastal or offshore space-use strategies. Finally, we examine stable isotope values and THg concentrations across the 5-year study period and through comparison of values from recaptured bears.

4.3 MATERIALS AND METHODS

4.3.1 *Study site and sampling*

The BB polar bear subpopulation occupies an area of close to 1 million km^2 bounded by Greenland to the east and Baffin Island, Canada, to the west (Taylor et al. 2005). Polar bears were captured in the fast and pack ice of West Greenland in March and April of 2009–2013. Briefly, helicopter searches occurred ~150 km from the coast and bears were temporarily sedated for sample collection (see Laidre et al. 2020a for capture methods). A premolar tooth was collected from each bear, excluding cubs-of-the-year, to estimate age from the tooth cementum layers (*e.g.*, Hensel & Sorensen 1980). Captured individuals (n = 131; Table 4.1; Figure 4.1) were grouped into five age classes: cub-of-the-year (COY), yearling (YRL), 2-year old (2YR), subadult (ages 3-4), and adult (ages 5+). Hair samples were trimmed from the coat about 2-5 mm from the skin on the captured bear's rump using scissors and frozen in a plastic bag. Total body mass (TBM) was estimated using axillary girth and body length (Table S4.1; Derocher and Wiig 2002). A Body Condition Index (BCI) was calculated for each bear using the TBM in kg and straight-line body length in cm (SLBL) in the equation specific to polar bears (Table S4.1; Cattet et al. 2002). BCIs were not calculated for six bears (1 adult male, 1 2YR, and 4 COYs) due to missing TBM estimates. All female bears (n = 42) were fitted with a Telonics TAW-4610H satellite radio collar to collect movement data (Laidre et al. 2018a b, 2020a). These movement data were used to differentiate between 'coastal bears' (n = 6) that remained resident on the fast ice in Melville Bay near glacier fronts and 'offshore bears' (n = 36) that used larger areas across the pack ice of Baffin Bay, between West Greenland and Baffin Island (Figure S4.1; see Laidre et al. 2018a, 2020a).

4.3.2 *Stable isotope and THg analysis*

For each captured bear, multiple guard hairs were pooled to meet the required minimum sample weight (450 μg) for chemical analysis. Field-collected hair samples consisted of both underfur and guard hair; prior to analysis, we separated and excluded underfur from analysis. Additional guard hair samples from a subset of adult females (n = 27) were measured and cut into 2 cm long segments. Two segments, the first nearest to the root (referred to as 'base', hereafter) and the second nearest to the tip of the hair were analyzed separately to evaluate isotope variation between the spring and summer seasons. We assumed that the collected guard hair was grown determinately during the gradual molting period, presumed to be between April and August (Kolenosky 1987, Born et al. 1991, St. Louis et al. 2011, personal observation), though the exact timing of polar bear hair growth is unknown and has never been quantified. For segemented guard hairs, the tip of the hair was assumed to roughly represent growth in spring (April - May), whereas the hair near the root represented growth in the summer (July - August), in the year prior to sampling (Born et al. 1991, Rogers et al. 2015). The subset of samples included all available coastal bears (n = 6) and a subset of offshore bears (n = 21) across the study period. We assume that the hair growth period does not overlap with the fasting period as adult female bears arrive on Baffin Island (and enter their fasting period) in early August (SWG 2016).

Hair samples processed for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ were first cleaned via immersion in 2:1 chloroform:methanol for 24 hr at 30 °C, then rinsed with a second aliquot of 2:1 chloroform:methanol, followed by three rinses with deionized water. After drying for 24 hr at 50 °C, hairs were cut into small pieces using surgical scissors. Approximately 450-600 μg of the hair was weighed and packed for analysis via a Costech 4010 elemental analyzer and a Thermo

Delta V Advantage ($\delta^{13}C$, $\delta^{15}N$) / Delta V Plus ($\delta^{34}S$) isotope ratio mass spectrometer in the Fisk lab at the University of Windsor using the method of McKinney et al. (2012) for stable isotope analyses. Precision was assessed by the standard deviation of replicate analyses of multiple standards for each element: NIST 1577c ($\delta^{13}C$, $\delta^{15}N$: $n = 16$; $\delta^{34}S$: $n = 4$), internal lab standard - tilapia muscle ($\delta^{13}C$, $\delta^{15}N$: $n = 16$; $\delta^{34}S$: $n = 4$), USGS 40 ($\delta^{13}C$, $\delta^{15}N$: $n = 16$), Urea ($\delta^{13}C$, $\delta^{15}N$: $n = 16$), USGS 42 ($\delta^{34}S$: $n = 4$), and NIST 8529 ($\delta^{34}S$: $n = 4$). For all standards, precision values averaged 0.21‰ for $\delta^{15}N$ and 0.11‰ for $\delta^{13}C$. Accuracy, based on the certified values of USGS 40 ($\delta^{13}C$, $\delta^{15}N$: $n = 16$) and USGS 42 ($\delta^{34}S$: $n = 4$), showed a mean absolute difference from the certified value of 0.09‰ for $\delta^{13}C$, 0.06‰ for $\delta^{15}N$, and 0.01‰ for $\delta^{34}S$.

For total mercury (THg) analysis, the cleaned hairs were acid-digested in plastic centrifuge tubes and then analyzed using a Perkin Elmer FIMS Cold-Vapor Atomic Absorption Spectrometer by the Metals Division at the University of Connecticut Center for Environmental Science and Engineering (McKinney et al. 2017b). All concentrations of THg are reported as μg g^{-1} dry weight (dw). Based on an average sample size of ~0.001 g, the detection limit was determined to be 0.2 μg g^{-1}. Only two samples were under the limit of detection and thus excluded from analysis. All blanks were below the detection limit. Precision was indicated by relative percent difference of duplicate samples and was between 4.4 and 11.2%. Recoveries of matrix spikes ranged from 85.1 to 88.3% and recoveries of laboratory control samples ranged from 95.4 to 105.2%. Accuracy was indicated by the percent THg measured relative to that of the certified standard values from the National Research Council of Canada and was 95.0 ± 12.6% for DOLT-4 ($n = 5$) and 88.4 % for DORM-3 ($n = 1$).

4.3.3 *Sea-ice metrics*

We calculated the March sea ice extent and area in hundred thousand km^2 within the BB subpopulation boundary using daily data from the National Snow and Ice Data Center (Cavalieri et al. 1996 [updated yearly], Stern & Laidre 2016). We used the initiation dates of spring sea ice retreat and fall sea ice advance, as well as the duration of the open water period as calculated in Stern and Laidre (2016). We defined spring sea ice retreat and fall sea ice advance dates as the date in which the sea ice concentration reached below/above 311×10^3 km^2, a threshold halfway between the historical (1979-2014) mean September and mean March sea ice areas in Baffin Bay (Stern & Laidre 2016). The open water period was defined as the number of days between the spring sea ice retreat and fall sea ice advance dates. Sea ice metrics fluctuated throughout the five-year study period with a full month (31.4 days) between the minimum and maximum open water periods. The March sea ice extent ranged from 628,347.3 km^2 to 656, 356.7 km^2. The March sea ice area ranged from 574,470.5 km^2 to 632,446.5 km^2.

4.3.4 *Statistical analysis*

Subadult and adult bears were separated by age and sex, whereas dependent bears were grouped for analysis by age class only (COY, YRL, 2YR). Adult females were further divided into the following reproductive categories: solitary, with COYs, with YRLs, and with 2YRs (Table 4.1). Summary statistics for all stable isotopes were reported as arithmetic means and standard errors of the mean. Normality and homogeneity of variances of CNS stable isotopes and THg were assessed using the Shapiro–Wilk test and Levene's test, respectively. Concentrations of THg were log transformed to meet normality prior to any statistical analysis. A Pearson's product-moment correlation was run between THg and both stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) for all adult age classes. Outliers were determined by identifying values that exceeded three times

the interquartile range (IQR). All statistical tests were run using program R v.4.0.3 (R Core Team 2017).

We used the isotopic niche width to examine variation in dietary breadth for each demographic class. Niche width, represented by the mode Bayesian estimate of the standard ellipse area (SEA_b), was calculated using SIBER (Stable Isotope Bayesian Ellipses in R) version 2.1.3 (Jackson et al. 2011). To calculate SEA_b and the 95% credible interval for each demographic class, two chains were used in the Markov Chain Monte Carlo process with a burn-in of 1,000 iterations, a thinning rate of 10, and 20,000 iterations for each posterior distribution. Space-use strategies (coastal vs. offshore) were pooled among adult female reproductive statuses for this niche analysis.

We fit either a generalized linear model (GLM) or generalized linear mixed model (GLMM) to separately examine variation in $\delta^{13}C$, $\delta^{15}N$ and log-transformed THg concentrations. Explanatory variables included demographic group/reproductive status of the bears referred to as *Class* (*i.e*., solitary adult female, female with COYs, female with YRLs, female with 2YRs, adult male, subadult female, subadult male) and sea ice metrics important to polar bears (Stern & Laidre 2016) and specific to Baffin Bay, either fall sea ice advance date of the previous year (*FreezeUp.lag*), spring sea ice retreat of the previous year (*BreakUp.lag*), open water period duration of the previous year (*OpenWater.lag*), March sea ice extent of the previous year (*IceExtent.lag*), or March sea ice area of the previous year (*IceArea.lag*). Models only included one sea ice variable to avoid autocorrelation and model selection was conducted using the function 'dredge' in the 'MuMIn' package (Bartoń 2017). Space-use strategies were pooled among adult female reproductive statuses for this analysis. The *BCI* was also included in THg models to account for variation related to body condition. Because $\delta^{34}S$ was only examined in

base and tip hair segments in a subset of adult females, no whole hair models were feasible to include in this study.

We conducted a likelihood ratio test with a parametric bootstrap approach (n = 1000) to construct the distribution of the likelihood ratio statistic (McLachlan 1987, Tekle et al. 2016) to determine whether a model was improved with *Capture Year* included as a random effect and if a GLMM should be used. If a model required a random effect, we used the 'lme4' package to fit a GLMM (Bates et al. 2015). If not, we used the 'stats' package to fit a GLM (R Core Team 2017).

The Akaike's Information Criterion (Akaike 1974), corrected for small sample size, was used to determine the models of best fit with penalties for overfitting (defined as $\Delta AIC_c = 0$). The estimate and 95% confidence interval are reported for each predictor in the models of best fit (Table S4.2). The residuals of every top model were checked for normality by examining the residual plots and using the Shapiro-Wilk Normality test using the 'stats' package (R Core Team 2017). Models with a ΔAIC_c of less than two were considered competing models (Table 4.2), and all models with ΔAIC_c less than four are reported (Table S4.3). We calculated the deviance explained (R^2) for the GLMs using the 'rsq' package (Zhang 2020) and the marginal and conditional R^2 values for GLMMs using the 'MuMin' package (Bartoń 2017). We used a Type II analysis (Yates's method of fitting constants) to calculate the relative amount of variance explained by each predictor (partial R^2) via the 'car' package (Langsrud 2003, Fox & Weisberg 2011).

The CNS stable isotopes and THg values of six coastal adult females were compared with values of thirty-six offshore females using Welch's two-sample *t*-tests (Table S4.4A). Niche width (SEA_b) and the 95% credible interval was calculated for coastal and offshore female polar

bears (Jackson et al. 2011). Additional separate GLMs were fit for only adult females in order to include an additional covariate (*Habitat)* derived from the satellite collar data (*i.e*., coastal or offshore movement patterns), and the top five models are reported (Table S4.5). For these analyses, we did not distinguish between reproductive statuses within space-use strategy groups.

The CNS stable isotopes and THg values in the base and tip segments of hair were compared among individual adult females using paired t-tests (Table S4.4B). Welch's two-sample *t*-tests were used to compare between coastal and offshore base sections and between coastal and offshore tip segments (Table S4.4B). We ran a Pearson's product-moment correlation for $\delta^{13}C$, $\delta^{15}N$, and THg for solitary adult females (as a representative group) across the 5-year study period. We also examined inter-annual differences in $\delta^{13}C$, $\delta^{15}N$, THg for seven bears (including one 'coastal bear') that were recaptured during the 5-year study period. The GLMs and GLMMs included data from only the first capture if a bear was captured more than once to avoid pseudo-replication.

4.4 RESULTS

4.4.1 *Demographic variation*

Polar bears in BB occupied a narrow range of carbon sources (2.1 ‰) and the 95% credible intervals of the niche width for all sex/age classes fully overlapped (Figure S4.2). Despite this, demographic group was important in all competing $\delta^{13}C$, $\delta^{15}N$, and THg models. There was variation in $\delta^{13}C$ ($F_{9,118} = 5.17$, $p < 1.31e\text{-}5$) and $\delta^{15}N$ ($F_{9,120} = 23.15$, $p < 2e\text{-}16$) among multiple age and sex classes (Table 4.1; Figure 4.2). Similar to $\delta^{13}C$ and $\delta^{15}N$ (CN) isotopes, THg concentrations varied between age and sex classes ($F_{9,114} = 69.94$, $p < 2e\text{-}16$). The Pearson's

product-moment correlation showed few significant linkages between THg and CN isotopes among demographic groups (Table S4.6).

The THg concentrations varied for all bears between 0.3 and 12.5 μg g^{-1} dw, with a median THg concentration of 5.1 ± 0.2 μg g^{-1} dw (Table 4.1). Only the median THg concentration of solitary adult females exceeded 5.4 μg g^{-1}, a concentration at which negative correlations with N-methyl-D-aspartate (NMDA) activity have been reported for East Greenland (EG) polar bears (Basu et al. 2009, Dietz et al. 2013). When examined individually, nearly half of the BB bears exceeded this threshold. Two-thirds (66.7%) of both solitary adult females and adult males exceeded the threshold. The lowest percentage of adult females exceeding the neurological effects level threshold was found for females with COYs (28.6%), as compared to percentages of females with YRLs (85.7%) and with 2YRs (88.9%). Of all cub age classes, only 2YRs (21.4%) exceeded the neurological effects level threshold.

4.4.2 *Overall model results*

There were three competing models for $\delta^{13}C$, which included *Class,* ice variables *(*either *OpenWater.lag* or *BreakUp.lag)* and *Capture Year* (Table 4.2). A GLMM was used in $\delta^{13}C$ model selection as $\delta^{13}C$ data supported the inclusion of capture year ($p < 0.001$) as a random effect. The variance of the random effect (*Capture Year*) was smaller than the residual variation of the GLMM ($s^2_{Capture\ Year} = 0.02$; $s^2_{residual} = 0.08$). The overall deviance explained (R^2) for the competing models ranged between 0.396 – 0.423 (Table 4.2). Limited variance was explained by *Class* in the top models for $\delta^{13}C$ (partial $R^2 = 0.161$). Two of the three competing models for $\delta^{13}C$ included ice metrics, *OpenWater.lag* or *BreakUp.lag* for $\delta^{13}C$. However, the confidence intervals for both *OpenWater.lag* and *BreakUp.lag* overlapped zero and therefore were not considered significant variables in their respective models.

There were four competing models for $\delta^{15}N$, which included *Class* and either *IceArea.lag, BreakUp.lag*, or *IceExtent.lag* as an ice variable (Table 4.2). A GLM was used in $\delta^{15}N$ model selection because the inclusion of capture year as a random effect was not supported ($p = 0.515$). The overall deviance explained (R^2) for the competing models ranged between 0.348 – 0.366 (Table 4.2). Most of the variance was explained by *Class* in the top models for $\delta^{15}N$ (partial R^2 = 0.318 –0.349). The confidence intervals for adult males did not overlap zero in any $\delta^{15}N$ models, and thus was considered important in explaining $\delta^{15}N$ variation. The confidence intervals for *IceArea.lag, BreakUp.lag*, and *IceExtent.lag* overlapped zero and therefore were not considered significant variables in their respective models.

There were three competing models for THg, which included *Class* and either *FreezeUp.lag* or *OpenWater.lag* as an ice variable (Table 2). A GLM was used in THg model selection because the inclusion of capture year as a random effect was not supported ($p = 0.926$). The overall deviance explained (R^2) for the competing models ranged between 0.198 – 0.202 (Table 4.2). Most of the variance was explained by *Class* in the models for THg (partial R^2 = 0.194 – 0.198). The confidence intervals for subadult males did not overlap zero in any THg models, and thus this age class was considered important in explaining THg variation. Two of the three top models for THg included ice metrics (Table 4.2), *FreezeUp.lag* or *OpenWater.lag* for THg. However, the confidence intervals for both *FreezeUp.lag* and *OpenWater.lag* overlapped zero and therefore were not considered significant variables in their respective models. The covariate *BCI* was not selected in the three competing THg models, and thus was not considered significant in describing THg variation (Table 4.2).

4.4.3 *Offshore versus coastal habitat use*

Coastal and offshore polar bears were similar in $\delta^{13}C$, $\delta^{15}N$ and THg. Whole hair means for $\delta^{13}C$, $\delta^{15}N$, and THg did not significantly differ between coastal ($\delta^{13}C$ =-16.3 ± 0.6 ‰, $\delta^{15}N$ = 19.1 ± 0.4 ‰, THg = 6.6 ± 2.1 μg g^{-1} dw; Table S4A) and offshore adult female bears ($\delta^{13}C$ = -16.2 ± 0.4 ‰, $\delta^{15}N$ = 18.8 ± 0.5 ‰, THg = 6.7 ± 2.3 μg g^{-1} dw; Table S4.4A). The 95% credible intervals of the niche widths for coastal polar bears [SEA_B = 0.8 $‰^2$ (0.3, 1.9)] and offshore polar bears [SEA_B = 0.5 $‰^2$ (0.4, 0.7)] fully overlapped (Figure S4.2). Of all the separate models for adult females to determine the influence of 'coastal' or 'offshore' space-use strategies, the *Habitat* covariate (partial R^2 value = 0.031) was retained in a single $\delta^{15}N$ model with a R^2 of 0.103 (ΔAIC_c = 1.02, Table S4.5). The inclusion of capture year was not supported by likelihood ratio tests (all $p > 0.4$) so all adult females were modeled using GLMs.

4.4.4 *Intra- and interannual variation*

For base and tip hair comparisons, outliers were detected for $\delta^{13}C$ and $\delta^{15}N$ for one individual and these values were excluded from the paired analysis. The $\delta^{34}S$ and THg values from this individual were retained as the analyses were separate and independent. The ^{13}C and ^{34}S in the base segments were significantly depleted compared to the tip segments for both coastal and offshore bears, while $\delta^{15}N$ and THg did not significantly differ (Figure 4.3; Table S4.4B). There were no significant differences between coastal and offshore base segments or between coastal and offshore tip segments (Table S4.4B).

We found interannual variation between $\delta^{13}C$, $\delta^{15}N$, and THg values for recaptured bears and no significant correlation between year and tracer values for solitary adult females over the 5-year study period. Recaptured bears (n = 7) showed interannual variation as they transitioned between age classes and/or reproductive status (Figure S4.3). The recaptured bear that

demonstrated the largest difference in $\delta^{13}C$ was a 'coastal' adult female bear that was without cubs in both capture years. This adult female increased in $\delta^{13}C$ by 0.3‰ and decreased in THg by 0.4 μg g^{-1} dw between 2011 and 2012.

4.5 DISCUSSION

We examined feeding habits of BB polar bears using $\delta^{13}C$, $\delta^{15}N$, and THg values from hair in relation to demographic class, sea ice, space-use strategy, season, and year. Our results suggest the explanatory power of sea ice dynamics on BB polar bear feeding habits was limited relative to demographic group and unknown drivers of variation. Of the variance explained by the model, most (at least 87%) was explained by demographic group for $\delta^{15}N$ and THg models. However, the overall deviance explained by the top model was relatively low for $\delta^{15}N$ ($R^2 = 0.348$) and THg ($R^2 = 0.197$). Only 40% of the variance in the $\delta^{13}C$ model (partial $R^2 = 0.161$; $R^2 = 0.408$) was explained by demographic group. Geographic location, ice thickness, and sympagic versus pelagic food sources for prey can affect $\delta^{13}C$ (Hobson et al. 2002, Tremblay et al. 2006, Horton et al. 2009, Boucher et al. 2019a b), and therefore could be considered in future models. The unclear link between sea ice dynamics and dietary tracers may be due to the low variability within isotopic tracers for the subpopulation or a potential phenological mismatch between the effect period of selected ice meterics and when hair grows. Base hair segments were significantly depleted in ^{13}C and ^{34}S compared to the tip segments for both coastal and offshore female bears, suggesting that season explains more variation in hair stable isotope values than space-use strategy. Habitat tracers ($\delta^{13}C$ and $\delta^{34}S$) were driven by season, whereas trophic tracers ($\delta^{15}N$ and THg) were driven by demographic group.

For $\delta^{15}N$, most of the differences between sex and age classes were small (< 1‰) suggesting limited variation in trophic position within the BB subpopulation. The exception was that COY $\delta^{15}N$ was higher than all other age groups, however nutrient transfer from ^{15}N–enriched milk from the mother is the primary contributor to ^{15}N–enriched values of COY hair (Polischuk et al. 2001). Yearlings were more ^{15}N–enriched than adult females with YRLs and females with 2YRs, likely because their hair was grown at a time when the YRLs were still nursing and therefore were feeding at a trophic level higher than their mother (Polischuk et al. 2001).

Similar to other polar bear subpopulations, variation in BB polar bear THg concentrations was related to sex, age class, and reproductive status (Cardona-Marek et al. 2009, St. Louis et al. 2011, Bechshoft et al. 2016, McKinney et al. 2017b). Hair THg concentrations increased with age for BB polar bears, following well with demographic variation reported in the western Hudson Bay (WHB) and Southern Beaufort Sea (SB) subpopulations (Bechshoft et al. 2016, McKinney et al. 2017b). In addition to age class, reproductive status played a role in determining THg concentrations, as the highest THg means were found in BB adult females with YRLs and 2YRs. This may indicate that adult female bears with cubs need to ingest more food than solitary females to feed their cubs.

In addition to use of THg as a tracer, polar bear hair THg concentrations can be interpreted in relation to effect thresholds (Dietz et al. 2011, 2013). Percentages of individuals exceeding the neurological effects threshold have previously been calculated for multiple subpopulations, including BB (Dietz et al. 2013), but not for distinct age and reproductive statuses. For THg accumulation, we report exceedance of the neurological effects threshold for all but two demographic groups ranging from 21.4% of 2YR cubs up to 88.9% of females with 2YR cubs. The median THg concentrations for subadult and adult BB polar bears in 2009–2013 was lower

than previously reported, ranging from 4.1 – 6.0 μg g^{-1} dw (Table 4.1) versus 7.6 μg g^{-1} dw in 1985–1994 (Dietz et al. 2006) and 9.4 μg g^{-1} dw in 2000–2008 (Dietz et al. 2011). However, the bears sampled by Dietz et al. (2006, 2011) were harvested in the Qaanaaq region, an area further north than capture locations in this study and were potentially more representative of bears in the Kane Basin subpopulation. The somewhat lower subadult and adult THg medians in recent years could be related to this difference in geography, changes in Hg transport, deposition, or biogeochemical cycling in the Arctic (Wang et al. 2019), and/or related to the long-term changes in the food web or BB polar bear diets, as documented in other subpopulations (*e.g.*, EG; McKinney et al. 2013).

Despite telemetry-based evidence of contrasting space-use strategies (Laidre et al. 2018a, 2020a), we did not detect any differences in $\delta^{13}C$, $\delta^{15}N$, and THg in hair between coastal and offshore polar bears although we are cautious to reach a firm conclusion due to low coastal sample size ($n = 6$). A lack of differences in $\delta^{13}C$ and $\delta^{15}N$ between space-use strategies was recently also found for Barents Sea (BS) and SB polar bears (Boucher et al. 2019a, Blévin et al. 2020). Only one BB adult female $\delta^{15}N$ model retained *Habitat* as a covariate, and even then space-use strategy explained little of the variation (partial $R^2 = 0.031$; $R^2 = 0.103$). However, we assume that movement strategies of the captured bears is consistent over two years (*i.e.,* coastal bears stay coastal bears) for the current year of satellite tracking and the lagged data of diet and ice metrics. Also, the foraging period reflected in the guard hair isotopic values of coastal and offshore BB bears may at least partially occur when the bears overlap in habitat use (*i.e.*, out on the ice in the spring and summer), although the exact timing of hair growth is not well understood in polar bears. We therefore suggest further investigation of hair growth rates in captive and wild polar bears, especially during the spring and summer seasons. An improved

understanding of the tissue growth timeline, a larger sample size of coastal polar bears, and/or the use of a higher-resolution tracer (*i.e.*, fatty acids, compound-specific stable isotopes, persistent organic pollutants) should be employed to detect differential patterns in feeding habits related to space-use strategies (Bowen et al. 2013).

Seasonal variation in dietary patterns was examined through comparisons of base and tip hair segments. For both coastal and offshore BB bears, the base end (grown in summer) was depleted in ^{34}S and ^{13}C when compared to the tip end (grown in spring). A nearshore-offshore/benthic-pelagic gradient of ^{13}C exists in the Baffin Bay food web, with depleted ^{13}C signifying an increased reliance on offshore/pelagic prey (Hobson et al. 2002, Fleming et al. 2018, Yurkowski et al. 2020). There is also a well-established benthic-pelagic gradient in ^{34}S in the opposite direction of ^{13}C, with depleted ^{34}S signifying an increased reliance on coastal/benthic-feeding prey (Peterson et al. 1985, Matthews & Ferguson 2015). We thus expected offshore BB bears would have depleted ^{13}C and enriched ^{34}S in both base and tip segments of the hair relative to coastal bears. We expected the offshore $\delta^{34}S$ value would be around 21‰, the value found in the well-mixed pool of sulfate in the open ocean (Böttcher et al. 2007, Barros et al. 2010). Conversely, we expected that coastal BB bears would exhibit a benthic isotopic signal via enriched ^{13}C and depleted ^{34}S in both base and tip segments of the hair.

Both offshore and coastal polar bears had a $\delta^{34}S$ tip value of 20.6‰ and values were more depleted in the base segment. This suggests that both coastal and offshore bears may feed on a higher proportion of nearshore/ benthic-feeding bearded seal later in the summer when remnant sea ice facilitates access to shallow, coastal areas. If interpreted using only the nearshore-offshore/benthic-pelagic gradient of ^{13}C, our results would imply that the depleted base end signifies an increased reliance on offshore/pelagic prey later in their primary feeding

season, a finding contrary to both our expectations and the $\delta^{34}S$ results. Szpak & Buckley (2020) also found $\delta^{13}C$ opposing $\delta^{34}S$ patterns and expectations for walrus (*Odobenus rosmarus*) and ringed seals across multiple regions. Our results support that $\delta^{34}S$ may be a more appropriate indicator of the contribution of benthic-feeding versus pelagic-feeding prey than $\delta^{13}C$ in Arctic consumers (Szpak & Buckley 2020).

The $\delta^{13}C$, $\delta^{15}N$, and THg concentrations were examined in seven bears recaptured after periods of 1-3 years to assess how values changed for bears transitioning between age classes and/or reproductive status. A solitary 'coastal' adult female had the highest increase in $\delta^{13}C$, which may indicate that this individual foraged over a larger area than the other recaptured bears. Both females captured with cubs were somewhat depleted in ^{15}N compared to when recaptured as solitary adults, though the magnitude of difference was small. We highlight the degree of interannual variation that can occur within an individual bear and the importance of including reproductive status and age class information in diet studies.

4.6 CONCLUSIONS

We examined feeding habits of BB polar bears using $\delta^{13}C$, $\delta^{15}N$, and THg values from hair in relation to demographic class, sea ice, space-use strategy, season, and year. Overall, there was little variation in feeding habits of BB polar bears across demographic groups, multiple years of sampling, and variable sea ice conditions. Demographic group was the most important predictor of the limited differences in $\delta^{15}N$ and THg concentrations. We found a high percentage of adult bears exceeded the neurological effects threshold, which confirms that BB polar bears will face multiple stressors in a rapidly warming Arctic. For adult females, seasonal variation of $\delta^{34}S$ between hair segments suggests bearded seal may be an increasingly important prey item in the

late summer which may have implications for phenological changes caused by climate change. We detected no differences in CNS stable isotopes and THg concentrations between adult female space-use strategies, suggesting that these tracers may not have sufficient resolution to distinguish more fine-scale variation in foraging patterns. Further investigation between coastal and offshore space-use strategies in BB will be important for understanding how differences in space use under climate change translate to diet and pollution levels. Continued monitoring of polar bear diet is necessary to understand the resilience of an apex predator across the changing Arctic ecosystem.

4.7 ACKNOWLEDGMENTS

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Polar Continental Shelf Project, Qaanaap Kommunia, Qikiqtaaluk Corporation, Quantum Murray LP, Royal Canadian Mounted Police, School of Aquatic & Fishery Sciences (University of Washington), Thule Air Force Base, US Department of Defense (National Defense Science & Engineering Graduate Fellowship), Universal Helicopters, University of Oslo, Upernavik Seafood, Uummannaq Sundhedscenter – Peqqik, Vetlesen Foundation, and World Wildlife Fund. Numerous hunters provided invaluable assistance in the field. Sniega Stapcinskaite (University of Connecticut) conducted THg instrumental analysis. Ben Cohen assisted with GIS maps and Harry Stern compiled ice metrics. We are grateful for the constructive comments of B. Popp, C. Clark, E. Escajeda, G. Holtgrieve, G. Stern, J. Hale, J. Lindsay, J. M. Stern, M. Arrington, R. James, S. Thurner, and anonymous reviewers.

4.8 FIGURES

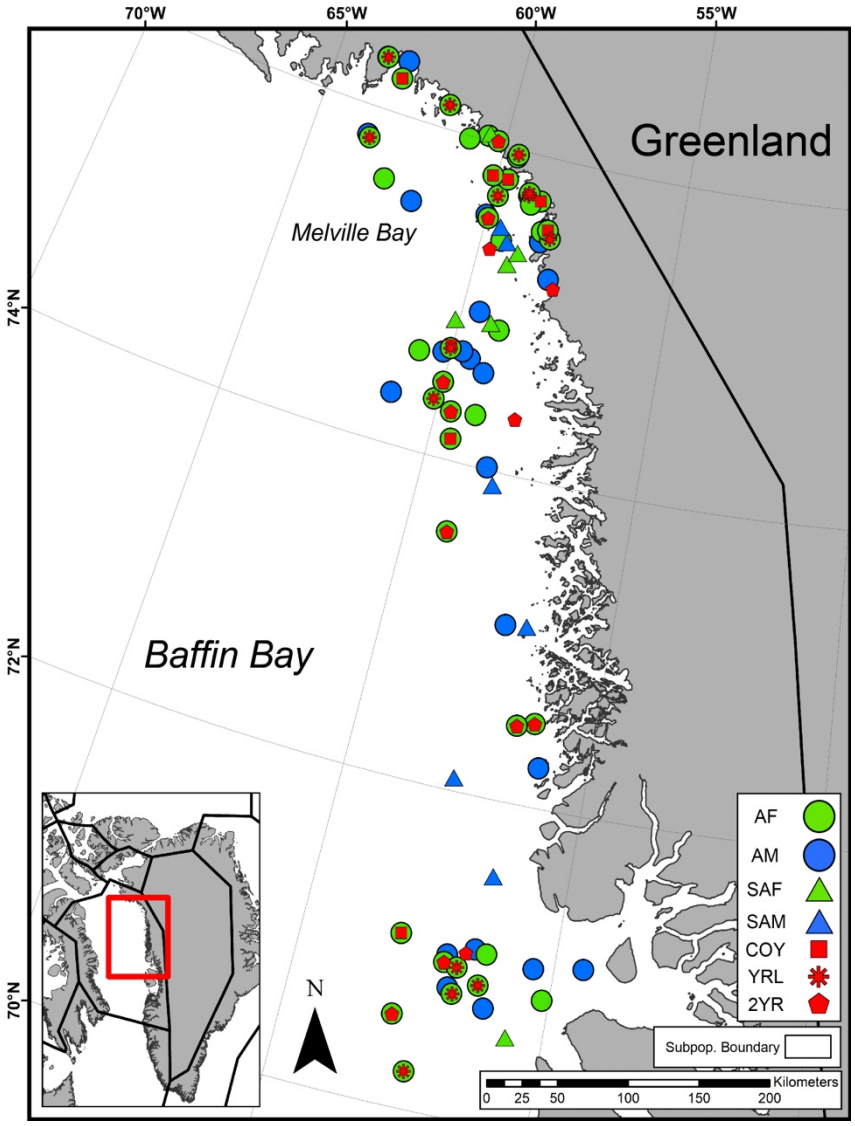

Figure 4.1 Capture and sampling locations (n = 131) of polar bears (*Ursus maritimus*) in Baffin Bay between 2009 - 2013 according to age and sex class. Demographic groups are defined as follows: Adult Female (AF), Adult Male (AM), Subadult Female (SAF), Subadult Male (SAM), Cub-of-the-year (COY), Yearling (YRL), and 2-year-old (2YR). The Polar Bear Specialist Group (2018) subpopulation boundaries are shown on the map with black lines.

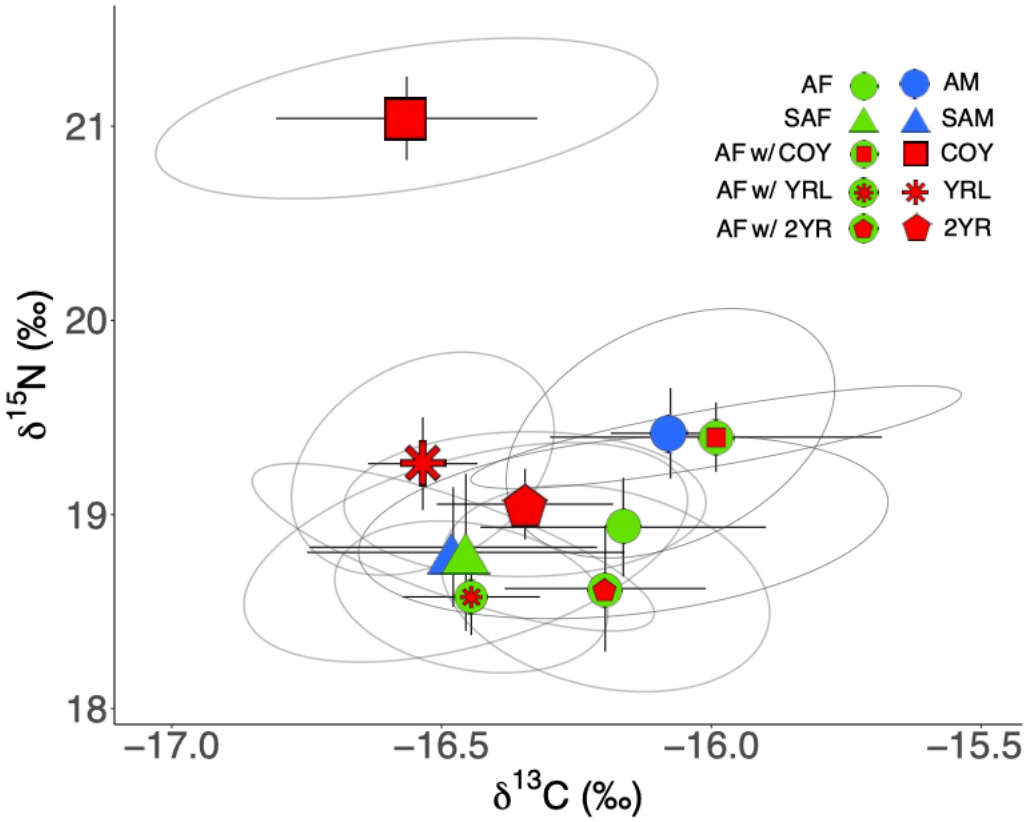

Figure 4.2 Mean guard hair $\delta^{13}C$ and $\delta^{15}N$ (‰) with standard error (SE) bars separated by age class, sex, and reproductive status in the Baffin Bay (BB) polar bear (*Ursus maritimus*) subpopulation. The demographic groups are defined as follows: Adult Female (AF), Adult Male (AM), Subadult Female (SAF), Subadult Male (SAM), Cub-of-the-year (COY), Yearling (YRL), and 2-year-old (2YR). Standard ellipses are shown for each demographic class in gray. Ellipses were calculated using SIBER (Stable Isotope Bayesian Ellipses in R) version 2.1.3 (Jackson et al. 2011) and contain approximately 95% of the data.

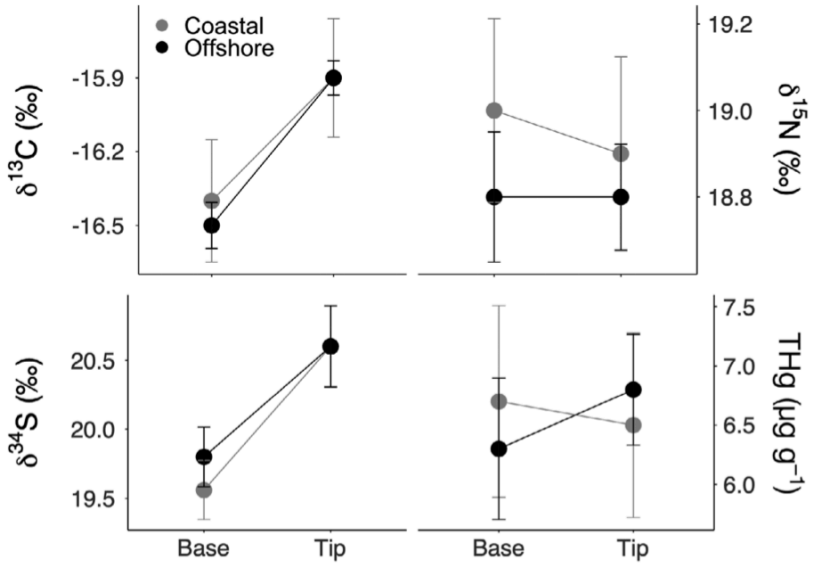

Figure 4.3 Mean (± SE) guard hair $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ (‰) and total mercury (THg) concentrations (ug g^{-1} dw) for both base and tip guard hair segments of adult female Baffin Bay (BB) bears. Values can also be found in Table S4B. Colors (gray, black) denote the space-use strategy (*i.e.*, coastal or offshore).

4.9 TABLES

Table 4.1 Mean guard hair $\delta^{13}C$ and $\delta^{15}N$ (‰) and median guard hair concentrations (μg g^{-1} dw) of total mercury (THg) with standard errors (SE), and THg concentration ranges (μg g^{-1} dw) for each class and sample size (*n* [THg *n*, if different]) in the Baffin Bay (BB) polar bear (*Ursus maritimus*) subpopulation.

Class	*n*	$\delta^{13}C$ mean ± SE	$\delta^{15}N$ mean ± SE	THg (med ± SE)	THg Range (min - max)
Adult females (solitary)	12	-16.2 ± 0.1	18.9 ± 0.1	6.0 ± 0.7	3.2 - 11.4
Adult female w/ COY	7	-16.0 ± 0.2	19.4 ± 0.1	5.1 ± 0.9	3.6 - 10.2
Adult female w/ YRL	14	-16.4 ± 0.1	18.6 ± 0.1	6.8 ± 0.5	4.8 - 12.2
Adult female w/ 2YR	9	-16.2 ± 0.1	18.6 ± 0.2	6.3 ± 0.9	4.5 - 12.3
Adult male	28 (27)	-16.1 ± 0.1	19.4 ± 0.1	5.8 ± 0.3	3.8 - 12.5
Subadult female	6	-16.5 ± 0.2	18.8 ± 0.2	5.0 ± 0.4	3.7 - 6.2
Subadult male	6	-16.5 ± 0.1	18.8 ± 0.2	4.1 ± 0.2	4.0 - 5.3
Cubs of the year (COY)	13 (8)	-16.6 ± 0.1	21.0 ± 0.1	0.4 ± 0.1	0.3 - 1.0
Yearling cubs (YRL)	21	-16.5 ± 0.1	19.3 ± 0.1	2.5 ± 0.2	1.6 - 4.4
2-Year old cubs (2YR)	15 (14)	-16.3 ± 0.1	19.1 ± 0.1	4.8 ± 0.4	2.0 - 7.5
All	131 (124)	-16.3 ± 0.03	19.3 ± 0.07	5.1 ± 0.2	0.3 - 12.5

Table 4.2 Model selection to assess demographic and environmental variables affecting $\delta^{13}C$, $\delta^{15}N$, and THg values of Baffin Bay polar bears (*Ursus maritimus*). Models with $\Delta AIC_c \leq 2$ are included and are considered to be competing. All models with $\Delta AIC_c < 4$ are shown in Table S4.2.

Response	Rank	Model	df	Deviance Explained (R^2)	AIC_c	ΔAIC_c
$\delta^{13}C$	1	*Class* + *OpenWater.lag* + (1 | *Capture Year*)	10	0.408	54.8	0
	2	*Class* + (1 | *Capture Year*)	9	0.396	54.9	0.08
	3	*Class* + *BreakUp.lag* + (1 | *Capture Year*)	10	0.423	55.5	0.64
$\delta^{15}N$	1	*Class*	8	0.348	131.4	0
	2	*Class* + *IceArea.lag*	9	0.366	131.6	0.26
	3	*Class* + *BreakUp.lag*	9	0.349	131.8	0.43
	4	*Class* + *IceExtent.lag*	9	0.338	131.9	0.50
log(THg)	1	*Class*	8	0.198	35.4	0
	2	*Class* + *OpenWater.lag*	9	0.202	37.4	2.01
	3	*Class* + *FreezeUp.lag*	9	0.202	37.4	2.03

4.10 SUPPLEMENTAL MATERIALS

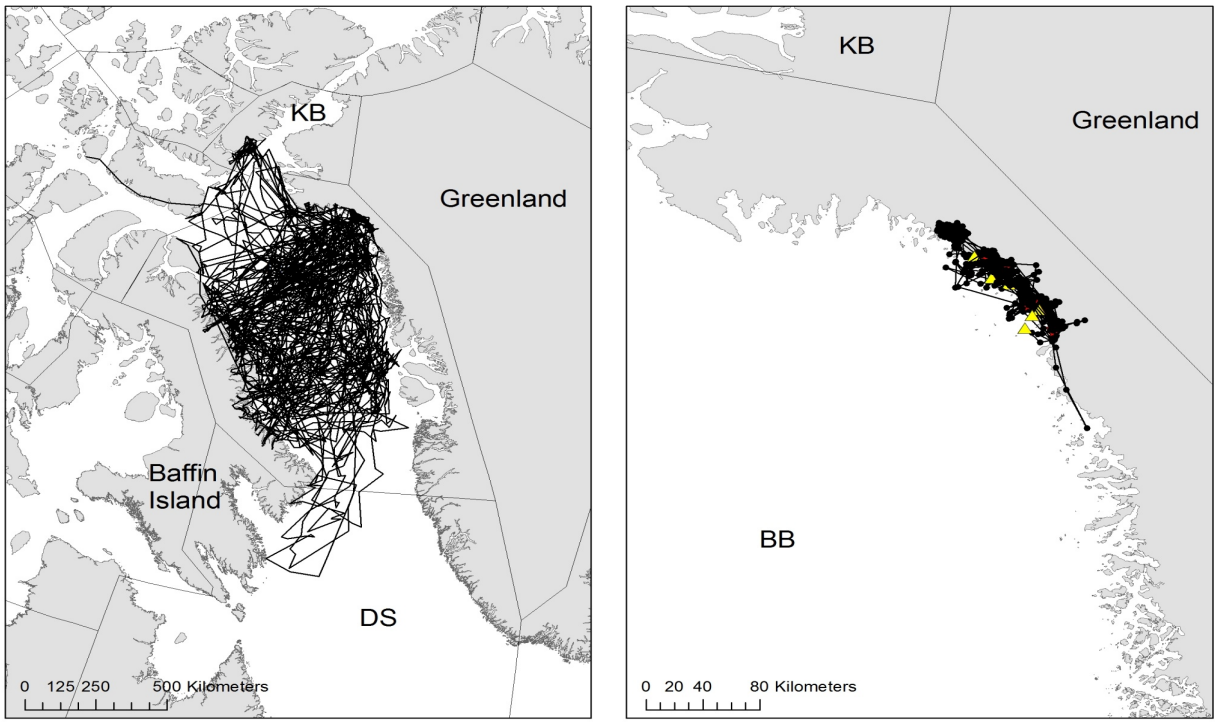

Figure S4.1 Adult female bears (n = 42) were fitted with a Telonics TAW-4610H satellite radio collar to collect movement data. These movement data were used to differentiate between 'offshore bears' (n = 36; left panel) that used larger areas across the pack ice of Baffin Bay and 'coastal bears' (n = 6; right panel) that remained resident on the fast ice in Melville Bay near glaciers.

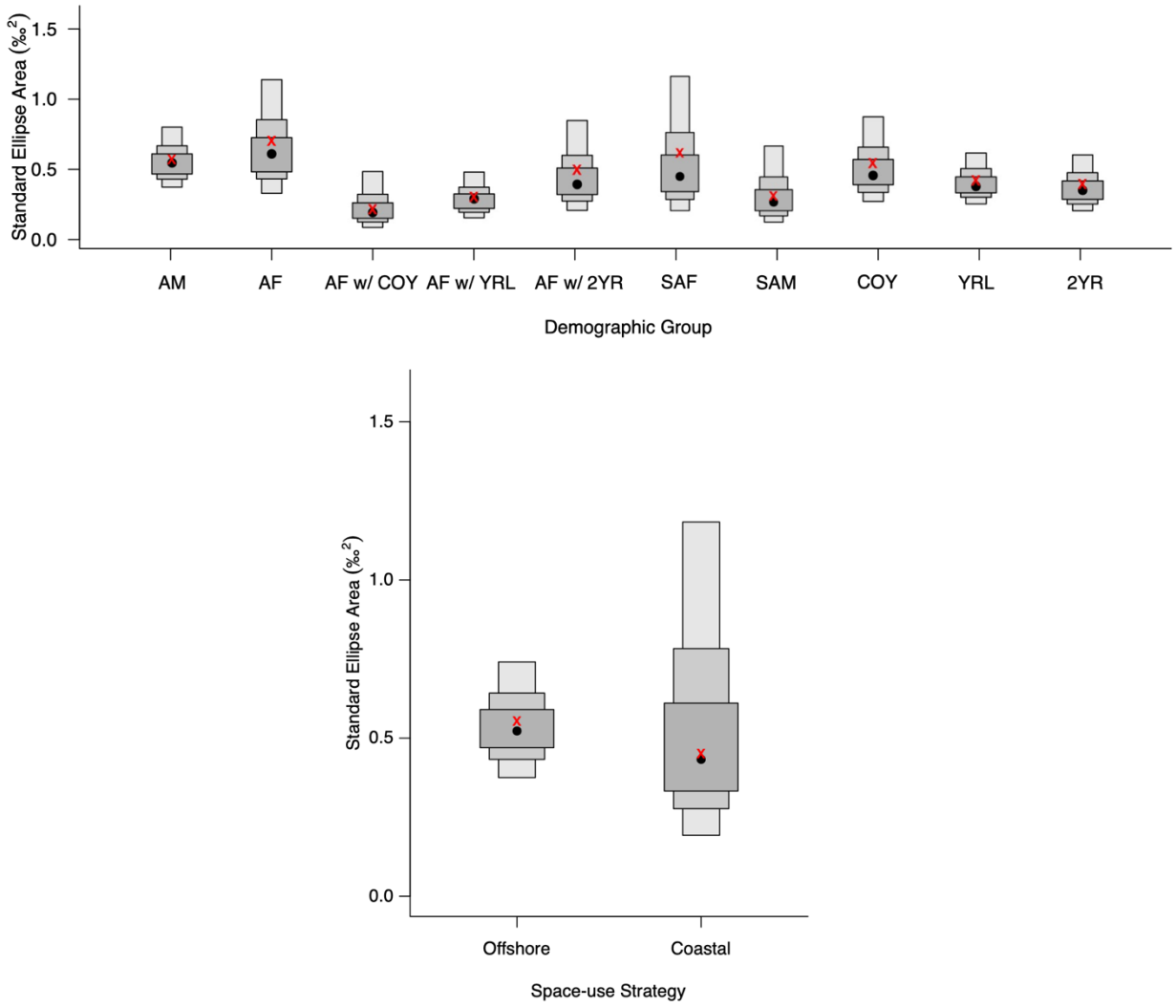

Figure S4.2 Density plot of the Bayesian estimates of the standard ellipse area [SEA_B] for each group (top panel) or space-use strategy (bottom panel). The mode SEA_B is represented by a black circle, the maximum likelihood estimate of the corrected standard ellipse area [SEA_c] is represented by a red x, and the 50, 75, and 95% credible intervals are represented as different shades of grey. Demographic groups are defined as follows: Adult Female (AF), Adult Male (AM), Subadult Female (SAF), Subadult Male (SAM), Cub-of-the-year (COY), Yearling (YRL), and 2-year-old (2YR).

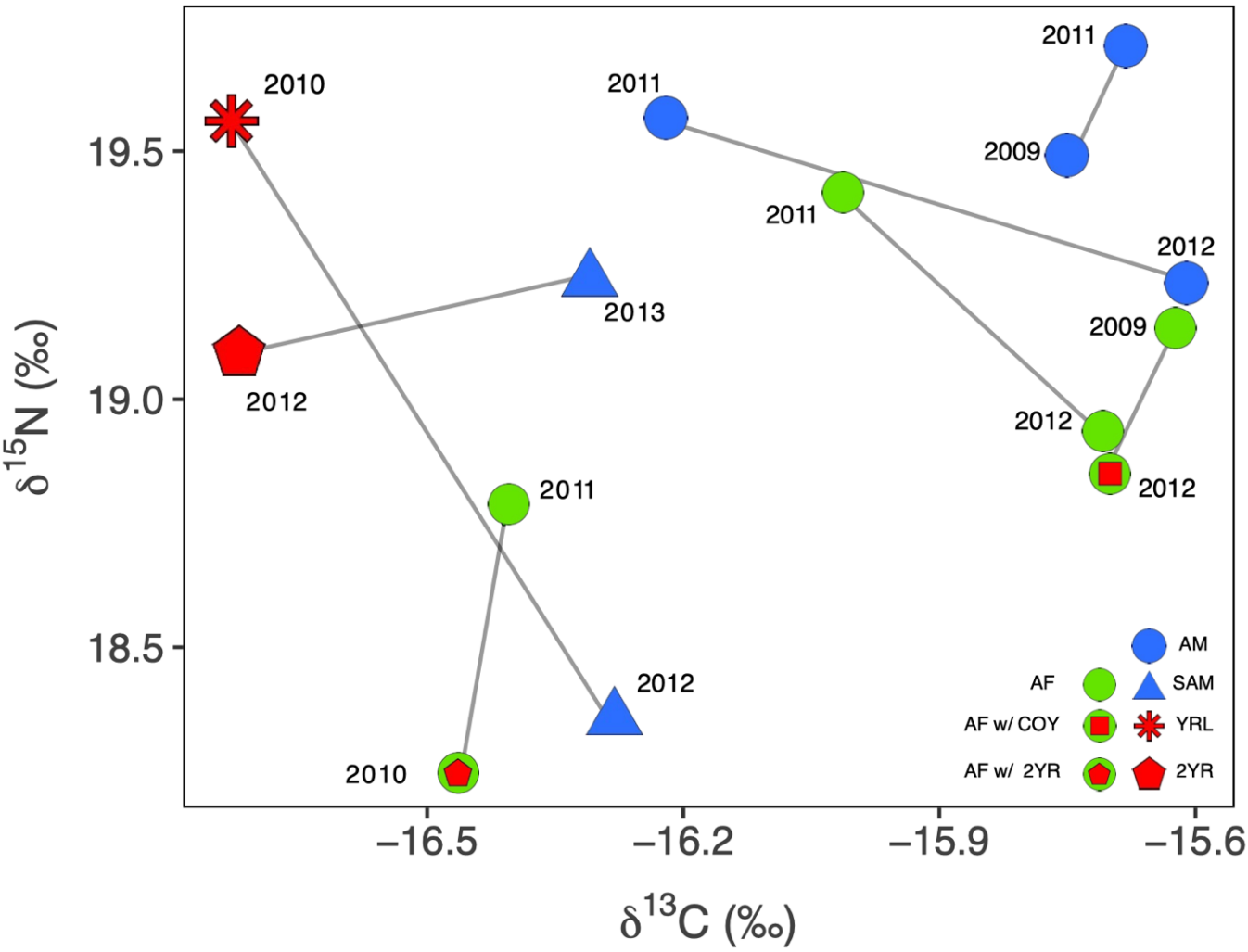

Figure S4.3 Biplot of guard hair $\delta^{13}C$ and $\delta^{15}N$ stable isotope values (‰) for individual bears that were captured and re-captured in the Baffin Bay (BB) polar bear (*Ursus maritimus*) subpopulation between 2009-2013. The demographic and reproductive status groups are defined as follows: Adult Female (AF), Adult Female with Cub-of-the-year (AF w/ COY), Adult Female with 2-year-old (AF w/ 2YR), Adult Male (AM), Subadult Male (SAM), Yearling (YRL), and 2-year-old (2YR).

Table S4.1 The equations used to estimate Total Body Mass (Derocher and Wiig 2002) and Body Condition Index (Cattet et al. 2002). The Body Condition Index was calculated for each bear using the TBM in kg and straight-line body length in cm.

	Equation	Variables	Source
Total Body Mass	$W\,(1- e^{-k(a-A)})^3$	a = age (years) W=asymptotic mass (kg) k=mass growth rate constant (years^{-1}) A= fitting constant (years)	(Derocher and Wiig 2002)
Body Condition Index	$\frac{\ln(TBM) - 3.07(\ln(SLBL)) + 10.76}{0.17+0.009(\ln(SLBL))}$	TBM = Total Body Mass (kg) SLBL = Straight-Line Body Length (cm)	(Cattet et al. 2002)

Table S4.2 The estimate and 95% confidence intervals for coefficients included in the model of best fit for guard hair $\delta^{13}C$, $\delta^{15}N$, and THg concentrations of Baffin Bay polar bears (*Ursus maritimus*), 2009 - 2013. The reference age class included in the intercept is Adult Female. Bold denotes that the confidence interval of the estimate does not overlap zero. The covariate abbreviation *OpenWater.lag* represents the open water period of the previous year (in days).

	$\delta^{13}C$		**$\delta^{15}N$**		**THg**	
	Class + *OpenWater.lag* + (1 | *Capture Year*)		*Class*		*Class*	
Variables	Estimate	Confidence Interval	Estimate	Confidence Interval	Estimate	Confidence Interval
(Intercept)	-14.5	**(-16.7, -12.3)**	18.9	**(18.6, 19.2)**	1.8	**(1.6, 1.9)**
Class (Adult Female with COY)	0.2	(-0.03, 0.5)	0.5	(-0.01, 0.9)	-0.1	(-0.4, 0.2)
Class (Adult Female with YRL)	-0.2	(-0.4, 0.03)	-0.4	(-0.7, 0.07)	0.1	(-0.1, 0.4)
Class (Adult Female with 2YR)	0.04	(-0.2, 0.3)	-0.3	(-0.8, 0.1)	0.2	(-0.1, 0.4)
Class (Adult Male)	0.1	(-0.1, 0.3)	0.5	**(0.1, 0.8)**	-0.01	(-0.2, 0.2)
Class (Subadult Female)	-0.2	(-0.5, 0.1)	-0.1	(-0.6, 0.4)	-0.2	(-0.5, 0.1)
Class (Subadult Male)	-0.2	(-0.5, 0.1)	-0.1	(-0.6, 0.4)	-0.3	**(-0.6, -0.02)**
OpenWater.lag	-0.01	(-0.02, 0.003)				

Table S4.3 Model selection to assess population and environmental variables affecting $\delta^{13}C$, $\delta^{15}N$ and THg of Baffin Bay polar bears (*Ursus maritimus*). Models are ranked by AIC_c, with $\Delta AIC_c \leq 2$ bolded. All models with $\Delta AIC_c < 4$ are shown.

Response	Rank	Model	df	AIC_c	ΔAIC_c	AIC_c Weight
$\delta^{13}C$	1	***Class + OpenWater.lag + (1 | Capture Year)***	10	54.8	0	0.256
	2	***Class + (1 | Capture Year)***	9	54.9	0.08	0.247
	3	***Class + BreakUp.lag + (1 | Capture Year)***	10	55.5	0.64	0.187
	4	*Class + IceExtent.lag* + (1 | *Capture Year*)	10	56.9	2.10	0.090
	5	*Class + IceArea.lag* + (1 | *Capture Year*)	10	57.1	2.27	0.082
	6	*BreakUp.lag* + (1 | *Capture Year*)	4	57.8	2.95	0.059
	7	*OpenWater.lag* + (1 | *Capture Year*)	4	58.5	3.65	0.041
	8	1 (null) + (1 | *Capture Year*)	3	58.6	3.81	0.038
$\delta^{15}N$	1	***Class***	8	131.4	0	0.243
	2	***Class + IceArea.lag***	9	131.6	0.26	0.214
	3	***Class + BreakUp.lag***	9	131.8	0.43	0.196
	4	***Class + IceExtent.lag***	9	131.9	0.50	0.189
	5	*Class + OpenWater.lag*	9	133.4	2.07	0.086
	6	*Class + FreezeUp.lag*	9	133.8	2.48	0.071
log(THg)	1	***Class***	8	35.4	0	0.330
	2	***Class + OpenWater.lag***	9	37.4	2.01	0.121
	3	***Class + FreezeUp.lag***	9	37.4	2.03	0.120
	4	*Class + BCI*	9	37.7	2.31	0.104
	5	*Class + BreakUp.lag*	9	37.9	2.50	0.095
	6	*Class + IceExtent.lag*	9	37.9	2.53	0.093
	7	*Class + IceArea.lag*	9	37.9	2.53	0.093
	8	1 (null)	2	39.4	3.98	0.045

Table S4.4 A) Mean guard hair $\delta^{13}C$ and $\delta^{15}N$ stable isotope values (‰) and mercury concentrations (μg g^{-1}) with standard deviations (SD), 95% confidence interval, and sample size (*n*) for each movement pattern in the adult female Baffin Bay (BB) polar bear (*Ursus maritimus*) subpopulation. B) Mean base and tip guard hair $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ stable isotope values (‰) and mercury concentrations (μg g^{-1}) with standard deviations (SD) and sample size (*n*) for each movement pattern in the adult female BB polar bear subpopulation. An outlier was excluded from the $\delta^{13}C$ and $\delta^{15}N$ stable isotope base and tip analyses. The 95% confidence intervals comparing base to tip segments and coastal base/tip to offshore base/tip are shown in the row and column margins, respectively; bold denotes significance, $\alpha = 0.05$.

A)

	Coastal *n* = 6	Offshore *n* = 36	Confidence Interval
$\delta^{13}C$	16.3 ± 0.6	16.2 ± 0.4	(-0.2, 0.7)
$\delta^{15}N$	19.1 ± 0.4	18.8 ± 0.5	(-2.3, 2.0)
THg	6.6 ± 2.1	6.7 ± 2.3	(-0.7,0.5)

B)

	Habitat	*n*	Base	Tip	
THg ± SD					
	Coastal	6	6.7 ± 2.0	6.5 ± 1.9	(-1.0, 0.6)
	Offshore	16	6.3 ± 2.4	6.8 ± 1.9	(-0.7,1.4)
			(-1.6, 2.7)	(-2.0, 2.0)	
$\delta^{13}C$ ± SD					
	Coastal	6	-16.4 ± 0.6	-15.9 ± 0.6	**(0.3, 0.8)**
	Offshore	21	-16.5 ± 0.4	-15.9 ± 0.3	**(0.4, 0.7)**
			(-0.6, 0.7)	(-0.6, 0.6)	
$\delta^{15}N$ ± SD					
	Coastal	6	19.0 ± 0.5	18.9 ± 0.6	(-0.3, 0.4)
	Offshore	21	18.8 ± 0.7	18.8 ± 0.6	(-0.3, 0.2)
			(-0.5, 0.6)	(-0.4, 0.7)	
$\delta^{34}S$ ± SD					
	Coastal	5	19.56 ± 0.5	20.6 ± 0.7	**(0.6, 1.5)**
	Offshore	7	19.8 ± 0.6	20.6 ± 0.8	**(0.7, 1.2)**
			(-1.0, 0.2)	(-1.1, 0.5)	

Table S4.5 Model selection to assess population and environmental variables affecting $\delta^{13}C$, $\delta^{15}N$ and THg of Baffin Bay adult female polar bears (*Ursus maritimus*). Models with a $\Delta AIC_c <$ 2 are shown through bolding, but only the top 5 models ranked by AIC_c are shown. An additional covariate (*Habitat)* was included and is derived from the satellite collar data (*i.e.*, coastal or offshore movement patterns).

Response	Rank	Model	df	AIC_c	ΔAIC_c	AIC_c Weight
$\delta^{13}C$	1	***OpenWater.lag***	3	40.0	0	0.366
	2	***BreakUp.lag***	3	41.4	1.44	0.178
	3	***FreezeUp.lag***	3	41.5	1.54	0.170
	4	**1 (null)**	2	41.5	1.56	0.168
	5	*OpenWater.lag + Habitat*	4	42.2	2.27	0.117
$\delta^{15}N$	1	***BreakUp.lag***	3	62.7	0	0.257
	2	***IceArea.lag***	3	62.8	0.09	0.246
	3	***IceExtent.lag***	3	63.5	0.78	0.174
	4	**1 (null)**	2	63.6	0.85	0.168
	5	***BreakUp.lag + Habitat***	4	63.8	1.02	0.154
THg	1	**1 (null)**	2	27.7	0	0.287
	2	***BCI***	3	27.9	0.16	0.266
	3	***IceExtent.lag***	3	28.9	1.25	0.154
	4	***IceArea.lag***	3	29.0	1.29	0.151
	5	***BCI + IceExtent.lag***	4	29.1	1.42	0.142

Table S4.6 The coefficient and 95% confidence intervals for the Pearson's product-moment correlation between log-transformed total mercury concentrations (THg) and CN stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) separated by adult sex and reproductive status of Baffin Bay polar bears (*Ursus maritimus*), 2009 - 2013. Bold denotes that the 95% confidence interval of the estimate does not overlap zero.

		$\delta^{13}C$ and THg		**$\delta^{15}N$ and THg**	
Class	*n*	Coefficient	Confidence Interval	Coefficient	Confidence Interval
Adult Female	10	**0.630**	**(0.088, 0.884)**	0.391	(-0.236, 0.788)
Adult Female with COY	5	**0.766**	**(0.0313, 0.963)**	0.431	(-0.477, 0.894)
Adult Female with YRL	12	0.019	(-0.517, 0.544)	**0.531**	**(0.0004, 0.828)**
Adult Female with 2YR	7	0.524	(-0.215, 0.881)	0.333	(-0.425, 0.817)
Adult Male	26	-0.0002	(-0.373, 0.373)	0.072	(-0.309, 0.434)

Chapter 5. SPACE-USE STRATEGIES DRIVE DIET COMPOSITION OF BAFFIN BAY POLAR BEARS

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5.1 ABSTRACT

Polar bears (*Ursus maritimus*) depend on sea ice to hunt their ice-associated prey. However, climate-induced sea ice loss is leading to changes in space-use strategies of polar bears, with bears in some subpopulations spending more time on land or selecting alternative habitats. One such documented alternative habitat is glacier ice, which provides year-round access to prey, although the feeding habits of polar bears using glacier ice relative to those following the retreating ice and/or seasonally moving onshore are not known. Here, we use adipose tissue from polar bears (n = 104) from the Baffin Bay subpopulation live-captured in Northwest Greenland during the springs of 2009 to 2013 to investigate dietary patterns between space-use strategies inferred from satellite telemetry data, while considering demographic and interannual variation. Using quantitative fatty acid signature analysis (QFASA) to generate diet estimates, ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) were estimated as the primary and secondary prey of Baffin Bay polar bears for all sex/age classes and sampling years, apart from a single anomalous year (2009) with a relatively high proportion of beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*). While demographic and short-term temporal variation was minimal, fatty acid signatures and QFASA-generated diet estimates clearly differed between polar bears using coastal and offshore space-use strategies. ‘Offshore’ adult

females, which make long-distance movements across the Baffin Bay pack ice, had high proportions of C22-chain length monosaturated fatty acids and diet estimates that included beluga, narwhal, harp (*Pagophilus groenlandicus*) and hooded seal (*Cystophora cristata*). 'Coastal' adult females which remain resident at glacier fronts in Northwest Greenland year-round, including during the sea ice-free season, consumed proportionally more ringed seals (+13%) and similar proportions of bearded seal, but essentially no beluga and narwhal or harp and hooded seal. Thus, space-use strategy is a driver of intrapopulation diet variability. As space-use strategies change with ongoing loss of sea ice habitat, our results suggest important ramifications for polar bear feeding patterns.

5.2 INTRODUCTION

Anthropogenic climate change is causing a decrease in the extent and seasonal duration of sea ice (Overland et al. 2019). Sea ice loss is expected to continue to decline at an accelerated rate (Stroeve & Notz 2018). As polar bears (*Ursus maritimus*) rely on sea ice to hunt their ice-associated prey, decreased sea ice equates to reductions in their traditional foraging habitat (Moore & Huntington 2008). To maximize access to prey in the reduced ice season, polar bears follow the receding sea ice edge or, in some subpopulations, move onto land or glacial fronts (PBSG [IUCN/SSC Polar Bear Specialist Group] 2018). Variation in polar bear feeding habitats and habits in response to reduced sea ice may be associated with geographic differences in sea ice conditions, the composition and status of regional prey populations, and ecosystem productivity (Rode et al. 2014, 2018, Hamilton et al. 2017).

Currently, polar bears are globally divided into 19 subpopulations which are pooled into four sea ice ecoregion types based on spatial-temporal sea ice dynamics and the responses of the polar

bear subpopulations to those patterns (Amstrup et al. 2008, Atwood et al. 2016a). In the divergent ice ecoregion, bears follow the sea ice as it retreats northward into the Arctic Basin, although some move onto land during the summer (Amstrup 2003, Atwood et al. 2016b). Polar bear subpopulations in the divergent ice ecoregion have increased their use of terrestrial habitat in recent years (Rode et al. 2015b, Atwood et al. 2016b). The Canadian Archipelago and convergent ice ecoregions are currently characterized by persistent multiyear sea ice, whereas the seasonal sea ice ecoregion is characterized by annual ice that melts entirely each year (Stirling & Archibald 1977, Derocher & Stirling 1990, Atwood et al. 2016a). In the seasonal ice ecoregion, polar bears are forced onto land and show limited or no terrestrial feeding until the sea ice reforms in the fall (Lunn & Stirling 1985, Amstrup 2003, Laidre et al. 2018a).

As one of five polar bear subpopulations within the seasonal sea ice ecoregion, Baffin Bay (BB) polar bears inhabit a region that is free of sea ice in the summer (Amstrup et al. 2008, Laidre et al. 2013, 2018ab). Typically, BB polar bears make long-distance movements across the pack ice from Northwest Greenland to spend their summers on land, largely on Baffin Island. With limited access to marine prey resources during summer, BB polar bears may fast for three or more months (Ferguson et al. 1997, Laidre et al. 2020a). This sea ice-free period in BB has increased by 12 days per decade since 1979 (Stern & Laidre 2016). Fewer ice-covered days may result in changing space-use strategies, such as more use of coastal habitats at glacier fronts (e.g., Laidre et al. 2022). The date of arrival to and departure from Baffin Island of 'offshore bears', those that cross the pack ice to over-summer on Baffin Island, closely correlates with the timing of sea ice retreat and advance (Laidre et al. 2013, 2020, SWG [Scientific Working Group to the Canada-Greenland Joint Commission on Polar Bear] 2016), such that time spent on land by BB polar bears has increased by over 30 days in the last few decades (SWG 2016, Laidre et al.

2018b). Yet, a subset of the BB bear subpopulation, which we refer to in this paper as 'coastal bears', do not follow the sea ice retreat and instead remain resident on the extensive glacial ice mélange in fjords or on land in Northwest Greenland (Born et al. 2011, SWG 2016, Laidre et al. 2020). This distinct space-use strategy of polar bears using glacier fjords has also been described for subsets of the Barents Sea (BS) subpopulation (Mauritzen et al. 2001, Freitas et al. 2012) and the newly identified Southeast Greenland subpopulation (Laidre et al. 2022). The use of this unique environment may increase with climate change in places where glacial ice is available to bears (Laidre et al. 2022), and thus it is essential to understand how diet composition of polar bears relates to coastal and offshore space-use strategies.

Stable isotopes analysis has been the primary tool to examine dietary patterns related to distinct coastal and offshore movement patterns within polar bear subpopulations (Rogers et al. 2015; Boucher et al. 2019; Blévin et al. 2020; Stern et al. 2021), but multiple methods are recommended to ensure reliable diet information (Bowen et al. 2013). Stern et al. (2021) detected no differences between coastal and offshore adult female BB polar bears in hair sample carbon, nitrogen, and sulfur stable isotope values and total mercury concentrations. The lack of difference may have been due to insufficient resolution of the tracers to distinguish fine-scale variation in foraging patterns. Alternatively, diets may not have been different during the spring-summer, the timescale likely represented by hair samples (Stern et al. 2021). Measurements from adipose tissue samples represent a period of time (weeks to months) closer to collection because fat has a higher turnover rate than hair (Kurle & Worthy 2002, Thiemann et al. 2022). The deposition of many fatty acids (FAs) in predator adipose tissue occurs in a predictable pattern with little modification (Budge et al. 2006), allowing the use of FAs as tracers of feeding patterns and food webs. Furthermore, the quantitative fatty acid signature analysis (QFASA) approach

can estimate the prey composition of a predator's diet by modeling the combination of different proportions of prey species that best match the observed predator FA signature after accounting for FA-specific patterns of metabolism (Iverson et al. 2004). Neither FA signatures nor QFASA has been applied to comparing the diets of coastal and offshore polar bears. Here, we investigated the feeding patterns of BB polar bears from 2009 to 2013 using adipose FA signatures collected in March-April each year and generated estimates of their diets using QFASA. We used satellite telemetry data of adult female bears to determine individual foraging area and space-use strategy. Our primary objective was to compare FA signature-based feeding patterns and diet estimates between polar bears that exhibit diverging space-use strategies, i.e., between coastal and offshore BB polar bears. We also examined FA patterns and diet estimates among demographic groups and across sampling years. Our study underscores the importance of understanding space use as a driver of diet variability.

5.3 MATERIALS AND METHODS

5.3.1 *Sample collection*

Subcutaneous adipose tissue samples were collected from the rump area of chemically immobilized BB polar bears (n = 110) using a 6 mm biopsy punch, leading to a full layer core. Polar bears were captured along the coast and up to ~150 km from the shore of Northwest Greenland in March and April 2009–2013 (see Laidre et al. 2020). Captured individuals were grouped into five age classes: cub-of-the-year (COY), yearling (YRL), 2-year old (2YR), ages 3−4 (subadult), and ages 5+ (adult). Ages for subadults and adults were determined from tooth cementum layers (*e.g.*, Hensel & Sorensen 1980), while COYs, YRLs, and 2YRs were aged from their size. Of the 2YRs (n = 10), three were captured without their mother. Movement data for

adult female bears (n = 39) were collected using Telonics TAW-4610H satellite radio collars (Laidre et al. 2018a b, 2020a). These data were used to differentiate habitat use and classify 'coastal' adult females (n = 6) that remained resident on the fast ice and glacial mélange near glacier fronts in Melville Bay and 'offshore' adult females (n = 31) that used large areas across the pack ice of BB (Figure 5.1; see Laidre et al. 2018a, 2020, Stern et al. 2021). Two captured adult females were not assigned to a space-use strategy because the collar did not fit the bear (n = 1), or satellite collar transmissions stopped after a single day (n = 1).

5.3.2 *Fatty acid analysis*

All adipose tissue samples were classified according to a visual extent of oxidation (McKinney et al. 2013, 2017). Lipid was extracted twice using 2:1 chloroform:methanol with 0.01 % butylated hydroxytoluene (BHT) as an antioxidant. Extracted FAs were derivatized to FA methyl esters (FAMEs) using the Hilditch reagent (0.5 N sulfuric acid in methanol) on a heating block at 100 °C for one hour. FAMEs were extracted and made to a final concentration of 50 mg/ml. Standard reference material (SRM) 1945, long-finned pilot whale (*Globicephala melas*) blubber, from the National Institute of Standards and Technology was extracted and derivatized with each batch of samples (n = 12). All FAME extracts and SRM 1945 were analyzed by gas chromatography with flame ionization detection (GC-FID). Peak identifications and quantification (as mass percent of total FAME) were performed using TotalChrom software (Version 6.3.2; PerkinElmer, Shelton, CT, USA) and were manually confirmed for each FA. The FAs are described with the nomenclature of X:YnZ, where X indicates the carbon chain length, Y denotes the number of double bonds, and Z indicates the position of the first double bond relative to the terminal methyl group. The relative percent difference of the renormalized FA mass percentages in SRM 1945 averaged 11% compared to the renormalized published values

(Kucklick et al. 2010). Because 22:6n3 is the FA monitored that is most subject to oxidative degradation, we examined 22:6n3 proportions together with the subjective oxidation class. We then excluded samples with 22:6n3 values below 1% from analyses to avoid including samples with biased FA signatures due to oxidation (McKinney et al. 2013) for a final sample size of 104 polar bears.

5.3.3 *QFASA diet modeling*

The QFASA method estimates the diet composition of a predator by modeling the combination of different proportions of prey species that best match the FA signature of each predator after accounting for FA-specific patterns of predator metabolism (Iverson et al. 2004). FA values were adjusted for differential metabolism and deposition using calibration coefficients derived from an American mink (*Neogale vison*) feeding trial, as done previously for polar bears (Thiemann et al. 2008). We used the Kullback–Leibler (KL) distance measure (Iverson et al. 2004) and computed QFASA diet estimates in R (version 3.4.1; (R Core Team 2017) using the qfasar package (Bromaghin 2017). QFASA analyses were done for all age classes except YRLs, as these dependent cubs were likely still nursing, resulting in a sample size of 87 polar bears. Summary statistics for all QFASA-generated estimates are reported as arithmetic means and standard deviations of the mean.

All prey species initially considered for inclusion in the model were collected from Baffin Bay or adjacent regions of East Greenland, Lancaster Sound, or Davis Strait between 1997 and 2018. We further refined the prey library by conducting a leave-one-prey-out (LOPO) analysis with the diagnostic function *lopo* in the qfasar package to cross-validate the prey library (Bromaghin 2017). The subsequent prey library included previously published values for 45 bearded seals (*Erignathus barbatus*; Davis Strait; collected from 1997-2003; Thiemann et al.

2008), 22 belugas (*Delphinapterus leucas*; Davis Strait, Lancaster Sound; collected from 2000-2001; Thiemann et al. 2008), 13 narwhals (*Monodon monoceros*; Baffin Bay, Lancaster Sound; collected from 1999-2001; Thiemann et al. 2008), and 9 ringed seals (*Pusa hispida*; Lancaster Sound; collected in 2018; Facciola et al. 2022), with 16 harp and hooded seals (*Pagophilus groenlandicus* and *Cystophora cristata*; East Greenland; collected in 2018; Land-Miller et al. 2023). Harbor seals (*Phoca vitulina*) were excluded as a potential prey item due to their low abundance in Greenland (Rosing-Asvid 2010); harbor seals were also excluded as a prey item in a recent study on BB polar bears (Galicia et al. 2021).

The LOPO analysis and the average of predator signatures outside of the prey signature space determined the final FA set to be used for QFASA estimation. We began with the 30 FAs considered to largely be of dietary origin (Iverson et al. 2004) (Table S5.1) and that were previously used to estimate the diet of BB polar bears by Galicia et al. (2015). We then reduced that set by retaining only those FAs of average mass percent > 0.1% in polar bear and prey samples to avoid introducing analytical error from low percentage FAs. This set of 18 retained FAs (Table S5.1), referred to hereafter as the 'full' dietary FA set, was used in preliminary diet estimations using the qfasar package (Bromaghin 2017) in R (version 3.4.1; (R Core Team 2017). After the initial run, we further refined the FA list by using the diagnostic function *pred_beyond_prey* in the qfasar package, which identifies the proportion of predator signatures beyond the range of the prey signatures (Bromaghin 2017). We then calculated the mean percentage of predator signatures out of range of the prey signatures for each FA. This resulted in the second set of 10 FAs (Table S5.1) used for modeling, referred to hereafter as the 'reduced' dietary FA set, in which at least 50% of the predator signatures overlapped with prey signatures.

This threshold was selected to minimize contributions to the KL distance measure by FAs outside the range of mean prey proportions (Bromaghin et al. 2015c).

5.3.4 *Statistical analysis of fatty acid signatures and diet estimates*

To evaluate differences in FA signatures and QFASA-generated diet estimates between diverging space-use strategies (coastal, offshore) of 37 radio-collared female polar bears, we used Welch's 2-sample *t*-tests adjusted with the false discovery rate controlling procedure described by Benjamini & Hochberg (1995). We ran a principal component analysis (PCA) for all adult females using the full dietary FA set in the FactoMineR package in R (Lê et al. 2008) to visualize the FA patterns of coastal versus offshore females. We further tested if the known space-use strategy could be correctly discerned using only FA signatures of radio-collared adult females and their associated YRLs by applying classification and regression trees (CART), following the methods of Iverson et al. (1997). We chose to examine associated YRLs as this age group likely remained close to their radio-collared mothers and provided the largest sample size (n = 17) of dependent cubs. To compare FA signatures and diet estimates between sex/age classes and sampling years, we ran permutational multivariate analyses of variance (PERMANOVAs) with both sex/age class and year as covariates in the vegan package in R (Oksanen et al. 2020). Further differences among age classes were examined using Tukey's Honest Significant Difference test. We used a significance level alpha of 0.05 for all comparisons. All statistics were done in R (version 4.0.3; R Core Team 2017).

5.4 RESULTS

5.4.1 *QFASA model inputs and diagnostics*

Diet estimates were generated using both the full dietary FA set (n = 18) and the reduced dietary FA set (n = 10) (Table S5.1). For both FA sets, the accuracy of identification of prey in the LOPO analysis was improved by grouping belugas and narwhals (referred to hereafter as beluga/narwhal) and grouping harp and hooded seals (referred to hereafter as harp/hooded seal). The subsequent LOPO analysis revealed that the prey species were generally well distinguished from one another with few misidentifications (Table S5.2) using either FA set. Nonetheless, the reduced dietary FA set showed higher accuracy in prey identifications than the full dietary FA set for beluga/narwhal (88% vs. 85%), harp/hooded seals (74% vs. 68%), and ringed seals (92% vs. 82%). The full FA set only outperformed the reduced set when identifying bearded seals (89% vs. 85%). Using the full FA set, 52% of polar bear FA signatures were outside the prey space in the *pred_beyond_prey* analysis. In contrast, only 28% of the polar bear FA signatures were beyond the prey signature space using the reduced dietary FA set. Based on these diagnostic outputs, the subsequently reported BB polar bear diet estimates are based on this reduced FA set.

5.4.2 *Diet estimates and fatty acid signatures of offshore and coastal space-use strategies*

The QFASA model estimated BB polar bear diets to consist of mostly ringed seals (55 ± 19%), supplemented with bearded seals (29 ± 10%) and small amounts of beluga/narwhal (10 ± 19%) and harp/hooded seals (6 ± 9%) (Table 5.1). Diet composition estimates by QFASA significantly differed between coastal and offshore adult female BB polar bears (Figure 5.2). Coastal adult females consumed proportionally more ringed seals than offshore adult females (70

± 6% vs. 57 ± 19%; p_{adj} = 0.007). Offshore adult females consumed a higher proportion of beluga/narwhal (8 ± 15%) and harp/hooded seals (8 ± 10%), as coastal adult females were estimated to consume little to none of these prey species (0 ± 0% and 1 ± 3%, respectively) (p_{adj} = 0.007). There were no significant differences in bearded seal consumption between coastal (29 ± 8%) and offshore (27 ± 10%) adult females (p_{adj} = 0.625).

Coastal and offshore adult females showed distinct FA patterns, which were primarily driven by differences in the proportions of three FAs. Offshore adult females had higher proportions of 22:1n7 (p_{adj} = 0.007) and 22:1n11 (p_{adj} = 0.01) than coastal adult females. Conversely, coastal adult females had higher proportions of 22:5n3 (p_{adj} = 0.04). Although the 95% confidence ellipses of dietary fatty acids fully overlap for coastal and offshore females in the PCA, coastal females are more tightly clustered than offshore females in multivariate space (Figure 5.3). The CART analyses correctly differentiated between coastal and offshore space-use strategies in adult females and their associated YRLs using FAs. Of the full dietary set of FAs considered for modeling, 22:1n11 explained the greatest deviance between groups. Thus 22:1n11 was chosen by the algorithm as the sole classifying variable in both analyses, with a FA proportion threshold of 0.025 in adult females and 0.021 in YRL cubs. Using only 22:1n11, CART correctly sorted 89% of adult females (33 out of 37 bears) and 94% of yearling cubs (16 out of 17 cubs) into their correct space use strategy.

5.4.3 *Demographic variation in diet composition and fatty acid signatures*

When diet composition was examined among demographic groups (n = 87; Table 5.1), we found no significant differences in estimated diets among sex/age classes (PERMANOVA, p = 0.205). Similarly, there were few significant differences in the FA proportions among BB polar bear demographic groups when coastal females were included in the analysis (PERMANOVA, p

= 0.04). Adult males showed lower proportions of 20:4n3 (p_{adj} = 0.007), 16:3n6 (p_{adj} = 0.041), and 21:5n3 (p_{adj} = 0.041) and higher proportions of 20:1n7 (p_{adj} = 0.041), 22:1n7 (p_{adj} = 0.041), and 22:1n9 (p_{adj} = 0.041) than adult females w/ YRL. Lastly, the proportions of 22:1n9 were higher in adult males compared to 2YRs (p_{adj} = 0.041). However, there were no significant differences when FA proportions were compared among BB polar bear demographic groups (PERMANOVA, p = 0.111). with all known coastal bears removed (n = 7: 2 adult females, 2 adult females w/ YRL, 1 adult female w/ 2YR, 1 adult female w/ COY, and 1 2YR).

5.4.4 *Temporal patterns in diet composition and fatty acid signatures*

QFASA-generated results showed that consumption across prey types was consistent from 2010 to 2013 for all sex/age classes but differed and was more variable in 2009 (Figure 5.4; PERMANOVA, p < 0.001). Mean ringed seal consumption was estimated at 58 ± 17% in 2010-2013, but 34 ± 26% in 2009, while mean consumption of beluga/narwhal in 2009 was estimated at 6% ± 12% in 2010-2013, but 43 ± 31% in 2009. Bearded seal and harp/hooded seal consumption were similar across all years. FA signatures for all sex/age classes significantly differed across the five sampling years of 2009 - 2013 (PERMANOVA, p = 0.01), with proportions of eight FAs (18:2n6, 18:3n3, 18:3n4, 18:4n3, 20:4n3, 21:5n3, 22:5n3, 22:6n3) being different (p_{adj} < 0.05) in 2009 relative to all other years.

Polar bears recaptured after periods of 1-3 years showed some apparent interannual variation in QFASA-generated diet estimates, although statistical analyses could not be performed due to low sample size (Figure S5.1). Among the recaptured bears (n = 5), one adult female that was solitary in 2009, but was resampled with COY in 2012, qualitatively showed the largest diet difference after resampling. This adult female increased proportional harp/hooded seal consumption by 40% and decreased beluga/narwhal consumption by 52%.

5.5 DISCUSSION

Ringed seals were estimated to be the primary prey, followed by bearded seals, for Baffin Bay polar bears of all sex/age classes and sampling years, apart from a single anomalous year (2009) with higher dietary proportions of beluga/narwhal. Nonetheless, both FA signatures and QFASA diet estimates indicated distinct feeding habits between polar bears using coastal versus offshore space-use strategies. Offshore adult females had higher proportions of 22-carbon chain length monounsaturated FAs (MUFAs) and were estimated to consume more beluga/narwhal and harp/hooded seal. Conversely, coastal adult females consumed proportionally more ringed seals than offshore females and almost no beluga/narwhal and harp/hooded seal. Thus, space-use strategy is an important driver of intrapopulation diet variability in this rapidly changing environment, with potentially important implications for understanding climate impacts on polar bear physiology and body condition.

5.5.1 *QFASA estimates are sensitive to prey libraries and fatty acid sets*

Our results corroborate the sensitivity of diet estimates to the particular FA set and prey library used in QFASA modeling (Bromaghin et al. 2015ab). Prey libraries in QFASA analyses are often collected from a larger geographic area than the predator samples (e.g., McKinney et al. 2013, Galicia et al. 2015, Florko et al. 2020); in our case, the prey library did not fully overlap with the spatial and temporal distribution of the BB polar bears. The spatiotemporal mismatch could bias diet estimations and may play a role in polar bear signatures lying partially beyond the prey signature space. The reduced dietary FA set had 24% more overlap between polar bear and prey than the full FA set. More research is needed to refine the selection of FA sets to improve

the accuracy of QFASA (Zhang et al. 2020). The difference in the overlap of FA signatures between predator and prey from 18 FAs to 10 FAs for this polar bear subpopulation highlights the particular FA set chosen as a critical area for ongoing refinement of the approach. Still, the FA signature approach provided insight into feeding differences between space-use strategies that were not found by other, lower-resolution tracers (Stern et al. 2021). Thus, multiple approaches are necessary to understand the variability of predator diets.

5.5.2 *Diet diverges between offshore versus coastal space-use strategies*

We found distinct adipose FA signatures between the telemetry-based coastal and offshore space-use strategies established in previous studies (Laidre et al. 2018a, 2020a). Offshore females showed strong links to the *Calanus*-based offshore food web with higher proportions of C22-chain length (22:1n7 and 22:1n11) MUFAs, which are synthesized by calanoid copepods (Kattner & Hagen 1995). Coastal females instead showed FA signatures relatively enriched in long-chain polyunsaturated FAs (LCPUFAs; 22:5n3, specifically), which are synthesized by diatoms (Baird 2022). MUFAs have been suggested to be better fuel sources than LCPUFAs because they produce more net energy when oxidized, whereas LCPUFAs have been hypothesized to be of physiological significance at the cellular level and serve as proxies for high-quality food (Sargent et al. 2003, Baird 2022). Offshore females that use energy while moving hundreds of kilometers on sea ice across Baffin Bay may benefit from metabolically accessible energy stores while seeking alternative prey. Coastal females, which have a much more restricted movement pattern, may have more consistent access to high-quality, energy-rich prey. Similar use of glacier fronts in Svalbard female polar bears has been hypothesized to provide access to predictable prey and for energy conservation (Freitas et al. 2012, Blanchet et al. 2020). The glacial habitat in southeast Greenland provides year-round access to ringed seals

and has supported a few hundred polar bears to persist for at least the last 200 years (Laidre et al. 2022).

The CART results further supported using 22-carbon length MUFAs, specifically 22:1n11, as representative tracers of space-use strategy. The present study successfully distinguished coastal and offshore adult females and YRLs using only 22:1n11. The FA proportion threshold for sorting the two space-use strategies was similar between the two age classes. While these results indicate that offshore adult females are feeding in *Calanus*-based offshore food webs, this analysis demonstrates that the offshore link is also detectable for dependent young. Calanoid FA tracers have been used to infer offshore feeding in Arctic cod, *Boreogadus saida* (Kelley et al. 2010), belugas (Choy et al. 2020), Greenland sharks, *Somniosus microcephalus* (McMeans et al. 2012), pagophilic phocid seals (Cooper et al. 2009), and northern fulmars, *Fulmarus glacialis* (Dahl et al. 2003). Smith et al. (1996) similarly used 22:1n11 to infer the feeding patterns of a freshwater harbor seal population from its marine counterparts.

The QFASA diet estimates, which complement the FA signature results, suggested the same divergence of feeding patterns for offshore and coastal adult females despite a reduced set of FAs. Ringed seals were estimated to be consumed proportionally more often by coastal females, which is consistent with observations of their availability as a prey item on the glacial fronts in Melville Bay (Born et al. 1999, Laidre et al. 2020a). Despite lower dietary proportions, offshore females also have access to large populations of ringed seals associated with the pack ice (Finley et al. 1983). Ringed seals living on glacial fronts have shown blubber enriched in LCPUFAs (McMeans et al. 2012), a finding that aligns with the LCPUFA-enriched coastal female polar bears in this study. Offshore females consuming higher proportions of beluga/narwhal using QFASA is also aligned with the FA signature results; similar to the MUFA-enriched offshore

females, belugas in the Beaufort Sea ecosystem were found to have enriched levels of 22-carbon length MUFAs in their blubber (Choy et al. 2020). The availability of beluga/narwhal and harp/hooded seals is higher in the pack ice as compared to the nearshore areas (Finley et al. 1990, Richard et al. 1998, Laidre et al. 2004, Andersen et al. 2009), which may have contributed to the higher proportions of alternative prey in the diet of offshore females. The higher proportion of alternative prey may also be a signal that offshore bears are eating less overall, a scenario illustrated by concurrent increases in dietary proportions of beluga and a decline in energy density for Southern Beaufort polar bears during periods of low bear survival (Rode et al. 2022).

5.5.3 *Few demographic differences in fatty acid signatures and diet estimates*

We did not identify demographic differences, as measured by sex and age class, in QFASA diet estimates for BB polar bears. In previous work, QFASA-generated diet estimates for 56 subsistence-harvested BB polar bears in 2010-2012 showed variation with both sex and age class (Galicia et al. 2015). Thiemann et al. (2008) reported QFASA-generated diet estimates for 101 BB polar bears in 1999-2004 differed by age class but not by sex. The lack of difference in diet estimates across demographic groups found in our study in contrast to these previous studies may be attributable to a different sampling period, year, or location; bears in these previous studies were primarily sampled by hunters on Baffin Island during fall, winter, and spring harvest and capture seasons (Thiemann et al. 2008, Galicia et al. 2015), which may lead to differences as many prey species vary spatially and temporally throughout the region. The present study represents a finer resolution of BB polar bear diet specific to a single season with an explicit consideration of bears that do not travel to Baffin Island. Prey library differences may have also contributed to differences between the studies. Both Galicia et al. (2015) and Thiemann et al.

(2008) included harbor seals as potential prey items, whereas Galicia et al. (2021) excluded harbor seals from the BB prey library. QFASA-generated diet estimates in the present study showed large individual variability within each demographic group (see Table 5.1); this variability suggests other factors, such as space-use strategy, may be driving dietary differences within groups.

The differences in adipose FA signatures between adult females with YRL and adult males were influenced by the inclusion of coastal females. The higher proportions of C20- and C22-chain length (20:1n7, 22:1n7, 22:1n9) monounsaturated FAs in adult males may indicate some similarities to the wider space use and more diverse feeding patterns of offshore adult females, which aligns with satellite telemetry data (Laidre et al. 2013). Similar to coastal females, adult females with dependent cubs have been shown to occupy a smaller area and rely heavily on ringed seals (Stirling et al. 1993, Freitas et al. 2012).

5.5.4 *Single anomalous year for diet composition across sampling year*

Overall, ringed seals were the primary prey for BB polar bears for all sampling years, apart from a single anomalous year in 2009. In 2009, BB polar bear diet for all sex/age classes was 43% beluga/narwhal compared with the mean of 6% from 2010-2013. Sea ice conditions are a possible cause of the 2009 anomaly in diet composition. However, the open water period and sea ice maximum (March) extent/area values in 2008 were close to the 5-year average for the lagged timeline of sea ice conditions. This study is unable to account for non-averaged climate or ice conditions or variability on a fine spatial scale. The factors driving increased dietary proportions of beluga/narwhal could be attributed to unusual entrapment events of beluga/narwhal or variation in overall availability during annual whale migrations (Heide-Jørgensen & Acquarone 2002, Heide-Jørgensen et al. 2003, Laidre et al. 2012). It is also possible that the high

proportions of beluga/narwhal indicate that the energy density of the diet decreased during this year (Rode et al. 2022). A high proportion of beluga whales, similar to this study's estimate in 2009, was estimated by QFASA in previous studies of BB polar bears (Thiemann et al. 2008, Galicia et al. 2015, 2021), as well as in other subpopulations (Florko et al. 2021, Galicia et al. 2021).

5.6 CONCLUSIONS

We demonstrate that FAs can be used as high-resolution feeding tracers that allow for an in-depth investigation of space-use strategy as a driver of diet. Our results reveal differences in the FA signatures and QFASA-generated diet estimates between coastal polar bears using glacier fronts and offshore bears using pack ice habitat. This finding contrasts with the lack of differences found between coastal and offshore adult females in hair sample carbon, nitrogen, and sulfur stable isotope values and total mercury concentrations during spring - summer by Stern et al. (2021). The combined use of FA signatures and QFASA-generated estimates emphasized the relative importance of space-use strategy as compared to demographic and temporal variation in influencing BB polar bear feeding patterns. As the open-water period becomes longer and sea ice travel platforms disappear, the implications of prey availability in coastal and offshore habitats will become increasingly important to manage and conserve polar bears effectively.

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5.8 DATA AVAILABILITY

The polar bear fatty acid data are available from Figshare: https://doi.org/10.6084/m9.figshare.24312622.

5.9 FIGURES

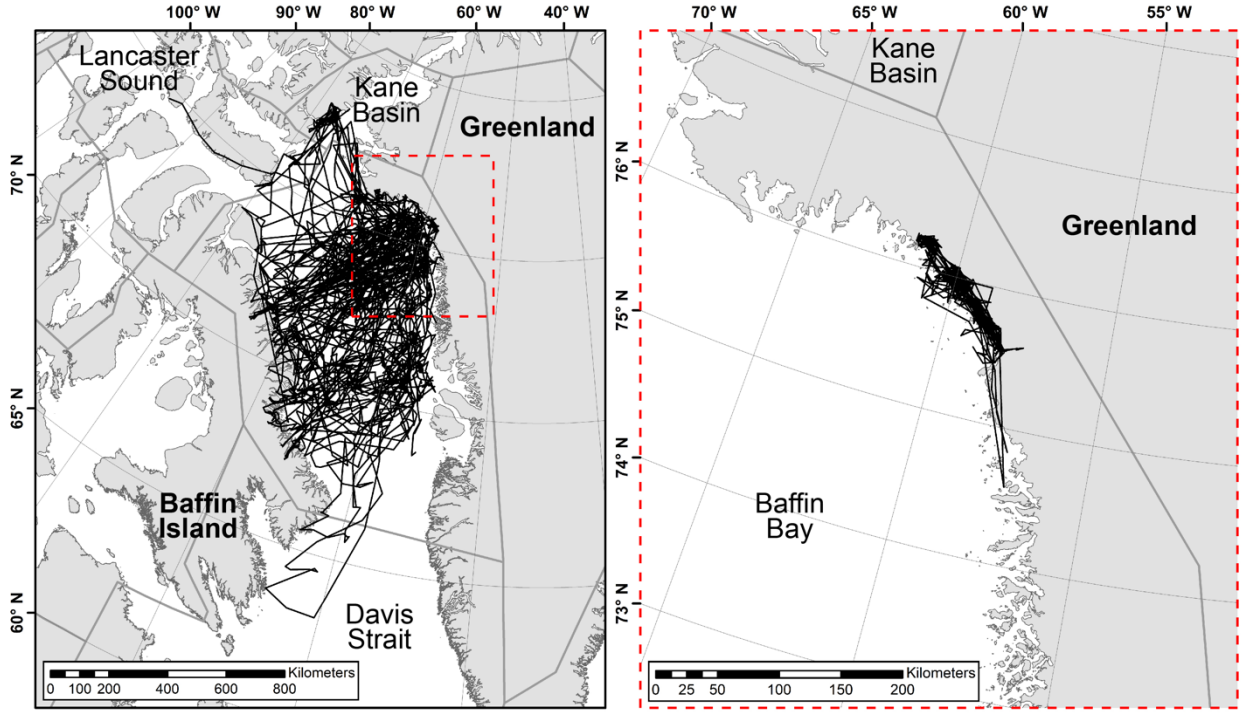

Figure 5.1 Adult female polar bears (n = 37) from the Baffin Bay subpopulation were fitted with Telonics TAW-4610H satellite radio collars in 2009–2013 to collect movement data. These data were used to differentiate between 'offshore' adult females (n = 31; left panel) that used larger areas across the pack ice of Baffin Bay and 'coastal' adult females (n = 6; right panel) that remained resident on the fast ice and glacial mélange in Melville Bay, Greenland. The dashed red line in the left panel denotes the area represented in the right panel.

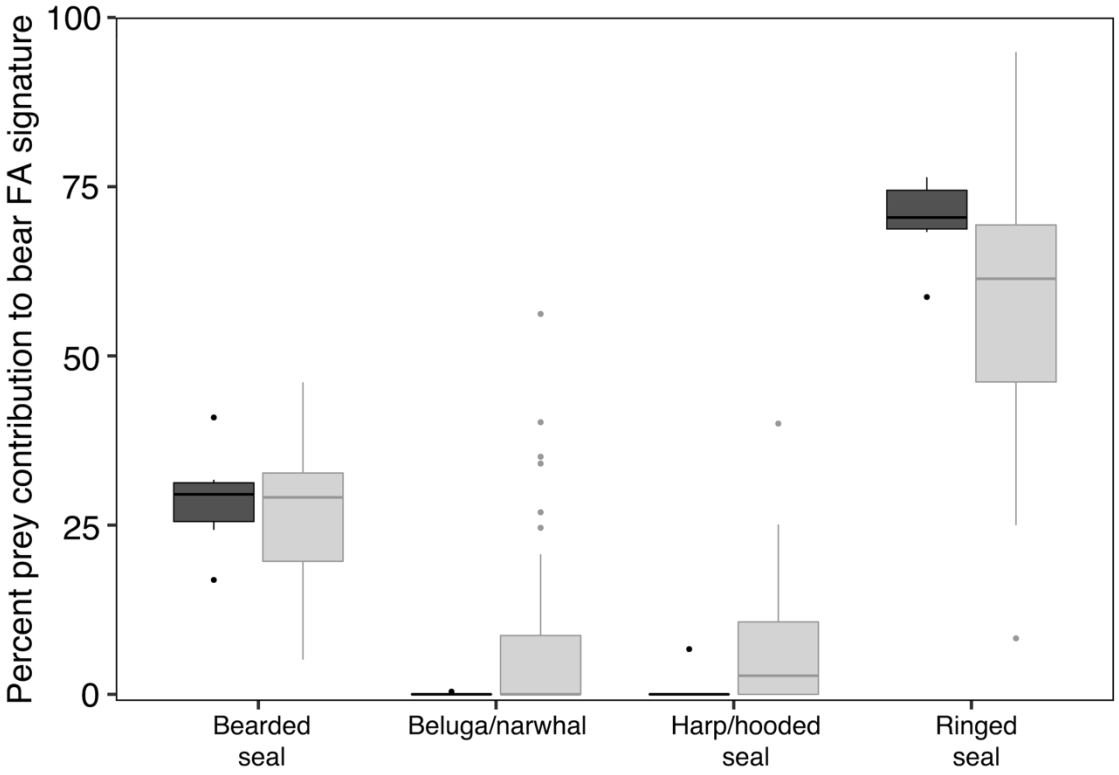

Figure 5.2 Percent diet composition estimated using quantitative fatty acid signature analysis (QFASA) for coastal (black; n = 6) and offshore (gray; n = 31) adult female Baffin Bay polar bears (n = 37) tracked with satellite collars in 2009–2013. The boxplots show the 25th quartile, median, 75th quartile, and outlying points.

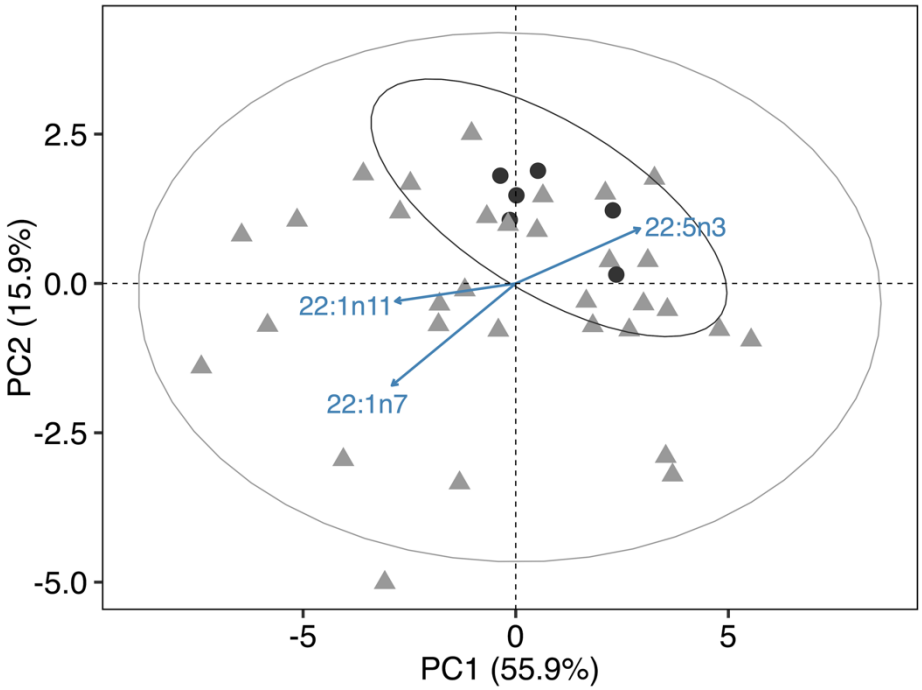

Figure 5.3 Principal Components Analysis and 95% confidence ellipses of full dietary fatty acid (FA) set in coastal (black circle; n = 6) and offshore (gray triangle; n = 31) adult female Baffin Bay polar bears. The only loadings displayed correspond with the FAs that significantly differed between coastal and offshore female polar bears (22:1n7, 22:1n11, and 22:5n3).

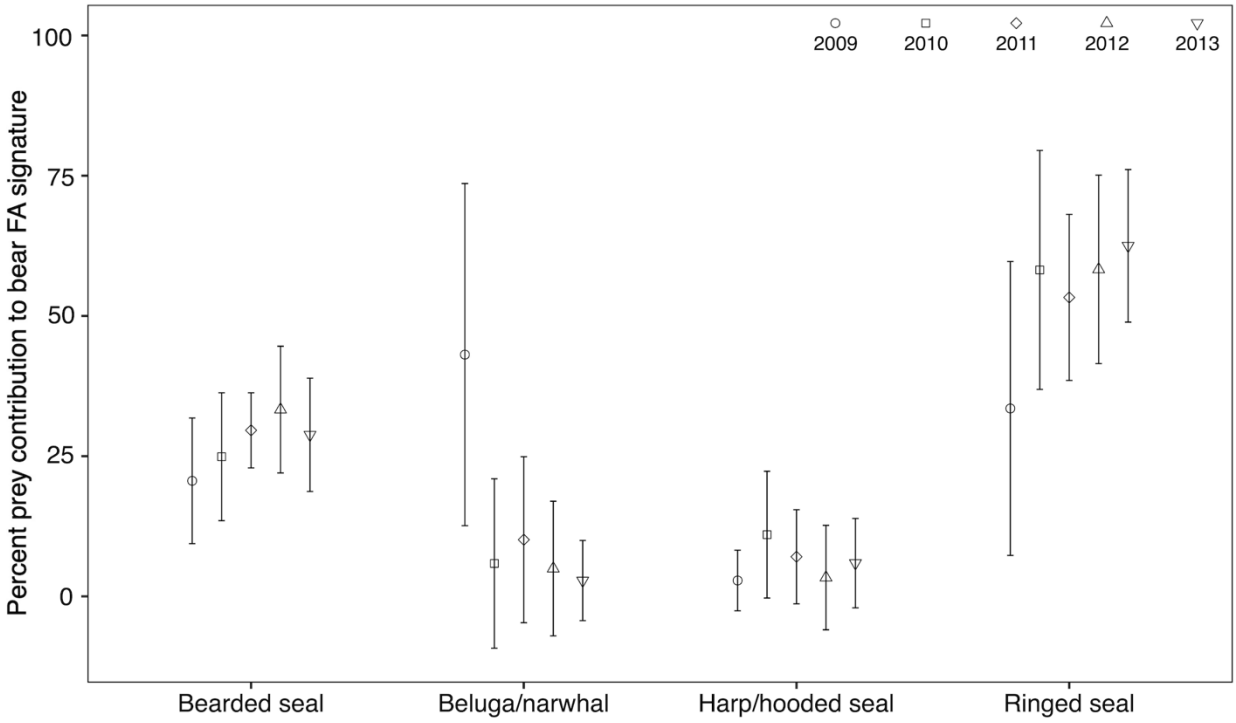

Figure 5.4 Temporal trends in polar bear diet composition estimated using quantitative fatty acid signature analysis (QFASA) as mean ± standard deviation (%) for adult, subadult, and 2-year-old Baffin Bay polar bears of both sexes captured in 2009 – 2013.

5.10 TABLES

Table 5.1 Sample size for different age/sex classes and family groups of Baffin Bay polar bears sampled in 2009–2013. Prey composition ± standard deviation (%) was estimated using quantitative fatty acid signature analysis (QFASA), and the minimum and maximum percent prey contributions are included in parentheses.

Age Class	**Sample Size**	**Percent prey contribution to bear FA signature ± SD (MIN, MAX)**			
		Ringed seal	Bearded seal	Beluga/ narwhal	Harp/ hooded seal
Adult Female	10	64 ± 12 (41, 76)	29 ± 3 (22, 33)	5 ± 10 (0, 27)	2 ± 4 (0, 11)
Adult Females with COY	8	48 ± 21 (8, 75)	32 ± 12 (16, 46)	10 ± 20 (0, 56)	10 ± 16 (0, 40)
Adult Female with YRL	14	64 ± 16 (29, 95)	23 ± 12 (5, 44)	4 ± 9 (0, 34)	9 ± 9 (0, 25)
Adult Female with 2YR	7	56 ± 19 (25, 75)	30 ± 6 (20, 38)	11 ± 18 (0, 40)	3 ± 3 (0, 7)
Adult Male	24	47 ± 20 (0, 82)	33 ± 10 (10, 55)	15 ± 22 (0, 81)	5 ± 7 (0, 26)
Subadult Female	6	59 ± 19 (29, 81)	24 ± 12 (13, 45)	8 ± 13 (0, 26)	9 ± 9 (0, 20)
Subadult Male	8	55 ± 17 (31, 84)	27 ± 11 (12, 49)	8 ± 17 (0, 47)	10 ± 13 (0, 38)
2YR	10	57 ± 23 (3, 88)	25 ± 11 (1, 38)	13 ± 30 (0, 96)	5 ± 8 (0, 22)
Overall	87	55 ± 19	29 ± 10	10 ± 19	6 ± 9

Note: Dependent cubs are denoted as cub-of-the-year (COY), yearling (YRL), or 2-year old (2YR).

5.11 SUPPLEMENTAL MATERIALS

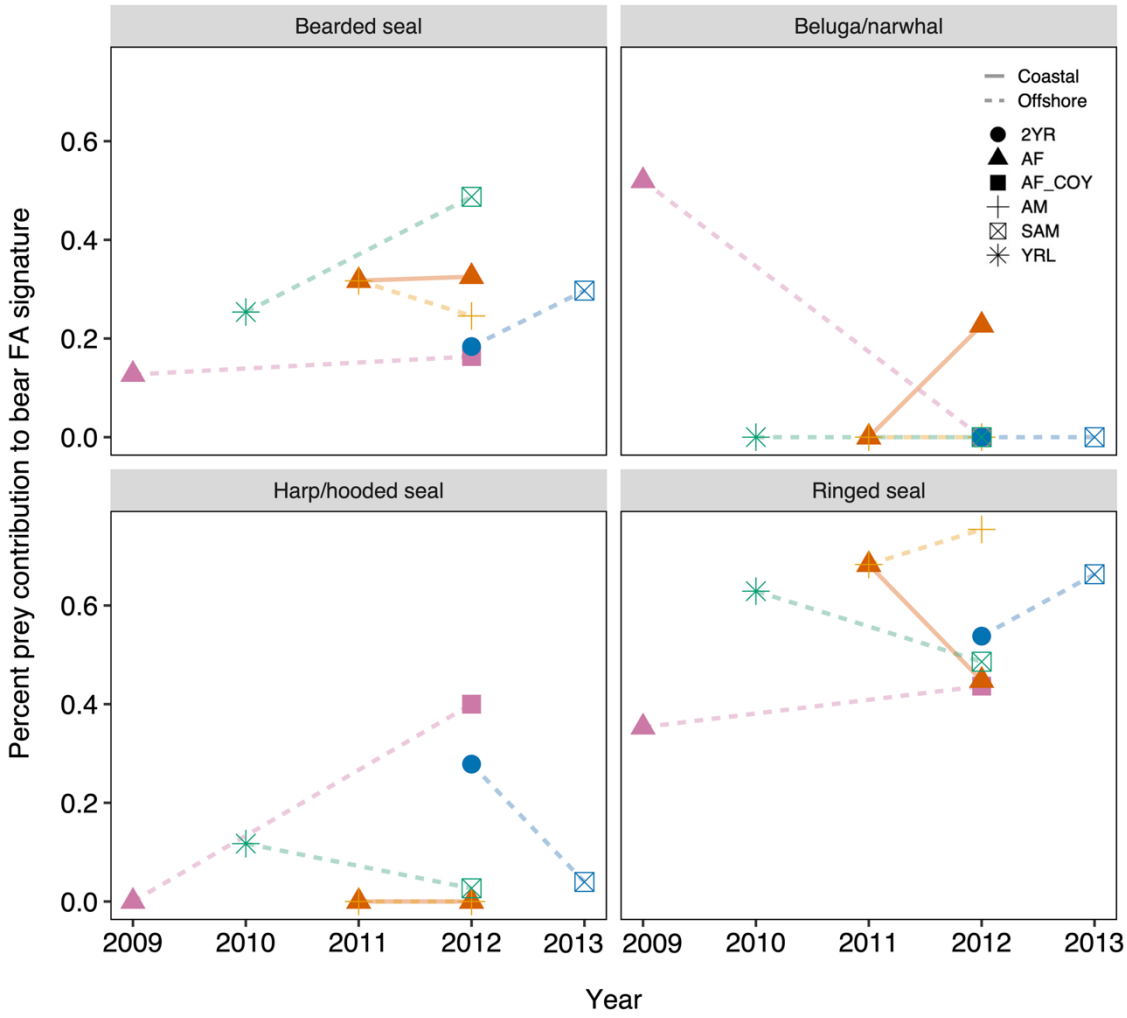

Figure S5.1 Interannual variation between prey consumption estimates for Baffin Bay polar bears (n = 5) recaptured after periods of 1-3 years. Each recaptured bear is represented by a different color and is connected by a line, either dashed (offshore habitat use) or solid (coastal habitat use). Demographic groups are defined as adult female (AF), adult male (AM), subadult male (SAM), 2-year old (2YR), yearling (YRL), and cub-of-the-year (COY).

Table S5.1 Average (± standard deviation) FA signatures (mass % of total FAME) for adipose tissues of adult, subadult, and 2-year-old Baffin Bay polar bears of both sexes collected in 2009–2013 (n = 87). The table includes the 30 dietary FAs used previously to estimate the diet of BB polar bears by Galicia et al. (2015). Bolded values indicate 18 FAs with an average mass percent > 0.1% in both polar bear and prey samples. Asterisk (*) indicates 10 FAs included in the reduced FA set used in the QFASA modeling.

Dietary FAs	Mean % ± SD
Polyunsaturated FAs (PUFAs)	
16:2n6	0.02 ± 0.01
***16:2n4**	0.13 ± 0.03
***16:3n6**	0.24 ± 0.09
16:3n4	0.03 ± 0.01
16:4n3	0.11 ± 0.02
16:4n1	0.04 ± 0.03
***18:2n6**	1.31 ± 0.19
18:3n6	0.02 ± 0.01
***18:3n4**	0.12 ± 0.05
18:3n3	0.44 ± 0.09
18:3n1	0.04 ± 0.01
***18:4n3**	0.36 ± 0.23
18:4n1	0.07 ± 0.04
***20:2n6**	0.23 ± 0.04
20:3n6	0.09 ± 0.02
***20:4n6**	0.17 ± 0.09
20:3n3	0.05 ± 0.01
20:4n3	0.31 ± 0.111
20:5n3	1.36 ± 1.02
***21:5n3**	0.19 ± 0.06
22:4n6	0.09 ± 0.03
22:5n6	0.10 ± 0.03
22:4n3	0.06 ± 0.01
***22:5n3**	4.46 ± 1.09
22:6n3	5.37 ± 2.06
Monounsaturated FAs (MUFAs)	
20:1n9	16.07 ± 3.204
***20:1n7**	1.23 ± 0.23
22:1n11	3.60 ± 1.21
22:1n9	1.20 ± 0.36
22:1n7	0.15 ± 0.05

Table S5.2 Leave-one-prey-out (LOPO) simulations for the prey library groups used to estimate the diets of adult, subadult, and 2-year-old Baffin Bay polar bears: bearded seal, beluga/narwhal, harp/hooded seal, and ringed seal. All prey samples were collected between 1997 and 2018. Bolded values represent the percent of prey correctly identified, and row values identify the percentage of misidentification as other prey groups.

Full Dietary FA Set

	Bearded seal	Beluga/ narwhal	Harp/hooded seal	Ringed seal
Bearded seal	**89%**	2%	5%	5%
Beluga/narwhal	3%	**85%**	10%	3%
Harp/hooded seal	11%	9%	**68%**	11%
Ringed seal	9%	4%	5%	**82%**

Reduced Dietary FA Set

	Bearded seal	Beluga/ narwhal	Harp/hooded seal	Ringed seal
Bearded seal	**84%**	4%	5%	6%
Beluga/narwhal	5%	**88%**	3%	5%
Harp/hooded seal	4%	12%	**74%**	10%
Ringed seal	1%	5%	2%	**92%**

Chapter 6. CONCLUSIONS

6.1 SUMMARY OF CONTRIBUTIONS TO THE FIELD

This dissertation addresses knowledge gaps in bear feeding ecology by bridging experimental and applied research to improve the accurate interpretation of hair samples and to provide insight into the ecological and environmental factors driving diet variability in wild polar bears. My collaborators and I began by developing two methods to document hair growth in black, grizzly, and polar bears: 1) applying a small patch of hair dye (or bleach) on the rump or foreleg, and 2) feeding an isotopically labeled glycine capsule that 'marks' time at a particular location as it is incorporated within the hair. We found that both methods detected individual and seasonal variation in hair growth rates, and the effectiveness of these methods was not dependent on the bear species. After validating these methods, we expanded this project into a systematic experimental approach on captive bears to complete the first comprehensive study on polar bear hair growth rates and timing. Our results showed that hair growth was detected in all seasons, with comparable hair growth rates across spring, summer, and fall, and slower growth rates during winter. These results were consistent with expected hair growth patterns in wild bears associated with an annual molt. Together, results from Chapters 2 and 3 inform our understanding of hair growth across three bear species and how this fine-scale information can be extrapolated to inform applied research in wild bear populations.

For Chapters 4 and 5, my collaborators and I used dietary tracers from two distinct tissues collected from the wild subpopulation of Baffin Bay polar bears to elucidate their feeding habits. We evaluated feeding patterns using stable isotopes and mercury in hair as tracers in wild polar bears with distinct coastal and offshore space-use strategies, and found no differences between carbon, nitrogen, and sulfur stable isotope values and total mercury concentrations between the

two movement patterns. Our results suggested limited variation in feeding habits among Baffin Bay polar bears despite wide fluctuations in inter-annual sea ice conditions. We also showed that habitat tracers, specifically carbon and sulfur stable isotopes, vary between the base and tip hair segments and thus fluctuate over the timescale proportional to the tissue growth rate. Next, we evaluated patterns of diet composition among Baffin Bay polar bears with distinct coastal and offshore space-use strategies using fatty acid signatures in fat samples, a tissue representing a different time period (winter-fall) than hair (spring-summer). Our analysis of fatty acid signatures revealed a difference in diet between coastal polar bears using freshwater glacier fronts and offshore bears using pack ice habitat, a distinction not observed in the timescale represented by hair. Ringed and bearded seals were the primary and secondary prey for all sex/age classes of Baffin Bay polar bears in sampling years, apart from a single anomalous year in 2009. Detailed studies of polar bear foraging using multiple tracers are necessary for a comparative and predictive understanding of how diets may change with a loss of sea ice habitat and increased use of coastal habitats. As sea ice continues to decline throughout the Arctic, understanding the intersection of sea-ice metrics, movement patterns, and resource use for a subpopulation that undergoes a completely ice-free season is increasingly important.

6.2 FUTURE RESEARCH DIRECTIONS

In this dissertation, my collaborators and I present the first assessment of hair dye/bleach and labeled-glycine methods for estimating seasonal hair growth rates, and the first comprehensive study on hair growth rates and timing in polar bears. We also provide the first quantitative data describing hair growth in black bears and strong seasonality of growth. Since the estimated hair growth rates for grizzly bears have either focused on a single rate for the entire growth period

(Mowat et al. 2017) or have been limited to specific seasons (Felicetti et al. 2004, Erlenbach 2020), variations in hair growth across body regions and throughout the year have not yet been explored. Thus, a comprehensive study on hair growth rates for black and grizzly bears across body regions and seasons is warranted. Further research is also needed to identify drivers of variation in polar bear hair growth rates and timing. With adequate sample sizes, studies measuring hair growth rates should consider factors that are thought to influence molt, such as sex, age, reproductive class, latitude, and food availability (Schwartz et al. 2003, Macbeth et al. 2010). A more comprehensive understanding of the causes of variation in polar bear hair growth will improve inference of seasonal dietary patterns, hormonal fluctuations, and other indicators of polar bear health in a changing climate.

Continued research on polar bears with coastal and offshore space-use strategies will be necessary to understand how habitat use differences translate to diet and pollution levels. The distinct space-use strategy of polar bears using glacier fjords is not unique to the Baffin Bay subpopulation; this movement pattern has been described for subsets of the Barents Sea subpopulation (Mauritzen et al. 2001, Freitas et al. 2012) and the newly identified Southeast Greenland subpopulation (Laidre et al. 2022). It has been hypothesized that glacier habitats provide access to predictable prey and energy conservation (Freitas et al. 2012, Blanchet et al. 2020). The use of this unique environment may increase with climate change in places where glacial ice is available to bears (Laidre et al. 2022). Therefore, future research should prioritize characterizing polar bear diet compositions and prey availability in these habitats and investigating how food web dynamics in glacial environments may shift in response to climate change.

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