DEVELOPMENT AND FITNESS CONSEQUENCES OF ONSHORE BEHAVIOR AMONG POLAR BEARS IN THE SOUTHERN BEAUFORT SEA

SUBPOPULATION

by

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in

Ecology

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ABSTRACT

Development and Fitness Consequences of Onshore Behavior Among Polar Bears in the Southern Beaufort Sea Subpopulation

by

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Utah State University, 2018

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Polar bears (*Ursus maritimus*) are experiencing rapid and substantial changes to their environment due to global climate change. Polar bears of the southern Beaufort Sea (SB) have historically spent most of the year on the sea ice. However, recent reports from Alaska indicate that the proportion of the SB subpopulation observed onshore during late summer and early fall has increased considerably. Previous research suggests that the number of polar bears onshore is linked to sea ice conditions and the availability of subsistence-harvested whale carcasses, which are referred to as bone piles. My objectives were to determine the development and fitness consequences for SB polar bears that come onshore. Furthermore, I aimed to reveal the number of polar bears that come onshore and feed at whale carcasses. I used a combination of genetic and behavioral data collected on SB polar bears from 2010-2013 to determine if onshore behavior developed through genetic inheritance, asocial learning, or social learning. I found that onshore behavior was primarily transmitted via mother-offspring social learning. I used hair
samples collected at bone piles near Kaktovik, Alaska from 2011-2014 and genetic capture-recapture techniques to estimate the annual number of polar bears that visited the bone piles and rates of apparent site fidelity to the bone pile. I estimated that as many as 146 (SE = 21) SB polar bears visited the bone piles near Kaktovik in 2012. Annual rates of apparent site fidelity to the bone pile for male polar bears ranged from 0.60 (SE = 0.07) to 0.61 (SE = 0.07), and female rates of apparent site fidelity was 0.69 (SE = 0.19). Lastly, I used quantitative fatty acid signature analysis to estimate the proportion of bowhead whale, ringed seal, bearded seal, and beluga whale in the diets of SB polar bears from 2004-2015. I revealed that polar bears achieved higher body condition by coming onshore and feeding at whale carcasses. Overall, my results indicated that SB polar bears are socially learning from their mother to come onshore and that this behavior is linked to increased body condition.
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Kate M. Lillie

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I thank Dr. Eric Gese whose guidance and knowledge was more than I could have asked for in a major advisor. He believed in me and supported me along the way with valuable suggestions and advice. I thank him for his patience with me with narrowing down a research topic and the countless revisions throughout my time at Utah State University. I feel honored that I got to be a part of his lab.

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CHAPTER 1

INTRODUCTION

Introduction

Polar bears (*Ursus maritimus*) are experiencing rapid and dramatic changes to their environment due to the warming global conditions produced by climate change (Durner *et al.* 2009). Polar bears are Arctic marine mammals that depend on sea ice as a platform for long-distance movements, mating, access to their primary prey, and some maternal denning (Amstrup 2003). However, the spatial extent of Arctic sea ice in September (when sea ice reaches its annual minima) has declined by 13.3% per decade due to warming temperatures (Serreze & Stroeve 2015). The decline in sea ice habitat puts polar bears at risk of becoming endangered and ultimately led to the listing of polar bears as “threatened” under the U.S. Endangered Species Act in 2008 (U.S. Fish and Wildlife Service 2008). Some polar bear subpopulations have been shown to be declining (Bromaghin *et al.* 2015), and experiencing reduced survival in relation to diminishing sea ice extent (Regehr *et al.* 2010).

Polar bears are predators that rely primarily on ringed seals (*Phoca hispida*) and, to a lesser extent, bearded seals (*Erignathus barbatus*) across their range (Amstrup 2003). This species represents the apex predator of the Arctic marine ecosystem. Apex predators play a fundamental role on influencing the structure and function of ecosystems (Ripple *et al.* 2014). Declines of predators can impact several trophic levels and can have devastating effects on ecosystems. For example, research on the predatory sea otter (*Enhydra lutris*) in coastal marine ecosystems of Alaska demonstrated that sea otters
were important for limiting herbivorous sea urchins, which in turn, enhanced the abundance and distribution of kelp and other macroalgae (Ripple et al. 2014). The higher levels of kelp influenced numerous other species primarily through creating a biogenic habitat, enhancing primary productivity, and dampening coastal waves and currents.

Other studies (Terborgh & Estes 2013; Ripple et al. 2014) have documented similar examples of the importance of predators in maintaining ecosystems [e.g., African lions (Panthera leo) and leopards (Panthera pardus) in Africa; dingoes (Canis dingo) in Australia, gray wolves (Canis lupus) in North America, and pumas (Puma concolor) in North America]. Thus, it is reasonable to assume that decreasing numbers of polar bears (i.e., an apex predator) will have severe effects on Arctic marine ecosystems.

There are 19 subpopulations of polar bears worldwide that still inhabit the majority of their historical range (Obbard et al. 2010). One subpopulation of polar bears that is likely declining is the southern Beaufort Sea (SB) subpopulation in Alaska (Bromaghin et al. 2015). Bromaghin et al. (2015) used data collected from 2001-2010 and reported reductions in survival and abundance from 2004 through 2007. Abundance was comparatively stable from 2008 to 2010, with ~900 bears in 2010. Survival of subadult bears declined throughout the entire study period. Moreover, the SB subpopulation has undergone declines in survival (Regehr et al. 2010), body condition, and reproduction (Rode, Amstrup & Regehr 2010), all of which were related to decreasing sea ice conditions. One study reported high metabolic rates coupled with low intake of prey resulted in an energy deficit for polar bears of the SB subpopulation (Pagano et al. 2018). The researchers predicted that the increasing energy demands
associated with declines in and fragmentation of sea ice are likely an important factor explaining the observed declines in body condition and survival.

Historically, polar bears of the SB subpopulation had a life history of spending the majority of the year on the sea ice (Amstrup et al. 2000). However, beginning in the early 2000s polar bear use of land in the summer and fall began to increase (Schliebe et al. 2008; Gleason & Rode 2009; Atwood et al. 2016). Atwood et al. (2016) reported that the proportion of radio-collared bears onshore was 20.0% during 2000-2014, which was an increase from 5.8% during 1986-1999. Furthermore, trends of earlier arrival onshore, increased length of stay onshore, and later departure back to the sea ice were detected and associated with sea ice conditions.

The number of onshore bears increased when sea ice retracted farther from the shore following the summer melt season (Schliebe et al. 2008). The spatial distribution of onshore bears was closely linked to the availability of subsistence-harvested bowhead whale (*Balaena mysticetus*) carcasses (Schliebe et al. 2008; Atwood et al. 2016; Wilson et al. 2017), which are harvested and deposited by indigenous communities of Alaska along the north coast. Numerous bears congregate and feed at these whale carcasses during the summer and fall (Herreman & Peacock 2013). Bowhead whales have thick blubber, which constitutes up to 50% of their body mass. Therefore, bowhead whale carcasses represent a persistent and reliable marine food subsidy for SB subpopulations. The availability of a food subsidy has the potential to influence the behavior, foraging ecology, and population dynamics of a species (Roth 2003; Herreman & Peacock 2013).

The focus of my dissertation was to determine how onshore behavior for polar bears of the SB subpopulation developed and its fitness consequences. I worked in
collaboration with faculty at Utah State University and staff of the U.S. Geological Survey-Alaska Science Center. Data for this research were obtained by field work conducted by primarily staff of the U.S. Geological Survey-Alaska Science Center. The U.S. Geological Survey-Alaska Science Center has been conducting ongoing research on SB polar bears for several decades, which provided me with access to a long-term data set for my dissertation research.

In chapter 2, I investigated the development of onshore behavior for polar bears of the SB subpopulation. I tested hypotheses to determine if onshore behavior developed through genetic inheritance, asocial learning, or through social learning mechanisms. I determined that onshore behavior for polar bears of the SB subpopulation was primarily transmitted via mother-offspring social learning. Thus, it appeared that onshore behavior for polar bears of the SB subpopulation developed because offspring learned to come onshore from their mother.

In chapter 3, I estimated the number of polar bears visiting bowhead whale carcasses deposited near Kaktovik, Alaska, which are referred to as “bone piles.” Furthermore, I estimated annual apparent site fidelity to the bone pile. I estimated that as many as 146 (SE = 21) polar bears (sexes combined) visited the bone pile near Kaktovik, Alaska in 2012, with an estimated low of 51 (SE = 13) bears in 2014. The estimated annual apparent site fidelity to the bone pile for males ranged from 0.60 (SE = 0.07) to 0.61 (SE = 0.07) and 0.69 (SE = 0.19) for females. However, my estimate of apparent site fidelity could be slightly confounded with survival.

In chapter 4, I determined if the proportion of bowhead whale in the diet of SB polar bears had a significant impact on body condition and reproductive output. In
addition, I investigated if the length of the open-water season from the prior year had a significant impact on body condition and reproductive output. I found that polar bears with a higher proportion of bowhead whale in the diet were in better body condition than bears that primarily fed on prey hunted from the sea ice. I revealed a concave association between body condition and the length of the prior year open-water season.

References


CHAPTER 2
DEVELOPMENT OF ONSHORE BEHAVIOR AMONG POLAR BEARS IN THE SOUTHERN BEAUFORT SEA

INTRODUCTION

The ability of a species to adapt is fundamental to being resilient to environmental change. A species can biologically respond to change by extinction, shifting its distribution, or adapting to new environmental conditions (Raia et al. 2012; Teplitzky and Millien 2014). Alterations in species distribution and abundance that follow shifting of climatic conditions have been documented in several plant and animal species (Parmesan and Yohe 2003; Root et al. 2003). Similarly, changes in species phenology in response to climate change have been reported (Inouye et al. 2000; Boutin and Lane 2014; Charmantier and Gienapp 2014). Polar bears (*Ursus maritimus*) are experiencing critical and rapid changes to their environment due to climatic warming (Stirling and Derocher 2012). This ice-dependent Arctic marine mammal (Amstrup 2003) was listed as “threatened” under the U.S. Endangered Species Act in 2008 (U.S. Fish and Wildlife Service 2008). The listing was primarily due to the observed and projected loss of sea ice habitat, which puts polar bears at risk of becoming endangered in the foreseeable future (i.e., by mid-century). During 1979-2014, the spatial extent of Arctic sea ice in September (when sea ice reaches its annual minima) declined by 13.3% per decade due to warming temperatures (Serreze and Stroeve 2015). Sea ice extent (and volume) is

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expected to continue to decline and the southern Beaufort Sea is predicted to become essentially seasonally ice-free (i.e., <1.0 \times 10^6 \text{ km}^2) during the summer before the end of the 21st century (Stroeve et al. 2012). Hence, conservation and management actions to understanding the ecology and behavior of species dependent on sea ice is necessary for ensure their population persistence.

Polar bears depend on sea ice for long-distance movements, mating, access to their primary prey of ringed seal (*Phoca hispida*) and bearded seal (*Erignathus barbatus*), and some maternal denning (Amstrup 2003). Numerous studies indicate that survival, (Regehr et al. 2010; Bromaghin et al. 2015), reproduction, and body condition (Rode et al. 2010) of the southern Beaufort Sea (SB) subpopulation is negatively affected by changing sea ice conditions. In addition, polar bears have been observed swimming increasingly longer distances as sea ice has, on average, retracted farther from shore during summer (Pilfold et al. 2017), resulting in potentially higher energetic costs (Pagano et al. 2012). Furthermore, the distribution of denning has shifted to include fewer denning sites on the pack ice and more sites on land in correspondence with a reduction in the availability and quality of pack ice serving as denning habitat (Fischbach et al. 2007).

Polar bears of the SB have historically spent most of the year on the sea ice with the exception of denning (Amstrup et al. 2000). However, recent research in Alaska indicates that polar bears of the SB subpopulation are becoming increasingly reliant on land during late summer and fall, when sea ice is no longer present over the biologically productive, shallow water of the continental shelf (Schliebe et al. 2008; Gleason and Rode 2009; Atwood et al. 2016). The estimated proportion of radio-collared bears from
the SB subpopulation observed onshore increased from 5.8% during 1986-1999 to 20.0% during 2000-2014, reaching a peak of 37.0% in 2013 (Atwood et al. 2016).

The number of bears observed onshore has been shown to increase when sea ice retracts farther from the shore following the summer melt season (Schliebe et al. 2008). Additionally, the spatial distribution of onshore bears appears to be linked to the accessibility of ringed seals in offshore waters and the availability of subsistence-harvested bowhead whale (*Balaena mysticetus*) carcasses (Schliebe et al. 2008; Atwood et al. 2016). Coastal Iñupiat communities of Alaska annually hunt bowhead whales and deposit the unused remains at localized “bone piles” onshore that consist of trimmed blubber, meat, and bones (Ashjian et al. 2010), thereby attracting polar bears and other wildlife. Onshore bears could be at a higher risk of human-bear conflicts with local residents, tourists, and from industrial activities (Laforge et al. 2017; Wilder et al. 2017), as well as increased exposure to certain pathogens (Atwood et al. 2017) and pollutants (Amstrup et al. 1989). Despite this marked increase of bears exhibiting onshore behavior, there remains a lack of research on how this behavior developed.

Recognizing how animals acquire different behavioral strategies is necessary for both basic and applied scientific disciplines such as wildlife management and conservation biology. Animal behavioral traits can be obtained through genetic inheritance (Arnold 1981), but frequently the acquisition of a behavior occurs via learning (Heyes 1994; Heyes and Galef 1996). Learning incorporates complex ontogenetic processes allowing animals to acquire, store, and use information about the environment (Galef and Laland 2005). Learning can occur socially or asocially, whereby social learning refers to knowledge acquired from the observation of others, typically a
conspecific or the products of their activities, and asocial learning refers to learning where no social interaction is required (Heyes 1994).

Recent studies have investigated the transmission of foraging behavior from mother to offspring in free-ranging black bears (*U. americanus*) using observational and genetic techniques (Breck et al. 2008; Mazur and Seher 2008; Hopkins 2013). Similarly, studies on grizzly bears (*U. arctos*) examined the transmission of habitat selection and conflict behavior from mother to offspring (Morehouse et al. 2016; Nielsen et al. 2013). Bears are good candidates for studying whether particular behaviors are transmitted from mother to offspring because bears are highly intelligent and solitary with the exception of a prolonged mother-offspring association (Gilbert 1999). Polar bear offspring typically remain with their mother up until 2.3 years of age (Ramsay and Stirling 1988). Therefore, it is feasible to determine that a bear is learning socially from its mother if bears display the same behavioral patterns as adults.

In light of the pronounced increase in the number of polar bears coming onshore and its potential to have both ecological and management implications, our objective was to elucidate how this behavior developed. We collected genetic and behavioral data from bears that come onshore (hereafter “onshore”) and those that remain on the pack ice (hereafter “off-shore”) during the fall season. Specifically, we addressed the following question: Was onshore behavior for polar bears in the SB subpopulation acquired via asocial learning, social learning, or genetic inheritance?

To answer this question, we tested hypotheses to determine how onshore behavior developed via three analyses: (1) genetic relatedness (i.e., quantitative estimate of the proportion of genes shared between the genomes of any two individuals); (2) 1st-order
relatives (i.e., parent-offspring or sibling pairs); (3) and parentage (i.e., mother-offspring and father-offspring pairs) within and between polar bears categorized as onshore and off-shore bears. We included transmission (i.e., the behavior was transmitted via social learning or genetic inheritance) as an additional hypothesis because not all analyses that we conducted could differentiate between social learning and genetic inheritance. It is important to note that these hypotheses are not mutually exclusive, thus evidence for one hypothesis does not indicate other mechanisms are not occurring but that the most supported hypothesis is more predominant.

**Hypothesis 1: Onshore behavior for polar bears developed via asocial learning.**—The asocial learning hypothesis from the genetic relatedness analyses predicts that female bears that exhibit onshore behavior do not have higher levels of genetic relatedness relative to the entire sampled population. Asocial learning of onshore and off-shore behavior from the parentage analysis would be evident if there was no association between the parent’s behavior and the offspring’s behavior.

**Hypothesis 2: Onshore behavior for polar bears developed via social learning.**—The transmission via social learning hypothesis from the genetic relatedness analyses predicts that female bears but not male bears that exhibit onshore behavior have higher levels of genetic relatedness relative to the sampled population. Furthermore, an association between the mother’s behavior and her offspring’s behavior, but no association between the father’s behavior and his offspring’s behavior (as male bears do not rear cubs), from the parentage analyses would be indicative of social learning for onshore and off-shore behavior.
Hypothesis 3: Onshore behavior for polar bears developed via genetic inheritance.—The transmission via genetic inheritance hypothesis from the genetic relatedness analyses predicts that both female and male bears that display onshore behavior have higher levels of genetic relatedness than the sampled population. In addition, a scenario of genetic inheritance of onshore and off-shore behavior from the parentage analyses would be if there was an association between both the mother’s behavior and her offspring’s behavior and the father’s behavior and his offspring’s behavior.

Hypothesis 4: Onshore behavior for polar bears developed via transmission (i.e., social learning or genetic inheritance).—The transmission hypothesis from the genetic relatedness analyses predicts that female bears that exhibit onshore behavior have a higher genetic relatedness than the sampled population. Secondly, a higher than expected number of 1st-order relatives that display onshore behavior would provide evidence of transmission for this behavior.

MATERIALS AND METHODS

Study area

The SB polar bear subpopulation inhabits a region encompassing areas along the north coast of Alaska and Canada from Icy Cape, Alaska, USA, (70.3°N, 161.9°W) in the west, to Tuktoyaktuk, Northwest Territories, Canada, (69.4°N, 133.0°W) in the east. The southern Beaufort Sea has a narrow continental shelf with a steep shelf-break that plunges to some of the deepest waters of the Arctic Ocean (Jakobsson et al. 2008). The SB is typically ice covered from October to June, and sea ice retreats to its minimum in
the summer and fall seasons from July to September. In recent years there has been a
trend in the SB of earlier melt onset, reduced summer sea ice extent, a lengthening of the
open-water season (i.e., sea ice retreats towards the pole during the annual sea ice
minimum), and later freeze-up (Stroeve et al. 2014).

Collection of genetic material

We collected genetic material from SB polar bears from 2010 to 2013 via direct
polar bear captures, remote biopsy darting, and hair snags. We used the contemporary
genetic data in conjunction with a long-term data set of SB polar bears captured nearly
every spring since the mid-1980s. We captured polar bears in coastal areas (e.g., within
150 km of the coast) of the SB from Utqiagvik (formerly known as Barrow), Alaska
(~157°W) to the U.S.-Canada border (~141°W). We conducted captures over the sea ice
during the spring season from March to early May over the study. We encountered adults
and subadults opportunistically while flying in a helicopter and immobilized them with
tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®, Fort Dodge and
Warner-Lambert Co.) using a projectile syringe fired from a dart gun. We collected blood
and tissue samples for genetic identification. Additionally, we fitted an Argos or global
positioning system (GPS) platform transmitter terminal (PTT) satellite radio-collars to a
subset of adult female polar bears to collect movement and spatial data (Durner et al.
2009).

During the spring, we conducted remote biopsy darting from a helicopter to
collect tissue samples from adult and subadult bears within approximately 150 km of the
coast between Utqiagvik, Alaska and the U.S.-Canada border. Additionally, we
conducted remote biopsy darting in the fall along the coastline, barrier islands, and inland areas within approximately 30 km of the coast (Pagano et al. 2014). The remote biopsies collected skin tissue samples for genetic identification. Hair snags were implemented in Utqiagvik, Alaska in the fall season of 2011 and Kaktovik, Alaska (~143°W) in the fall seasons of 2012 and 2013 to collect hair samples for genetic identification (see [Herreman and Peacock 2013] for details).

**Genetic identification**

We genotyped blood, tissue, and hair samples at 20 microsatellite loci and a ZFX/ZFY sex identification marker by Wildlife Genetics International (Nelson, British Columbia, Canada). The DNA was extracted using a Qiagen DNeasy kit (QIAGEN Inc., Valencia, California, USA). The DNA was extracted from hair samples using a minimum of 10 guard hair roots, if available, or up to 30 whole underfur hairs if needed to supplement guard hairs. The DNA was extracted from the dry blood and tissue samples using a clipped piece ~3mm² from the end of a Q-tip or ear punch. The DNA extracts were initially amplified at 11 hypervariable microsatellite markers to identify individuals: G1A, G10B, G10C, CX110, G1D, G10L, G10M, MU59, G10P (Paetkau and Strobeck 1994; Taberlet et al. 1997; Proctor et al. 2002); and G10H and G10J (GenBank accession numbers U22086.1 and U22087.1, respectively). Any DNA extracts that were amplified at <11 loci were considered unsuccessful and excluded from further analyses. After individuals were identified, each individual was amplified at nine additional markers including a sex-linked locus: MSUT-2, CPH9, CXX20, MU50, MU51, G10X, CXX173 (Ostrander et al. 1993; Paetkau et al. 1995; Taberlet et al. 1997; Kitahara et al. 2000;
Proctor et al. 2002; An et al. 2010); and 14RENP07 and G10U (GenBank accession numbers AJ411284, and U22092.1, respectively).

**Onshore and off-shore bears**

We categorized polar bears based on their behavior as onshore or off-shore individuals both pooled over the duration of the study and on an annual basis. For the pooled data set, we considered bears as onshore individuals if they were identified onshore during the study. We identified bears onshore during the fall season using information from the remote biopsy, hair snag, or GPS locations (see [Atwood et al. 2016] for details). We restricted the fall season to July 1-October 31 as this was when the sea ice was not contiguous to the coast. We categorized bears as off-shore individuals if they were identified on the sea ice during the spring remote biopsy or direct capture and were not observed onshore at any time during the study. For the annual data set, we considered bears as onshore individuals if they were identified onshore for a given year from the fall season remote biopsy, hair snag, or GPS locations. We categorized bears as off-shore individuals if they were not identified onshore for that respective year. We conducted the annual categorization because some bears switched behavioral strategies during the four years of sampling. We conducted identical analyses on the pooled and the annual data sets to ascertain if comparable results would be obtained.

We estimated the age of individual bears from analysis of cementum annuli (Calvert and Ramsay 1998), or they were classed as a known age bear if they were originally captured as dependent young with their mother (Ramsay and Stirling 1988). We conducted three separate analyses to determine how onshore behavior was acquired:
genetic relatedness, 1st-order relatives, and parentage (Breck et al. 2008; Hopkins 2013). We conducted all statistical tests using $\alpha = 0.05$ in R (R Core Team 2016). We included an individual bear only once in all analyses after it was categorized as an onshore or offshore bear. In addition, we included only bears considered independent in all analyses since dependent young had no choice but to remain with their mother. We considered bears as independent if they were $\geq 2$ years old or if they were observed without their mother when captured.

**Genetic relatedness**

We calculated pairwise relatedness (Queller and Goodnight 1989) between all possible pairings of individuals using Genalex (Peakall and Smouse 2006; Peakall and Smouse 2012). Theoretical values of relatedness range from -1 to 1, with negative values indicating the gene frequencies of the two compared individuals differ from the population mean in opposite directions, zero representing random associations between individuals, and increasing values corresponding to increased relatedness. Relatedness values are affected by genetic structure, as these values measure genetic differences in overall allelic frequencies (Queller and Goodnight 1989). Polar bears are weakly structured throughout their circumpolar distribution (Peacock et al. 2015). No differentiation observed at microsatellite loci among southern Beaufort and adjacent (northern Beaufort and Chukchi Sea) subpopulations was observed; therefore, we conducted analyses among bears across all sampled sites.

We used bootstrap resampling for the genetic relatedness analysis because the relatedness distributions were non-normal and each behavioral group was a subset of the
entire sampled population (Hopkins 2013). The behavioral groups tested were onshore/onshore, onshore/off-shore, and off-shore/off-shore with mean relatedness determined for the entire sampled population, and females and males, separately. We randomly selected a subset of bears for each behavioral group from the sampled population matrix 10,000 times and calculated relatedness. We then used every relatedness value to generate the bootstrap distribution of the sample mean. We calculated the $P$-value by the number of times the bootstrap relatedness estimate was greater than or equal to the mean relatedness for the entire sampled population.

**Parentage**

We identified mother-offspring and father-offspring pairs (Breck et al. 2008) using Cervus 3.0 (Marshall et al. 1998). We considered bears as mothers or fathers if they were estimated to be ≥ 3 years older than the bear presumed to be the offspring, there were no genotype inconsistencies between parent-offspring pairs, and if parentage assignments were made with ≥80% confidence. We used either a chi-square goodness-of-fit test or a Fisher’s exact test (when sample size in at least 1 category was ≤5) to test the null hypothesis that there was no association between the parent’s behavior and the offspring’s behavior.

**First-order relatives**

We used the pairwise relatedness values to identify individual pairs that were 1st-order relatives (Breck et al. 2008). Based on relatedness values from known mother-offspring ($n = 27$) and sibling ($n = 6$) pairs, we used a value of relatedness ≥ 0.42 to indicate pairs related at the level of 1st-order relatives. We categorized 1st-order relatives
into the same onshore/onshore, onshore/off-shore, and off-shore/off-shore behavioral
groups examined previously. We used either a chi-square goodness-of-fit test or an exact
test for multinomial (when sample size in at least 1 category was ≤5) to determine if the
number of observed related pairs differed from the number of expected for each
behavioral group. We calculated the expected numbers by multiplying the observed
number of bears for each behavioral group by the proportion of all possible pairings
within a behavioral group. Thus, the expected number of 1st-order relative pairs assumed
no relationship between 1st-order relative status and the behavioral category
(onshore/offshore).

RESULTS

A total of 231 independent (i.e., ≥2 years old or if they were observed without
their mother when captured) polar bears for the pooled data set were successfully
genotyped at a number of loci sufficient to provide individual identity (11) and could be
categorized as onshore or off-shore individuals from the behavioral data; of these 123
bears were categorized as off-shore (59 females and 64 males) and 108 bears were
categorized as onshore (58 females and 50 males). Over the duration of the study, 12.6%
(n = 29/231) of the identified bears switched behaviors among the years. We conducted
an annual analysis solely for 2011, because sample size for independent bears was the
highest (2010: n = 81, 2011: n = 103, 2012: n = 97, 2013: n = 57) and we had sufficient
data for mother-offspring and father-offspring pairs to conduct the Fisher’s exact test. In
2011, there were 103 identified independent bears with behavioral data; we categorized
47 bears as off-shore (24 females and 23 males) and 56 bears as onshore (28 females and 28 males).

Female onshore/onshore pairs had the highest mean relatedness of all behavioral groups (Table 2.1), which was significantly higher than the mean relatedness of the entire sampled population. Male onshore/onshore pairs did not have a significantly higher mean relatedness than the mean relatedness of the entire sampled population, which provided evidence of social learning of onshore behavior given that the female onshore/onshore pairs had significantly higher relatedness than the sampled population. A similar pattern was observed for the 2011 annual analysis. Among the 2011 analyses, only female onshore/onshore pairs had significantly higher mean relatedness than the mean relatedness for the entire sampled population (and the highest mean relatedness of all behavioral groups). In contrast, male onshore/onshore pairs did not have a significantly higher mean relatedness than the mean relatedness of the entire sampled population.

There was evidence of an association between a mother’s behavior and her offspring’s behavior (Table 2.2). The numbers of onshore/onshore and off-shore/off-shore mother-offspring pairs were higher than expected. The number of onshore/off-shore mother-offspring pairs was lower than expected consistent with the pattern of offspring retaining the behavioral strategy of their mother. The same pattern was observed for the 2011 data set, though the signal was not as strong. The number of onshore/onshore and off-shore/off-shore mother-offspring pairs was higher than expected, while the number of onshore/off-shore mother-offspring pairs was lower than expected. There was no significant association between a father’s behavior and his offspring’s behavior (Table 2.3) for the pooled data set or for the 2011 data set; though
the sample size was low for 2011 and may limit the power of the test. Collectively, the parentage findings provide evidence for mother-offspring social learning of onshore behavior.

The observed number of 1st-order relatives deviated from the expectation for both the pooled and 2011 data sets (Table 2.4). The number of onshore/onshore 1st-order relatives was higher than expected, which provided evidence for transmission via genetic inheritance or social learning of onshore behavior. Conversely, the number of onshore/off-shore and off-shore/off-shore 1st-order relatives was lower than expected.

**DISCUSSION**

Analyses testing relationships based on genetic relatedness and parentage estimates revealed that social learning was the primary mechanism responsible for onshore behavior. This was revealed by the finding that the female onshore/onshore behavioral category had a significantly higher mean relatedness than the entire sampled population, while the male onshore/onshore behavioral category did not (Table 2.1). Thus, female polar bears exhibiting onshore behavior had higher relatedness; while onshore males were not more related than the general population. Furthermore, a significant association between a mother’s behavior and her offspring’s behavior was observed (Table 2.2), while no association between a father’s behavior and his offspring’s behavior was found (Table 2.3). In combination, the parentage results indicated that the transmission of onshore and off-shore behavior was through mother-offspring social learning because independent offspring generally continued to follow the same behavioral strategy of their mother.
All three analyses from both the pooled and annual data sets suggested transmission, via social learning or genetic inheritance, of onshore behavior for the SB polar bear subpopulation. The pooled and annual data sets had concordant results indicating that bears switching behavior among the years did not alter the overall conclusions. Analysis based on 1st-order relatives revealed higher than expected onshore/onshore 1st-order relatives and lower than expected onshore/off-shore and off-shore/off-shore 1st-order relatives (Table 2.4). Close relatives exhibiting the same behavior indicated transmission of onshore behavior because closely related individuals were likely socially learning from each other or there was a genetic basis for onshore behavior.

A high proportion of male polar bears leaving the study area could have resulted in similar patterns in our genetic relatedness analysis; thereby erroneously producing a signature of social learning. For example, male grizzly bears travel widely during breeding season (Ciarniello et al. 2007) and generally have longer natal dispersal distances than females (McLellan and Hovey 2001; Proctor et al. 2004), which would likely result in a higher level of genetic relatedness among female bears in a region. Generally, movements of male and female polar bears do not differ greatly (Amstrup et al. 2001) but female polar bears can have larger breeding range sizes than males (Laidre et al. 2013); whereas Zeyl et al. (2009) found that polar bears of the Barents Sea exhibit male-biased natal dispersal. Thus, because dispersal distance is sex-biased in polar bears, the scenario of higher genetic relatedness among female bears exhibiting onshore behavior could be a result of greater male dispersal. Nonetheless, the mother-offspring findings provided evidence of social learning despite the uncertainty regarding the
genetic relatedness results since offspring generally followed the same behavioral strategy as their mother.

Lower survival of off-shore polar bears could also generate equivalent results. That is, if onshore bears have higher survival, and therefore onshore females have a higher recruitment rate of cubs than off-shore bears, then higher genetic relatedness among onshore bears, a higher proportion of onshore/onshore 1st-order relatives, and more onshore/onshore mother-offspring pairs would be observed. Thus far, no studies have been conducted on survival and recruitment comparing onshore and off-shore polar bear subpopulations. However, research on SB polar bears found similar activity patterns and physiological condition for onshore and off-shore bears, which suggests that neither the onshore or off-shore group realizes a greater benefit than the other (Whiteman et al. 2015). While the mother-offspring data suggest onshore behavior was acquired through social learning, we cannot rule out the possibility that off-shore mothers experienced a high incidence of reproductive failure, which then contributed to the clustering of relatives onshore.

Behavioral or physiological modifications in response to climate-driven changes in their environment have been observed in other species (Bradshaw and Holzapfel 2006) with both positive and negative fitness consequences (Réale et al. 2003; Halupka et al. 2008; Both et al. 2006). The increase in SB polar bears coming onshore (Atwood et al. 2016) and the transmission of this behavior via mother-offspring social learning may be a behavioral modification in response to climate change and suggests that some SB polar bears are altering their behavior in response to a changing climate. Furthermore, some bears were observed switching behaviors over the duration of the study revealing that
these behaviors are dynamic. Bears may alter their behavior for a multitude of reasons, such as annual sea ice conditions, food availability, and reproductive status. Plasticity in onshore/off-shore behavior may provide an avenue for polar bears to respond to changing sea-ice conditions on an annual basis.

Onshore bears may be exposed to additional risks, including a greater potential for human-bear conflicts and increased exposure to contaminants and diseases (Stirling and Derocher 2012). There are several villages along the north coast of Alaska and an industrial footprint associated with oil exploration and extraction, all of which can occur in relatively close proximity to onshore bears. Also in close proximity to human settlements are the remains of subsistence-harvested bowhead whale carcasses, which are deposited on land and attract large aggregations of bears (Herreman and Peacock 2013). Therefore, human-bear conflicts will likely increase as the sea ice continues to decline and more bears come ashore. Human-wildlife conflicts can have broad effects: negatively impacting wildlife populations, changing the structure of ecosystems (Woodroffe et al. 2005), and endangering public safety (Thirgood et al. 2005). Other polar bear populations, such as the Western Hudson Bay population, have experienced increases in the number of problem bears correlated with delayed sea ice formation and changes in polar bear distribution and declining body condition. Additionally, polar bears that were highly motivated to obtain food appeared more willing to risk interacting with humans (Towns et al. 2009).

The proportion of SB polar bears exhibiting onshore behavior during the fall season has increased over time (Atwood et al. 2016; Pongracz and Derocher 2016). Furthermore, trends of earlier arrival onshore, increased length of stay, and later
departure back to the sea ice have been detected, which are all related to declines in the availability of sea ice habitat over the continental shelf and changes to sea ice phenology. The Arctic is expected to continue to warm given the current trends in global greenhouse emissions (Larsen et al. 2014). Thus, SB polar bears will likely continue to experience changes to their environment resulting in more bears coming onshore. Therefore, it will be important to monitor the population-level consequences of extended land use. Properly managing polar bear mother-offspring pairs, when feasible, will be important to ensure their continued persistence in a rapidly changing environment and mitigate human-bear conflicts for this apex predator in the changing Arctic.

REFERENCES


TABLES

Table 2.1.
Mean relatedness and corresponding $P$-values of behavioral groups by category for polar bears of the southern Beaufort Sea, pooled for 2010-2013 and annually for 2011. The $P$-value was calculated by the number of times the bootstrap relatedness estimate for each behavioral category was greater than or equal to the mean relatedness for the entire sampled population.

<table>
<thead>
<tr>
<th>Behavioral groups</th>
<th>$n$</th>
<th>Mean relatedness</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pooled</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sampled population</td>
<td>231</td>
<td>-0.0043</td>
<td>0.082</td>
</tr>
<tr>
<td>Onshore/onshore</td>
<td></td>
<td>0.0066</td>
<td></td>
</tr>
<tr>
<td>Onshore/off-shore</td>
<td></td>
<td>-0.0075</td>
<td>0.726</td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td></td>
<td>-0.0072</td>
<td>0.648</td>
</tr>
<tr>
<td>Female bears</td>
<td>117</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onshore/onshore</td>
<td></td>
<td>0.0151</td>
<td>0.039</td>
</tr>
<tr>
<td>Onshore/off-shore</td>
<td></td>
<td>-0.0005</td>
<td>0.298</td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td></td>
<td>-0.0020</td>
<td>0.406</td>
</tr>
<tr>
<td>Male bears</td>
<td>114</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onshore/onshore</td>
<td></td>
<td>-0.0018</td>
<td>0.406</td>
</tr>
<tr>
<td>Onshore/off-shore</td>
<td></td>
<td>-0.0141</td>
<td>0.904</td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td></td>
<td>-0.0147</td>
<td>0.849</td>
</tr>
<tr>
<td><strong>2011</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sampled population</td>
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<td>-0.0098</td>
<td>0.192</td>
</tr>
<tr>
<td>Onshore/onshore</td>
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<td>-0.0007</td>
<td>0.192</td>
</tr>
<tr>
<td>Onshore/off-shore</td>
<td></td>
<td>-0.0129</td>
<td>0.657</td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td></td>
<td>-0.0151</td>
<td>0.678</td>
</tr>
<tr>
<td>Female bears</td>
<td>52</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onshore/onshore</td>
<td></td>
<td>0.0110</td>
<td>0.089</td>
</tr>
<tr>
<td>Onshore/off-shore</td>
<td></td>
<td>-0.0196</td>
<td>0.810</td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td></td>
<td>-0.0109</td>
<td>0.524</td>
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<td>Male bears</td>
<td>51</td>
<td></td>
<td></td>
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<tr>
<td>Onshore/onshore</td>
<td></td>
<td>-0.0083</td>
<td>0.459</td>
</tr>
<tr>
<td>Onshore/off-shore</td>
<td></td>
<td>-0.0241</td>
<td>0.894</td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td></td>
<td>-0.0079</td>
<td>0.458</td>
</tr>
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</table>
Table 2.2.
Observed and expected mother-offspring pairs by behavioral group for polar bears of the southern Beaufort Sea, pooled for 2010-2013 and annually for 2011. A chi-square goodness-of-fit test or a Fisher’s exact test (when sample size in at least 1 category was ≤5) was used to test the null hypothesis that there is no association between the parent’s behavior and the offspring’s behavior.

<table>
<thead>
<tr>
<th>Relationship</th>
<th>Observed</th>
<th>Expected</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pooled</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mother-offspring</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onshore/onshore</td>
<td>32</td>
<td>28</td>
<td>0.004</td>
</tr>
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<td>Off-shore/onshore</td>
<td>4</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Onshore/off-shore</td>
<td>6</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td>7</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mother-offspring</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onshore/onshore</td>
<td>14</td>
<td>13</td>
<td>0.056</td>
</tr>
<tr>
<td>Off-shore/onshore</td>
<td>1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Onshore/off-shore</td>
<td>1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.3.
Observed and expected father-offspring pairs by behavioral group for polar bears of the southern Beaufort Sea, pooled for 2010-2013 and annually for 2011. A chi-square goodness-of-fit test or a Fisher’s exact test (when sample size in at least 1 category was ≤5) was used to test the null hypothesis that there is no association between the parent’s behavior and the offspring’s behavior.

<table>
<thead>
<tr>
<th>Relationship</th>
<th>Observed</th>
<th>Expected</th>
<th>$\chi^2$</th>
<th>P-value</th>
</tr>
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<tr>
<td><strong>Pooled</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Father-offspring</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onshore/onshore</td>
<td>17</td>
<td>15</td>
<td>0.876</td>
<td>0.349</td>
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<tr>
<td>Off-shore/onshore</td>
<td>7</td>
<td>9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onshore/off-shore</td>
<td>7</td>
<td>9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td>7</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>2011</strong></td>
<td></td>
<td></td>
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<tr>
<td>Father-offspring</td>
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<tr>
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<td>2</td>
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<td></td>
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<td>Onshore/off-shore</td>
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<td>2</td>
<td></td>
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<tr>
<td>Off-shore/off-shore</td>
<td>1</td>
<td>0</td>
<td></td>
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Table 2.4.
Observed and expected 1st-order relatives by behavioral group for polar bears of the southern Beaufort Sea, pooled for 2010-2013 and annually for 2011. A chi-square goodness-of-fit test or an exact test for multinomial (when sample size in at least 1 category was ≤5) was used to determine if the number of observed related pairs differed from the number of expected for each behavioral group.

<table>
<thead>
<tr>
<th>Behavioral groups</th>
<th>Observed</th>
<th>Expected</th>
<th>$\chi^2$</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pooled</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Onshore/onshore</td>
<td>64</td>
<td>25</td>
<td>80.892</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Onshore/off-shore</td>
<td>30</td>
<td>57</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td>19</td>
<td>32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onshore/onshore</td>
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<td>8</td>
<td>33.295</td>
<td>&lt;0.001</td>
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<td>13</td>
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<td></td>
</tr>
<tr>
<td>Off-shore/off-shore</td>
<td>2</td>
<td>5</td>
<td></td>
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</table>
CHAPTER 3
USE OF SUBSISTENCE-HARVESTED WHALE CARCASSES BY POLAR BEARS
IN THE SOUTHERN BEAUFORT SEA

INTRODUCTION

The ability of a species to utilize a food subsidy can greatly influence individual behavior, foraging ecology, fitness, and population dynamics (Roth 2003; Herreman and Peacock 2013). Due to climate change, polar bears (*Ursus maritimus*) are undergoing rapid changes to their environment (Stirling and Derocher 2012). As a result of decreasing sea ice extent, an increasing proportion of polar bears from the southern Beaufort Sea (SB) subpopulation are being observed onshore during the late summer and fall in Alaska (Schliebe et al. 2008; Gleason and Rode 2009; Atwood et al. 2016). One of the main food resources for bears onshore appears to be the availability of subsistence-harvested bowhead whale (*Balaena mysticetus*) carcasses (Schliebe et al. 2008; Herreman and Peacock 2013; Atwood et al. 2016; Wilson et al. 2017). Indigenous communities along the coast of northern Alaska annually harvest bowhead whales and deposit unused remains onshore at local “bone piles” which are comprised of trimmed blubber, meat, and bones (Ashjian et al. 2010). Diet analyses suggested that a high proportion of the SB subpopulation feed on these bowhead whale carcasses (Rogers et al. 2015; McKinney et al. 2017), which could potentially affect population dynamics. Therefore, it is important to understand the annual usage of this marine food subsidy by SB polar bears for conservation and management purposes.
Summer sea ice conditions in the Arctic have changed substantially in recent decades (Serreze and Stroeve 2015). The spatial extent of Arctic sea ice in September (when sea ice reaches its annual minimum) has declined by 13.3% per decade over the period 1979-2014 due to warming temperatures (Serreze and Stroeve 2015). Polar bears of the SB subpopulation have historically spent the majority of the year on the sea ice (Amstrup et al. 2000). Polar bears rely on sea ice for access to their primary prey of ringed (*Phoca hispida*) and bearded (*Erignathus barbatus*) seals, long-distance movements, mating, and some maternal denning (Amstrup 2003). Along with other areas of the Arctic, the SB has experienced pronounced declines in September sea ice extent and a lengthening of the melt season (i.e., period of time between sea ice break-up and freeze-up) since the 2000’s (Stroeve et al. 2014). Recent research in Alaska found that the estimated proportion of bears observed onshore increased from 5.8% during 1986-1999 to 20.0% during 2000-2014 (Atwood et al. 2016). Atwood et al. (2016) found trends of earlier arrival onshore, increased length of stay while onshore, and later departure back to the sea ice, all of which were associated with declines in the availability of sea ice habitat over the continental shelf and changes to sea ice phenology. Furthermore, the number of bears onshore appears to increase when sea ice retracts farther from the shore following the melt season (Schliebe et al. 2008; Wilson et al. 2017).

Numerous polar bears congregate at the energy-rich bone piles while onshore (Herreman and Peacock 2013; Wilson et al. 2017). Bone piles are present in Alaska in the fall near Cross Island (~147°W) and the community of Kaktovik (~143°W). An average of 38.9 (SD = 7.1) whales were harvested in Alaska per year from 2002 to 2011 and ranged in size from roughly 6 to nearly 20 m long (Suydam and George 2012). Bowhead
whales have thicker blubber than other cetaceans, comprising up to 50% of their body mass (George 2009). Bone piles constitute a persistent and reliable marine food subsidy for polar bears as they are available each year at the same locations.

Human-wildlife conflicts can have broad consequences such as negatively impacting wildlife populations, altering the structure of ecosystems (Woodroffe et al. 2005), and endangering public safety (Thirgood et al. 2005). The bone piles in Alaska occur near villages and oil exploration and extraction infrastructure, which increases the risk of human-bear interactions and conflict. Towns et al. (2009) found that an increase in human-polar bear interactions in Churchill, Manitoba, was associated with an increase in the length of the ice-free season and declines in bear body condition. Land use by polar bears and anthropogenic activities along Alaska’s Beaufort Sea coast are both likely to increase [e.g., (Raynolds et al. 2014)], thus it is important to understand the number and fidelity of polar bears using the bone piles in light of the management implications for minimizing human-bear conflicts.

Our objective was to use genetic mark-recapture techniques to determine the annual number of SB polar bears utilizing the bone pile near Kaktovik, Alaska, and the annual apparent site fidelity to the bone pile, over a period of four years: 2011-2014. Specifically, we used the POPAN model to estimate the annual number of polar bears visiting the bone pile and the Cormack-Jolly-Seber (CJS) model to estimate annual apparent site fidelity to the bone pile. Lastly, we aimed to characterize the demographics and temporal dynamics of bears at the bone pile. The results of this study will provide beneficial information important for making informed management decisions regarding the SB polar bear subpopulation.
MATERIALS AND METHODS

Study area.—The SB subpopulation extends from Icy Cape, Alaska, USA, (70.3°N, 161.9°W) in the west, to Tuktoyaktuk, Northwest Territories, Canada, (69.4°N, 133.0°W) in the east. We collected data in Kaktovik, Alaska, which is a community of approximately 300 inhabitants along the coast of the southern Beaufort Sea. Indigenous people of Kaktovik annually harvest bowhead whales during the fall and deposit the unused whale remains on a spit approximately 2 km northeast of the village. Bowhead whales have been harvested since 1964, with 2-4 whales harvested annually, with few exceptions, since 1989 (Koski et al. 2005). Published accounts of polar bears observed feeding at the Kaktovik bone pile date back to 1986 (Amstrup et al. 1986). The average daily temperature during the study periods while the hair snag was operated was -10.5°C with a maximum of 4°C in years 2011 and 2014 and a minimum of -33.9°C in 2013 (http://www.arh.noaa.gov/clim/). Kaktovik whalers harvested 3 bowhead whales per year during the fall for all 4 years of the study period (Suydam et al. 2012; 2013; 2014; 2015). Harvested whales ranged in length from 6.6 m in 2011 (Suydam et al. 2012) to 14.3 m in 2012 (Suydam et al. 2013) with an average length of 10.1 m (Suydam et al. 2012; 2013; 2014; 2015).

Data collection.—Hair snags were deployed in Kaktovik, Alaska (Herreman and Peacock 2013) in the fall of 2011, 2012, 2013, and 2014, to collect hair samples for genetic identification. Collection of hair samples continued through the fall and winter for each year and ceased somewhere between early and late winter. The hair snag was a barbed wire corral erected around the bowhead whale carcasses. The hair snag consisted
of a single continuous strand of 4-point, 12-gauge barbed wire attached to metal t-posts spaced approximately 10 m apart and pounded into the gravel at a minimum depth of 40 cm. Bailing wire or fence clips were used to attach the barbed wire to the t-posts at a height of 0.65 m. The hair snag was checked daily for the first 4 days of sampling. After the first 4 days, the snag was checked at least weekly to ensure integrity of the wire. We collected samples by plucking hairs from a single barb and putting them inside a small paper coin envelope. Samples were not collected if a single barb had large quantities of hair since it could have come from more than one individual. We collected only one sample within a 0.75 m section of fence to avoid collecting multiple samples from a single crossing event. All remaining hairs that were not collected from the fence at each visit were removed via plucking or burning with a gas torch. The samples were air-dried and stored at room temperature until DNA extraction.

Genetic identification.—Hair samples were genotyped at 20 microsatellite loci and a ZFX/ZFY sex identification marker by Wildlife Genetics International (Nelson, British Columbia, Canada). The DNA was extracted using a Qiagen DNeasy kit (QIAGEN Inc., Valencia, California, USA) per the manufacturer’s instructions. Initially, the DNA extracts were amplified at 11 hypervariable microsatellite markers to identify individual polar bears: G1A, G10B, G10C, CX110, G1D, G10L, G10M, MU59, G10P (Paetkau and Strobeck 1994; Taberlet et al. 1997; Proctor et al. 2002); and G10H and G10J (GenBank accession numbers U22086.1 and U22087.1, respectively). A minimum of 10 guard hair roots were used to extract DNA, if available, or up to 30 whole underfur hairs if needed to supplement guard hairs. DNA extracts that were amplified at <11 loci were considered unsuccessful and excluded from any further analyses. After individual polar bears were
identified, each individual was amplified at an additional 9 markers including a sex-linked locus: MSUT-2, CPH9, CXX20, MU50, MU51, G10X, CXX173 (Ostrander et al. 1993; Paetkau et al. 1995; Taberlet et al. 1997; Kitahara et al. 2000; Proctor et al. 2002; An et al. 2010); and 14RENP07 and G10U (GenBank accession numbers AJ411284, and U22092.1, respectively).

Capture-recapture analyses.—Our first objective was to estimate the number of SB polar bears that annually visited the Kaktovik bone pile. Secondly, we aimed to estimate the annual apparent site fidelity to the bone pile. Thus, we performed 2 separate capture-recapture analyses. We used the open-population model POPAN (Schwarz and Arnason 1996), which is a parameterization of the Jolly-Seber model, to estimate the total number of bears visiting the Kaktovik bone pile for each year of our study. In addition, we used the open-population CJS model (Cormack 1964; Jolly 1965; Seber 1965) to estimate annual apparent site fidelity to the bone pile. Both capture-recapture analyses were conducted with Program MARK 8.1 (Cooch and White 2017; White and Burnham 1999). We used open-population capture-recapture methods because preliminary analyses using Program CloseTest revealed that bears visiting the Kaktovik bone pile did not represent a closed population (Stanley and Burnham 1999).

To estimate the annual number (N) of polar bears at the Kaktovik bone pile we used the POPAN model and conducted separate analyses for each year of our study: 2011, 2012, 2013, and 2014. Thus, we produced individual capture histories for each polar bear identified in the sample set for each year. The sampling occasions were bi-weekly or monthly depending on the amount of captures over a given amount of time. The POPAN model assumes the individuals represent a portion of a larger
superpopulation (Kendall 1999), which was appropriate for our analyses because we found that bears using the bone pile did not represent a closed population. The POPAN model estimates abundance ($N$), apparent survival ($\phi$), detection probability ($p$), and probability of entry ($pent$). $N$ can be thought of as either the total number of animals available for capture at any time during the study or as the total number of animals ever in the sampled area between the first and last occasion of the study. For our study, we interpreted $N$ as the total annual number of bears that visited the bone pile. Furthermore, we interpreted the value of $\phi$ from the POPAN model as polar bear site fidelity to the bone pile from one sampling occasion to the next during the sampling period. Apparent survival ($\phi$) is defined as the product of the true survival probability and the probability of being available for capture, which in this case is probability the animals remain on the study area (site fidelity). The probability of permanently leaving the bone pile would be much greater than the probability an individual would die over the course of the period that the hair snag was implemented each year (i.e., ~2 to 5 months). We constructed a series of models and fit them to the capture data for each year. We used every possible combination of models in which $p$, $pent$, and $\phi$ were held constant (.) or were allowed to vary by gender ($g$) and time ($t$), and $N$ was allowed to vary by gender ($g$). We had 23 a priori models for year 2011, 45 for 2012, 52 for 2013, and 35 for 2014. For each year, we estimated overdispersion ($\hat{\epsilon}$) to determine goodness–of–fit of the global POPAN model that converged well {$\phi(g^*t) p(g^*t) pent(.)$} by using Program RELEASE. Program RELEASE performs a series of Chi-square tests to evaluate model fit, with $\hat{\epsilon}$ estimated as $\frac{\chi^2}{df}$, where $\chi^2$ is the sum over all chi-squared tests and df is the sum of the degrees of
freedom. When \( \hat{c} \) was >1, we used QAIC\(_c\) for model selection and \( \hat{c} \) to inflate variances of parameter estimates (Burnham and Anderson 2002). Lastly, to properly account for model uncertainty, the annual \( N \) estimates of bears visiting the bone pile were obtained by model averaging, in which each model contributed to the final estimate according to its AIC\(_c\) weight (Burnham and Anderson 2002).

To estimate the annual apparent site fidelity to the bone pile we used the open-population CJS model (Cormack 1964; Jolly 1965; Seber 1965). Specifically, we constructed individual capture histories for each bear identified in our sample set, in which each year represented a sampling occasion: 2011-2014. Thus, we had 4 sampling occasions. The CJS model estimates apparent survival \( (\phi) \) and recapture probabilities \( (p) \) between each sampling occasion. Apparent survival is the probability that an animal survived the time period and was available for capture later. However, here \( \phi \) represents the probability that an animal survived the time period between the hair snag sampling periods, and returned to the bone pile and was, consequently, available for recapture.

Similar to the POPAN model, we interpreted the value of \( \phi \) from the CJS model as apparent site fidelity to the bone pile due to the relatively short duration of our study compared to the average lifespan of a polar bear. We constructed a series of models and fit them to the capture data. We used every possible combination of models in which \( p \) and \( \phi \) were held constant (.) or were allowed to vary by gender (\( g \)) and time (\( t \)). We had 18 \textit{a priori} models. We estimated overdispersion (\( \hat{c} \)) to determine goodness–of–fit of the most global CJS model that converged well \( \{\phi(g+t) p(g+t)\} \) by using the median \( \hat{c} \) simulation procedure in Program MARK. We simulated data sets over a range of
overdispersion levels and compared \( \hat{c} \) (calculated as deviance divided by deviance degrees of freedom) from these simulations with the observed \( \hat{c} \). We simulated 100 data sets at each of 10 levels of overdispersion \((c)\) and estimated \( \hat{c} \) using logistic regression, as the value where half of the simulated data sets had \( \hat{c} \) greater than the observed \( \hat{c} \) (median \( \hat{c} \)). When median \( \hat{c} \) was >1, we used QAIC\(_c\) for model selection and \( \hat{c} \) to inflate variances of parameter estimates (Burnham and Anderson 2002). We used model averaging to obtain estimates of apparent fidelity \((\phi)\) and recapture probabilities \((p)\) to account for model uncertainty (Burnham and Anderson 2002).

**RESULTS**

We collected 1,477 hair samples over the 4-year study period during the fall and early winter. The hair snag was implemented throughout the following time-periods for year 1, year 2, year 3, and year 4, respectively: 15 Sep 2011-9 Dec 2011 (85 days), 13 Oct 2012-27 Feb 2013 (137 days), 8 Oct 2013-20 Jan 2014 (104 days), and 13 Sep 2014-17 Nov 2014 (65 days). Genetic analysis identified 158 individuals (77 males and 81 females) over the study from the hair samples. The average length of stay at the bone pile (sexes combined) was 14 days \((SE = 1.3)\). The average length of stay at the bone pile for males was 14 days \((SE = 1.7)\) and 13 days \((SE = 1.9)\) for females. The length of stay that an individual was detected at the bone pile was from the first day to the last day of detection during a given year but does not imply continuous use of the bone pile. Furthermore, our length of stay estimate was also likely an underestimate of the true length of stay, as bears are not always detected when they are present.
Annual number of polar bears.—Estimates of \( \hat{c} \) were <1.0 for all years, suggesting no overdispersion and no lack of fit (range 0.72-0.87). Therefore, we used AIC\(_c\) model selection for POPAN models. We estimated all parameters from the POPAN model with model averaging (Table 3.1). We found 63 (SE = 8) male polar bears and 45 (SE = 5) females visited the Kaktovik bone pile in 2011 (Fig. 3.1). For 2012, we estimated 71 males (SE = 10) and 75 females (SE = 11) used the bone pile. Insufficient data prevented us from obtaining parameter estimates for year 2013. We estimated 24 (SE = 2) males and 27 (SE = 11) females visited the bone pile (Fig. 3.1) in 2014. Thus, combining sexes, we estimated that as many as 146 (SE = 21) SB polar bears visited the Kaktovik bone pile in 2012 and estimated a low of 51 (SE = 13) bears in 2014.

Apparent site fidelity of polar bears.—Median \( \hat{c} \) was 1.65, suggesting some overdispersion and lack of fit. Therefore, we used QAIC\(_c\) model selection and adjusted estimated standard errors and model parameter estimates using estimates of \( c \) and increased the number of parameters (\( K \)) in each model by 1 to account for estimation of \( c \). We estimated all parameters from the CJS model with model averaging (Table 3.2). We found rates of apparent site fidelity (\( \phi \)) for male polar bears ranged from 0.60 (SE = 0.07) for the interval 2012-13 to 0.61 for the interval 2011-12 and 2013-14 (SE = 0.07, SE = 0.08, respectively; Fig. 3.2). Rates of apparent site fidelity (\( \phi \)) for females was slightly higher than males and estimated at 0.69 (SE = 0.19) for all intervals (Fig. 3.2). Recapture probability (\( p \)) for male polar bears ranged from 0.41 (SE = 0.14) for the interval 2012-13 to 0.93 (SE = 0.08) for 2011-12 (Fig. 4). Recapture probability (\( p \)) for females ranged from 0.11 (SE = 0.08) for 2013 to 0.71 (SE = 0.18) for 2012 (Fig. 3.3).
The POPAN model (Schwarz and Arnason 1996) estimated that as many as 146 (SE = 21) polar bears (sexes combined) of the SB subpopulation used the bone pile located at Kaktovik, Alaska (Fig. 3.1) in 2012. This represents approximately 16% of the SB subpopulation using the most recent subpopulation estimate of ~ 900 bears in 2010 (Bromaghin et al. 2015). In addition, we obtained similar estimates for the proportion of males and females visiting the bone pile across all years, which implied that both sexes make use of the food subsidy. Our estimated proportion of SB bears utilizing the bone pile from 2012 is similar to a previous estimate of bears using the bone pile near Utqiagvik, Alaska, during the winter of 2010-2011 (Herreman and Peacock 2013). Herreman and Peacock (2013) estimated that approximately 15% of the SB subpopulation used the Utqiagvik bone pile using the subpopulation estimate of 1,526 bears from 2006 (Regehr et al. 2006). We estimated a low of 51 (SE = 13) bears (sexes combined) using the bone pile in 2014. Previous research demonstrated that the number of bears onshore was related to sea ice conditions (Atwood et al. 2016). Hence, we suspect that the number of polar bears visiting the bone pile likely fluctuated among years due to other factors (e.g., sea ice conditions and quantity of subsistence-harvested whale remains). Lastly, we found that the average length of stay at the bone pile (sexes combined) was roughly two weeks. Movement of the bears before and after visiting the bone pile remains unknown. For instance, we are unsure if the bears that visited the bone pile remain onshore and visit other bone locations or utilize other onshore resources (e.g., human refuse or sea birds) or if the bears swim to offshore sea ice. We recommend that
future research investigate movement of bears before and after visiting the bone pile with the use of GPS collars.

Likely, there are more SB polar bears using subsistence-harvested bowhead whale carcasses than we estimated because bone piles have been present near the communities of Cross Island and Utqiagvik (until 2012) in addition to Kaktovik (Suydam and George 2012). Diet analysis on the SB subpopulation revealed that many polar bears are feeding on bowhead whale carcasses (Rogers et al. 2015; McKinney et al. 2017). For example, researchers reported that bowhead whale was detected via quantitative fatty acid signature analysis (QFASA) in ~79% of the winter-spring diets for SB polar bears, which was nearly as high as the detection rates for their primary prey of ice seals (McKinney et al. 2017). Another diet study used tissue samples and investigated carbon and stable isotope profiles in adult female polar bears of the SB subpopulation. The researchers found that a number of samples were depleted in $^{15}$N relative to the mean, which they suggested was due to the consumption of bowhead whale carcasses (Rogers et al. 2015).

Thus, our estimate for the number of SB polar bears utilizing the bone pile in Kaktovik, Alaska, is a conservative estimate in regards to the entire subpopulation of bears using bowhead whale carcasses along the northern coast of Alaska.

Polar bears that feed at the Kaktovik bone pile are in close proximity to a human settlement, which creates the potential for human-bear conflicts. The other bone pile (e.g., Cross Island) is also in close proximity to human settlements (i.e., the Prudhoe Bay and Kuparuk oil fields). The spatial overlap of polar bears and people has the potential to increase the risk of human-bear interactions and conflicts. The Arctic is expected to continue to warm (Larsen et al. 2014), thus we expect polar bears will continue utilizing
subsistence-harvested bowhead whale carcasses with a potential increase in numbers. Properly managing polar bears at the bone piles and adjacent areas will be critical to reduce the potential for human-bear conflicts. For instance, communities that hunt whales may want to consider situating bone piles further away from human settlements for the safety of people and polar bears.

Our estimates of annual apparent site fidelity to the bone pile for male polar bears were similar among years with a high of 0.61 (SE = 0.08) during 2013-14 (Fig. 3.2). Females had slightly higher estimates of annual apparent site fidelity to the bone pile, which was estimated at 0.69 (SE = 0.19) for all time intervals. Thus, we concluded that ~61% for males and ~69% for females of the SB subpopulation returned to the bone pile each year. To our knowledge, no other studies have investigated annual fidelity to the bone pile. Hence, our estimates of apparent site fidelity provide meaningful management information as we expect more bears to come onshore and feed at subsistence-harvested whale carcasses. When interpreting our estimates of annual apparent site fidelity to the bone pile, it is noteworthy to mention that our estimates could be slightly confounded with survival. We interpreted our estimates of apparent survival from the CJS model as primarily site fidelity due to the relatively short duration of the study compared to the average lifespan of polar bears. Therefore, we recommend that data continue to be collected at the Kaktovik bone pile for additional years with the goal of using other genetic capture-recapture models (e.g., multi-state open robust design), which can accurately separate estimates of true survival from fidelity. Multi-state open robust design models use capture-mark-recapture data and have provided highly reliable estimates of
survival for other species, but typically require long-term data sets (Dutton et al. 2005; Troëng and Chaloupka 2007).

Our results indicated that as many as 146 polar bears visited the bone pile in a given year with a relatively high rate of site fidelity. We believe that it will be important to monitor for human-bear interactions and conflicts along the north coast of Alaska as more polar bears come onshore. If human-bear conflicts increase and are found to be associated with polar bears using the bone piles, we suggest evaluating the advantages and disadvantages of providing polar bears with access to the bone piles, and/or dispersing whale remains over a broader area away from the community (e.g., Wilson et al. 2017). Previous studies on grizzly (Ursus arctos) and black bears (Ursus americanus) found that human-bear conflicts markedly decreased when bear access to anthropogenic food sources (e.g., garbage) was essentially eliminated, though loss of access to an important food subsidy can adversely affect population dynamics (Gunther 1994; Stringham 1986). Managing the risk of human-polar bear conflict resulting from bears visiting the bone pile will require collaboration between resource managers and the community, along with regular monitoring for the potential of adverse population-level effects.

**LITERATURE CITED**


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melt season and implications for sea ice loss. Geophysical Research Letters
41:1216–1225.


Suydam, R., et al. 2015. Subsistence harvest of bowhead whales (*Balaena mysticetus*) by


### Table 3.1

Model selection results from capture-mark-recapture analysis of polar bears that used the Kaktovik, Alaska bone pile for 2011, 2012, and 2014, from the POPAN model. Constant (.), gender (g), and time (t) effects were considered on detection probability (p), entry probability (pent), and site fidelity (φ) either as main effect, in an additive, or in an interactive fashion. Abundance (N) was allowed to vary by g. Estimates of the annual number of bears (N) visiting the Kaktovik, Alaska bone pile presented in this paper were model-averaged over models in this table.

<table>
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<th>Model</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td>φ(.)p(.)pent(.)N(g)</td>
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<td>301.74</td>
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<tr>
<td>2012</td>
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<td></td>
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<tr>
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Table 3.2.—Model selection results from capture-mark-recapture analysis of polar bears that used the Kaktovik, Alaska bone pile for 2011-2014, from the CJS model. Constant (.), gender (g), and time (t) effects were considered on site fidelity (φ) and recapture probability (p) either as main effect, in an additive, or in an interactive fashion. Estimates of φ for bears visiting the Kaktovik, Alaska bone pile presented in this paper were model-averaged over models in this table.

<table>
<thead>
<tr>
<th>Model</th>
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<th>ΔQAICc</th>
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Fig. 3.1.—Model-averaged estimates of the annual number of female and male polar bears ($N$) using the bone pile near Kaktovik, Alaska, with 95% confidence intervals for 2011, 2012, and 2014, from the POPAN model.
Fig. 3.2.—Model-averaged apparent site fidelity probability ($\phi$) estimates with 95% confidence intervals for female and male polar bears to the bone pile near Kaktovik, Alaska, 2011-2014, from the CJS model.
Fig. 3.3.—Model-averaged estimates of recapture probability (p) estimates with 95% confidence intervals for female and male polar bears at the bone pile near Kaktovik, Alaska, 2011-2014, from the CJS model.
CHAPTER 4

BODY CONDITION IN POLAR BEARS ASSOCIATED WITH AN ALTERNATIVE FORAGING STRATEGY

Introduction

Understanding the capacity of a species to adapt to climate change is essential for conservation purposes. Polar bears (Ursus maritimus) are ice-dependent Arctic marine mammals (Amstrup 2003) and were listed as “threatened” under the U.S. Endangered Species Act in 2008 due to the observed and projected loss of sea ice habitat (U.S. Fish and Wildlife Service 2008). Polar bears of the southern Beaufort Sea (SB) subpopulation appear to be negatively impacted by changing sea ice conditions (Regehr et al. 2010; Rode et al. 2010; Bromaghin et al. 2015). Historically, bears of the SB subpopulation have spent the majority of the year on the sea ice with the exception of denning (Amstrup et al. 2000). However, several studies indicate that a higher proportion of SB polar bears are being observed onshore and feeding at subsistence-harvested bowhead whale (Balaena mysticetus) carcasses during late summer and fall when sea ice reaches its annual minima (Schliebe et al. 2008; Gleason & Rode 2009; Atwood et al. 2016; Wilson et al. 2017). The proportion of SB polar bears observed onshore appears to be linked to sea ice conditions (Atwood et al. 2016). Hence, it is critical to determine the fitness consequences (e.g., body condition and reproduction) of SB polar bears that come onshore and feed at whale carcasses as sea ice is predicted to continue to decline (Stroeve et al. 2012) and we expect more polar bears to respond to declining sea ice by coming onshore.
Polar bears depend on sea ice for mating, movement, and access to their primary prey of ringed seal (*Phoca hispida*) and bearded (*Erignathus barbatus*) seal (Amstrup 2003). The Arctic sea ice minimum extent is decreasing at a rate of 14% per decade with spring break-up occurring earlier and fall freeze-up occurring later (Stroeve *et al.* 2014), which is likely reducing the accessibility of seal prey for polar bears (Stirling & Derocher 1993). The optimal habitat for polar bears occurs over the shallow waters of the continental shelf (Durner *et al.* 2009) due to high biological productivity and seal densities (Reeves 1998; Wang, Cota & Comiso 2005). However, the length of time that ice is absent over the biologically productive waters is lengthening due to warming temperatures. Thus, access to optimal habitats for polar bears has decreased and is expected to continue to decline (Durner *et al.* 2009). Research indicates that decreasing sea ice is negatively influencing survival (Regehr *et al.* 2010; Bromaghin *et al.* 2015), body condition, and reproduction (Rode *et al.* 2010) for the SB polar bear subpopulation.

Another consequence of reducing sea ice conditions is a higher proportion of SB polar bears becoming increasingly reliant on land during the summer and fall when sea ice retracts to its annual minima (Atwood *et al.* 2016). The proportion of SB radio-collared polar bears observed onshore has tripled over a period of 15 years, increasing from 5.8% during 1986-1999 to 20.0% during 2000-2014, with a peak of 37.0% in 2013. Furthermore, researchers detected trends of earlier arrival onshore, increased length of stay, and later departure back to the sea ice. All of the trends were related to declines in sea ice habitat over the biologically productive continental shelf and changes to sea ice phenology (Atwood *et al.* 2016).
The proportion of SB polar bears observed onshore increases when sea ice retracts farther from the shore during the summer melt season (Schliebe et al. 2008; Wilson et al. 2017). In addition, the spatial distribution of onshore bears appears to be linked to the reduced accessibility of ringed seals in offshore waters and the availability of subsistence-harvested bowhead whale carcasses (Schliebe et al. 2008; Atwood et al. 2016; Wilson et al. 2017). Coastal indigenous communities annually hunt bowhead whale and deposit the unused remains at localized “bone piles” (Ashjian et al. 2010), which attract polar bears and other wildlife species. Bone piles are comprised of trimmed blubber, meat, and bones (Ashjian et al. 2010).

Diet analyses found that a high proportion of SB polar bears are feeding at bowhead whale remains (Rogers et al. 2015; McKinney et al. 2017), with the proportion of bowhead whale detected in the winter-spring diets of SB bears reaching 79% (McKinney et al. 2017). Bone piles occur in Alaska at Cross Island (~147°W) and Kaktovik (~143°W). Bowhead whales have thick blubber, which comprises up to 50% of their body mass (George 2009). Therefore, the whale carcasses in Alaska represent a persistent and reliable marine food subsidy during the fall for SB polar bears, which can potentially influence increments of fitness (e.g., body condition and reproduction).

The increase in SB polar bears coming onshore when sea ice retracts during the summer and fall (Atwood et al. 2016) may be a behavioral modification in response to climate change. Numerous studies have documented a species’ response to climate change (Bradshaw & Holzapfel 2006) with varying fitness consequences. For instance, reed warblers (Acrocephalus scirpaceus) in Europe have started breeding progressively earlier, which corresponded to increasing temperatures (Halupka, Dyrcz & Borowiec
Researchers predicted that the increasing temperatures would ultimately lead to increased fitness for reed warblers due to higher re-nesting potential and fewer nest losses in warmer seasons. Another study found that earlier breeding increased the development rate of a yellow-bellied marmot (Marmota flaviventris) population, which increased reproductive output and a rapid increase in population size (Ozgul et al. 2010). In contrast, another study determined that the mean fitness for a roe deer (Capreolus capreolus) population decreased because of a mismatch between the timing of roe deer births and the increasingly earlier availability of peak resources induced by climate change (Plard et al. 2014).

Limited information is available on the fitness consequences for SB polar bears that come onshore and feed at bowhead whale carcasses when sea ice reaches its annual minima in summer and fall. One study placed telemetry transmitters and activity loggers on SB bears and found similar activity patterns and physiological condition for onshore and offshore bears, which suggested that neither onshore or offshore bears realizes a greater benefit than the other (Whiteman et al. 2015). Alternatively, researchers discovered that polar bears that consumed less seal prey and/or more bowhead whale were in better body condition than those that consumed less bowhead whale (McKinney et al. 2017). However, the latter study used subjective fatness index as a measure of body condition, while calculated measures of body mass relative to body size have been shown to accurately reflect body condition for polar bears (Cattet et al. 2002) but may have certain limitations (Pagano, Rode & Atkinson 2017). It is important to note that these studies used different methodology when making inferences about fitness (i.e., activity patterns and subjective fatness index), which might explain the contradicting conclusions.
To our knowledge, no study has investigated reproduction for bears that come onshore and feed at whale carcasses for the SB subpopulation.

Our objective was to examine body condition and reproduction for polar bears in the SB subpopulation that come onshore and feed at bowhead whale carcasses when the sea ice retracts to its annual minima. Moreover, we aimed to determine if the length of the prior year open-water season had an effect on body condition and reproductive output since the number of onshore bears was previously linked to sea ice conditions and the availability of whale carcasses (Atwood et al. 2016). Specifically, we addressed the following questions: 1) Does the proportion of bowhead whale in the diet have a significant effect on the body condition for polar bears? 2) Does the proportion of bowhead whale in the diet have a significant effect on the reproductive output (i.e., litter mass and litter size) for polar bears? 3) Does the length of the open-water season from the prior year have a significant effect on the body condition and reproductive output for polar bears?

Materials and methods

STUDY AREA

Polar bears of the SB subpopulation inhabit regions along the north coast of Alaska and Canada from Icy Cape, Alaska, USA, (70.3°N, 161.9°W) in the west, to Tuktoyaktuk, Northwest Territories, Canada, (69.4°N, 133.0°W) in the east. We studied polar bears of the SB subpopulation from 2004 to 2015 along the north coast of Alaska from Utqiagvik in the west to Kaktovik in the east (141-157°W). Shallow, productive waters of the southern Beaufort Sea over the narrow continental shelf characterize the
nearshore environment (Jakobsson et al. 2008). The southern Beaufort Sea is typically ice covered during the winter months from October to June, and sea ice retracts to its annual minima in the summer and fall from July to September. There has been a trend for earlier melt onset, reduced summer sea ice extent, a lengthening of the open-water period (i.e., sea ice retracts towards the pole during the annual sea ice minimum), and later freeze-up in recent years (Stroeve et al. 2014).

The communities of Utqiagvik, Cross Island, and Kaktovik in Alaska annually harvest bowhead whales in the study area during the fall season. The locations of the whale carcasses have been shown to influence the onshore distribution for polar bears of the SB subpopulation (Schliebe et al. 2008; Atwood et al. 2016; Wilson et al. 2017). The three communities landed a combined average of 23 bowhead whales per year from 2004 to 2014 (Suydam & George 2012; Suydam et al. 2013; 2014; 2015), with whales ranging in length from ~5 to 20 m (Suydam & George 2012).

SAMPLING

We captured polar bears in the spring from March to mid-May from 2004 to 2015 in coastal areas (i.e., within 150 km of the coast) along northern Alaska. Adults and subadults were encountered opportunistically from a helicopter and immobilized with tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®, Fort Dodge and Warner-Lambert Co.) using a projectile syringe fired from a dart gun. Yearlings and cubs-of-the-year were captured by darting from the ground or hand injection. Argos or global positioning system (GPS) platform transmitter terminal (PTT) satellite radio-collars were fitted to a subset of adult female polar bears to collect spatial and movement
data (Durner et al. 2009). During the spring of 2012, remote biopsy darting from a helicopter was also conducted to collect tissue samples from adult and subadult bears (Pagano, Peacock & McKinney 2014). We recorded age class and determined sex through genetic analysis for samples collected via remote biopsy darting. Additionally, we recorded the number and age class of accompanying cubs, when applicable.

We recorded location of capture, sex, girth, body length, subjective fatness index, mass, skull width (i.e., zygomatic width) and length, number and age class of accompanying cubs, cub sex, cub weight, and cub skull width and/or length (Rode et al. 2010). Body length was measured as the straight-line distance from the tip of the nose to the end of the last tail vertebrae. Bears were weighed with a spring or dynamometer scale. We determined ages for captured polar bears by counting the growth layer groups in the cementum of a vestigial premolar tooth (Calvert & Ramsay 1998). Additionally, we collected subcutaneous adipose tissues from the rump region of captured polar bears by biopsy punch, which were frozen at -80°C for long-term storage (McKinney et al. 2017). Individual polar bears were identified via genetic analysis (Pagano et al. 2014).

BODY CONDITION AND REPRODUCTIVE OUTPUT

We used a body condition index (BCI) to quantify body condition (Cattet et al. 2002). This index has been empirically validated in polar bears to accurately reflect their body condition (Cattet et al. 2002) and has been used in recent studies to investigate polar bear body condition (Rode et al. 2014; Obbard et al. 2016). The BCI uses standardized residuals from the regression of body mass (BM) and straight-line body length (BL) as a measure of condition, with a potential range from -3 to +3. We applied an equation for
BCI established for polar bears of the southern Beaufort Sea subpopulation (Rode et al. 2014), where $\text{BCI} = (\ln BM - 2.29 \times \ln BL + 6.7)/(2.58 - 0.45 \times \ln BL)$. We used the established equation for BCI since our sample size was insufficient to generate a BCI equation with our data set. We verified that comparable results would be obtained using Quetelet’s index ($W/L^2$) as a second condition index (Rode et al. 2010) due to the limitation of being unable to generate a BCI equation specific to our data set.

Polar bears are seasonal breeders that typically mate in the spring and summer and produce cubs in dens during the winter months (Amstrup 2003). Larger female polar bears have been shown to produce larger litters and heavier cubs (Derocher & Stirling 1994), because larger females are likely in better condition. Furthermore, larger cubs-of-the-year (COY) and yearlings have been shown to have higher rates of survival (Derocher & Stirling 1996). Thus, we described reproductive output by litter mass and litter size (Rode et al. 2010; 2014). We recorded litter mass and litter size for COY and yearlings accompanying adult females during spring captures. Spring captures overlapped with the timing of den emergence but lasted beyond the period of time when all females would have emerged from dens.

QUANTITATIVE FATTY ACID SIGNATURE ANALYSIS

The quantitative fatty acid signature analysis (QFASA) approach was used to estimate polar bear diets for bears captured from 2004 to 2015 [see (McKinney et al. 2017) for details; all QFASA work was conducted by the McKinney Lab: https://mckinneylab.weebly.com/the-mckinney-lab.html]. QFASA estimates the proportions of individual prey species consumed by determining the weighted mixture of
prey fatty acid signatures that best matches each individual polar bear signature after accounting for disparities between predator and prey due to predator metabolism. Specifically, we estimated the proportion of bowhead whale, beluga whale (*Delphinapterus leucas*), ringed seal, and bearded seal in the diets of individual polar bears. We used diet estimates from spring-sampled polar bears in all analyses because samples collected during this period roughly represent winter-spring diets. We used the variation of the estimates of bowhead whale in the diet among bears to calculate the standard errors (SE).

We verified that polar bears known to use the bowhead whale carcasses had a signature of bowhead whale in their diet from data obtained from separate studies on the SB subpopulation. A previous study implemented hair snags during the fall and early winter seasons at the bowhead whale carcasses and identified individuals through genetic analysis (Herreman & Peacock 2013). Thus, we confirmed that polar bears known to feed at the bowhead whale carcasses from data collected at the hair snag had bowhead whale detected in their diet from the QFASA approach the following spring that the bear was captured.

**OPEN-WATER SEASON**

We hypothesized that the body condition and reproductive output for SB polar bears that come onshore and feed at whale carcasses in the fall season were influenced by sea ice conditions. Specifically, we estimated the length of the open-water season when sea ice reached its annual minima. The length of the open-water season was defined as the length in days starting at when the proportion of the continental shelf covered by
>50% sea ice concentration decreases below ≤50% and ending when it increases >50%.

Daily sea ice data from the National Snow and Ice Data Center (NSIDC; Boulder, Colorado, USA) were used to develop concentration and distance metrics. We estimated sea ice concentrations from a 25 x 25 km resolution raster of passive microwave satellite imagery (Cavalieri et al. 1996). The shelf break and shelf area were delineated by the 300 m isobath for the offshore region. We defined areas covered by sea ice based on an ice concentration of >50%, which is most often used as a threshold above which sea ice habitat is most suitable for polar bears (Stirling, Lunn & Iacozza 1999). Sea ice data were acquired, processed, and analyzed by D. Douglas, U.S. Geological Survey, Alaska Science Center.

STATISTICAL ANALYSES

We used linear mixed-effects models to test for relationships between BCI and the length of the prior year open-water season (ow) and the proportion of bowhead whale (bowhead) detected in the diet of an individual bear. We provide a description of all covariates in Table 4.1. We included bear as a random effect (intercept only) to account for some bears occurring multiple times in the data set. We tested for relationships between BCI and ow during the previous year (t – 1), because our captures were conducted in the spring. We controlled for the factors of social class (social) and capture date (cdate), which can affect BCI. We designated bears to a social class based on age and the presence of cubs: adult males (≥5 years), adult females accompanied by cubs, solitary adult females (≥5 years), subadults (2-4 years) and yearlings. We included models with interactions between bowhead and ow, because we expected that changes in
BCI in relation to the proportion of bowhead whale detected in the diet of an individual might differ with the length of the open-water season. In addition, we included models with interactions between bowhead and cdate, because we expected that changes in BCI in relation to the proportion of bowhead whale detected in the diet might differ with capture date. We performed all statistical analyses in R version 3.4.3 (R Development Core Team 2016) and mixed-effects models were fitted using functions implemented in the ‘lme4’ package (Bates et al. 2014). We report the conditional R² for the top models, R²GLMM(c), which is considered an indication of the goodness-of-fit for each linear mixed-effects model. We estimated the conditional R² using the ‘MuMin’ package in R (Barton 2016).

We used generalized linear models to test for relationships between litter mass and ow and litter mass and bowhead. We controlled for the factors of litter size (lsize), cdate, maternal age (mage), and maternal body condition (mcondition) because they can affect litter mass (Derocher & Stirling 1998). We included models with interactions between bowhead and ow and interactions between bowhead and cdate. Separate analyses were conducted for COY and yearlings. We report the adjusted R² for the top models.

To determine if ow and bowhead affected litter size, we used logistic regression to model the probability that a female had more than one dependent young. Litter size was a binary categorical variable where “0” represented 1 dependent young and “1” represented 2 or more dependent young. We controlled for the factors of cdate, mage, and mcondition because they can affect litter size. We included models with interactions between bowhead and ow and interactions between bowhead and cdate. Separate analyses were
conducted for COY and yearlings. We report the Nagelkerke’s $R^2$ for the top models, which was determined using the ‘fmsb’ package in R (Nakazawa 2017).

To facilitate comparison of a reasonable number of models and avoid overfitting, we used a tiered approach for model selection and assessed relative support for competing models at each tier using $\Delta$AICc values (Burnham & Anderson 2002). Models that had the lowest AIC values were considered to explain the most variation with the fewest parameters (Burnham & Anderson 2002). We used this tiered approach to model selection to avoid including spurious effects in final models. First, we constructed a suite of models for each response variable (i.e., BCI, litter mass, and litter size) that contained the additive effects of the “control” covariates (e.g., social, cdate, ls, age, and mcondition). If the control covariates were not well supported individually (i.e., did not perform better than a model omitting those effects), we did not include them in more complex additive or interactive models with other covariates. Next, we believed that bowhead, ow, and cdate had the potential for non-linear relationships with our response variables. Thus, we compared candidate models which included first order, second order (quadratic), and third order (cubic) terms for bowhead, ow, and cdate in addition to the other factors, to determine the appropriate order for each predictor.

We constructed a suite of candidate models a priori to test our hypotheses while controlling for other covariates we found to affect our response variables. Specifically, we built candidate models that included none, one, or both of our explanatory variables of interest: bowhead and ow. We report models with $\Delta$AICc <2, because models with $\Delta$AICc <2 should receive consideration when making inferences (Burnham & Anderson 2002). When faced with model uncertainty (i.e., a non-significant variable was within the
top models), we calculated 85% confidence intervals for parameter estimates, and considered parameters whose 85% confidence intervals overlapped with zero to be uninformative (Arnold 2010). Our rationale was that if there was no bowhead or ow effect on our response variables then they would not be included in the top models following model selection procedures. We tested for collinearity between all predictor variables, examined regression residuals for evidence of heteroscedasticity, and examined quantile-quantile plots for evidence of non-normality.

Results

We analyzed 550 biopsy samples via the QFASA approach to obtain estimates of the proportion of bowhead whale, beluga whale, bearded seal, and ringed seal in the diets from 413 polar bears of the SB subpopulation from 2004 to 2015. We obtained an average of 46 (SE = 3) samples per year, which provided diet estimates. We found 331 of 413 (~80%) individual bears had a bowhead whale signature in their diet. We found that ~46% of all sampled individual bears within a given year had ≥ 0.10 proportion of bowhead whale detected in their diet, with a low of ~34% and a high of ~63% of sampled bears. The average proportion of bowhead whale in the diet for all social classes was ~0.17 (SE = 0.008). Adult male polar bears (n = 207 samples) had the highest estimated proportion of bowhead whale in their diet of ~0.21 (SE = 0.014), while yearlings (n = 38 samples) had the lowest with an estimate of ~0.11 (SE = 0.022). Values of the proportion of bowhead whale detected in the diet ranged from 0.00 to ~0.98, indicative that polar bears varied greatly in their consumption of bowhead whale. We found that the average proportion of bowhead whale in the diets of bears known to visit
the bowhead whale carcasses \( (n = 15) \) was \(~ 0.28\) (SE = 0.058) based on data collected from the hair snag. Bowhead whale was detected in the diet of \(~ 93\%\) of the polar bears known to feed at the bowhead whale carcasses (i.e., 14/15) via the hair snag. The average length of the open-water season was \(~ 126\) (SE = 3) days from 2003 to 2014, with a minimum of 105 days in 2006 and a maximum of 143 days in 2010.

**BODY CONDITION**

We had 367 observations from 285 (140 males and 145 females) individuals that provided sufficient data to calculate BCI. The top-ranked model (Table 4.2) for BCI had a positive and linear *bowhead* effect (\( \beta = 0.50, \ SE = 0.25, \ P = 0.05; \) Table 4.3), which suggested that bears with higher proportions of bowhead whale in their diet had a higher BCI (Fig. 4.1). We found that *ow* was associated with BCI in a non-linear fashion (Fig. 4.2), which implied that BCI varied with the length of the open-water season from the prior year. Specifically, *ow* was positive (\( \beta = 3.5, \ SE = 0.96, \ P < 0.001; \) Table 4.3) and \( ow^2 \) was negative (\( \beta = -2.2, \ SE = 0.97, \ P = 0.02; \) Table 4.3), which taken collectively, suggested a concave relationship between BCI and the length of the prior year open-water season, with BCI declining as the length of the open-water season increased past a maximum of 134 days (Fig. 4.2). The 3 top-ranked models accounted for \(~ 89\%\) of the model weight (Table 4.2). Comparable results were obtained with Quetelet’s index, which corroborated our BCI findings.

**LITTER MASS**

We had 48 observations that provided sufficient data to determine litter mass of COY. We controlled for *lsize, mage*, and *mcondition*, as we found these covariates had an
impact on litter mass of COY and yearlings. The top-ranked model for litter mass of COY included the control covariates: litter size was intuitively influencing litter mass (i.e., more cubs, higher litter mass), and litter mass increased with maternal age and condition (Table 4.3). The second-ranked model included a positive and linear $ow$ effect ($\beta = 0.15, SE = 0.11, P = 0.18$; Table 4.2) in addition to the control covariates. However, the 85% confidence intervals for $ow$ overlapped zero, indicating $ow$ was an uninformative covariate. The 2 top-ranked models for litter mass of COY accounted for 79% of the model weight. We had 29 observations that provided sufficient data to determine litter mass of yearlings from polar bears of the SB subpopulation, with the top-ranked model including the control covariates (i.e., $lsize$, $mage$, $mcondition$). We did not find evidence for any effects of $bowhead$ or $ow$ on litter mass of yearlings.

LITTER SIZE

We had 52 observations that provided data on litter size of COY from polar bears of the SB subpopulation. We controlled for $mage$ and $mcondition$ for litter size of COY and yearlings, since we found that these covariates influenced litter size. The top-ranked model for litter size of COY included the control covariates (Table 4.2): maternal age was positively related to litter size and maternal condition was negatively related to litter size (Table 4.3). We found a positive and linear $bowhead$ effect on COY litter size ($\beta = 3.5, SE = 2.7, P = 0.20$) in the second-ranked model (Table 4.2) in addition to the control covariates. However, the 85% confidence intervals for $bowhead$ overlapped zero, suggesting it was an uninformative covariate. The 2 top-ranked models accounted for 74% of the model weight. We had 44 observations that provided data on litter size of
yearlings from polar bears of the SB subpopulation. We found a negative and linear ow effect on yearling litter size ($\beta = -0.045$, SE = 0.04, $P = 0.28$) in the second-ranked model (Table 4.2), in addition to the control covariates. However, the 85% confidence intervals for ow overlapped zero. The 2 top-ranked models for litter size of yearlings accounted for 77% of the model weight.

**Discussion**

We found that SB polar bears with higher proportions of subsistence-harvested bowhead whale in their diet were in better body condition the following spring (Fig. 4.1). Thus, polar bears realized better body condition from an alternative foraging strategy by feeding at a marine food subsidy. Alternatively, polar bears that consumed higher proportions of prey hunted from the sea ice had lower body condition. Therefore, our findings demonstrated that polar bears that fed primarily on prey items hunted from sea ice and likely remained on the sea ice year-round had lower body condition than bears coming onshore and feeding at bowhead whale carcasses. However, the presence of whale carcasses is entirely dependent on human activity and therefore a limited food resource and will not sustain the entire SB subpopulation as more polar bears adopt onshore behavior in response to declining sea ice conditions.

Our body condition results corroborate a previous study that examined body condition via subjective fatness index for SB polar bears from 2004-2012 (McKinney et al. 2017). The researchers estimated the proportions of bowhead whale, ringed seal, bearded seal, and beluga whale in polar bear diets using the QFASA approach and reported that bears with higher proportions of bowhead whale and lower proportions of
ringed seal in their diets were in better condition (McKinney et al. 2017). We speculate that the increased body condition that we observed for bears feeding at subsistence-harvested whale carcasses was linked to limited access to prey for bears that remained on the sea ice year-round. For instance, another study measured field metabolic rates of SB polar bears on the spring sea ice and found that high metabolic rates coupled with low intake of prey resulted in an energy deficit for more than half of the bears examined (Pagano et al. 2018). The researchers concluded that energy demands for polar bears will likely increase as sea ice continues to decline and become more fragmented, which could lead to declines in body condition and survival. Thus, we concluded from our findings that polar bears that came onshore and fed at an energy-rich marine food subsidy achieved better body condition than bears that remained on the sea ice year-round, which likely experienced energy deficits and limited access to prey. We believe that polar bears that continue to feed primarily on prey items from the sea ice and remain on the sea ice year-round will continue to undergo declines in body condition as sea ice is predicted to continue to decrease (Stroeve et al. 2012).

We also demonstrated SB polar bears were in better body condition the following spring as the length of the prior year open-water season increased, however, the relationship was concave (Fig. 4.2). It is plausible that polar bears fed more heavily at bowhead whale carcasses as the length of the open-water season increased (e.g., visiting the whale carcasses more frequently and at greater numbers), since it has been shown that there is a positive relationship between the length of stay onshore for radio-collared bears and the open-water season (Atwood et al. 2016). Therefore, polar bears potentially achieved better body condition by coming onshore in greater numbers and feeding at
bowhead whale carcasses as the length of the open-water season increased. However, we did not find a significant interaction between the proportion of bowhead whale in the diet and the open-water season, likely because of the quadratic relationship of the open-water season. The concave relationship between BCI and the length of the open-water season suggested that polar bears were in better body condition as the length of the open-water season increased until the open-water season reached ~ 134 days, at which point, the association became negative. Hence, our findings revealed that body condition for SB polar bears began to decline as the length of the open-water season exceeded a threshold of ~ 134 days. Sea ice extent is expected to continue to decline and the southern Beaufort Sea is predicted to become essentially seasonally ice-free (i.e., <1.0 x 10^6 km^2) during the summer before the end of the 21st century (Stroeve et al. 2012), which our findings demonstrated, will likely have negative impacts on body condition for SB polar bears.

A prior study used mechanistic models for polar bears of the Western Hudson Bay to make predictions regarding survival and reproduction under climate change and reported that survival and reproduction are predicted to respond non-linearly to changing environmental conditions (Molnár et al. 2010; 2014). Specifically, researchers predicted that 2-3% of adult male polar bears would die with a fasting period of 120 days, and that 9-21% would die with a fasting period of 180 days (Molnár et al. 2014). Our findings seem to support this claim such that we found a non-linear response (i.e., concave) of body condition to sea ice conditions with the association reaching a maximum at ~ 134 days. We agree with the previously mentioned study that non-linearities can exist when relating vital rates to sea ice conditions and need to be considered to facilitate accurate projections for polar bears. Another study (Regehr et al. 2010) estimated survival for
polar bears of the SB subpopulation from 2001 to 2006 and reported little variation in survival up to about 127 ice-free days over the continental shelf (i.e., open-water season). However, the researchers found that survival declined beyond 127 ice-free days. Our body condition results support this finding, as we found body condition for polar bears appeared relatively insensitive to the length of the open-water season up to ~ 134 days, but beyond ~ 134 days, body condition declined (Fig. 4.2).

Previous research showed reduced reproductive output and body condition associated with declining sea ice for the SB subpopulation from 1982 to 2006 (Rode et al. 2010). Our findings are inconsistent with the aforementioned study as we found a concave association between body condition and open-water season. However, our data was collected more recently and over a shorter duration. The mean length of the open-water season from 1982 to 2006 was ~ 91 (SE = 6) days, whereas the mean length of the open-water season for our study was ~ 126 (SE = 3) days. Thus, polar bears during our study were experiencing, on average, much longer open-water seasons than the prior study. It is unclear whether the concave association we found for body condition and the open-water season was due to the disparate sea ice conditions during our study or the shorter duration in which we collected data. Moreover, SB polar bears have been observed onshore and feeding at whale carcasses in greater numbers over recent years (Atwood et al. 2016) and ringed seals appear to be in better body condition earlier in the spring in portions of their range (Harwood et al. 2012), which further complicates matters when interpreting our results. Lastly, it is also plausible that we are more likely to capture polar bears in the spring that summered onshore and visited the bone pile, which creates a sampling bias. We recommend future research investigate whether a sampling bias exists
during the SB polar bear capture effort. Earlier research on the SB polar bear subpopulation concluded that factors other than solely sea ice conditions influenced survival (Bromaghin et al. 2015). Likewise, we believe that the association between body condition with sea ice conditions can be complicated by other factors such as the availability of subsistence-harvested whale carcasses. Although sea ice conditions are expected to be the dominant driver of population dynamics over the long-term (Stirling & Derocher 2012), other region-specific factors need to be considered when developing appropriate strategies for management and conservation purposes.

We did not find that the proportion of bowhead whale in the maternal diet or the length of the open-water season from the prior year had an effect on litter mass or litter size of COY and yearlings. Thus, we concluded that SB polar bears did not have higher reproductive output by utilizing an alternative foraging strategy. Furthermore, sea ice conditions from the prior year had no impact on reproductive output from our study. We need to consider the relatively low goodness-of-fit values for our reproduction findings (Table 4.2), which implied that other covariates could be more important for reproductive output that were not accounted for in our models (e.g., den phenology, den distribution, and prey availability). Previous research on the SB subpopulation found that female polar bears of the SB subpopulation have shifted to more land-based denning between 1985 and 2013, and the frequency of land-based denning was associated with the distance that the sea ice retreated from the coast (Olson et al. 2017). In addition, female polar bears that came onshore during the summer subsequently denned on land, whereas females that remained on the sea ice during the summer were less likely to den on land. Furthermore, female polar bears that denned on land had higher reproductive success than females that
denned on the sea ice (Rode et al. 2018). We found approximately half of the pregnant females during our study denned on land based on GPS and Argos locations of collared females (i.e., 6/11). Insufficient data prevented us from conducting statistical analyses relating land-based denning to sea ice conditions and reproductive output. However, we believe that den phenology and den distribution are important to reproductive output, and we recommend that future research include these covariates, when feasible.

Our results revealed that SB polar bears achieved higher body condition by coming onshore and feeding at a marine subsidy than bears that supposedly remained primarily on the sea ice. We concluded that polar bears of the SB subpopulation achieved higher increments of fitness by utilizing onshore habitat during the summer and fall. We expect more polar bears to come onshore as sea ice continues to decline. Onshore habitat and marine food subsidies represent a potential refugia for SB polar bears to avoid the deleterious consequences of remaining on the sea ice. However, the presence of the marine food subsidy is entirely dependent on human activity, is a limited food resource, and therefore and we believe this resource will be unable to sustain the entire subpopulation as more polar bears adopt an onshore behavioral strategy. Thus, overall, we expect polar bears in the SB subpopulation will ultimately suffer in terms of body condition due to diminishing sea ice. We urge continued monitoring of body condition, reproduction, and survival on polar bears in the SB subpopulation in order to make informed management decisions in response to changing global temperatures.
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*Biological Conservation*, 214, 288–294.
Tables and figures

Table 4.1. Description of the covariates used to model their influence on BCI, litter mass, and litter size for polar bears in the SB subpopulation.

<table>
<thead>
<tr>
<th>Covariates</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>bowhead</td>
<td>Continuous variable representing the proportion of bowhead whale in the diet of individual bears</td>
</tr>
<tr>
<td>ow</td>
<td>Integer variable representing the length in days of the open-water season</td>
</tr>
<tr>
<td>cdate</td>
<td>Integer variable of the day of the year in which capture occurred (0-365)</td>
</tr>
<tr>
<td>social</td>
<td>Categorical variable where: AM = adult males ≥ 5 years, AC = female with cubs, SF = solitary females ≥ 5 years, S = subadults 2-4 years, and Y = yearlings</td>
</tr>
<tr>
<td>mage</td>
<td>Integer variable representing the age of cub's mother at the time of capture</td>
</tr>
<tr>
<td>Mcondition</td>
<td>Continuous variable representing the body condition (i.e., BCI) of cub's mother at time of capture</td>
</tr>
<tr>
<td>lsize</td>
<td>Binary categorical variable representing the number of cubs in a litter where 0 = 1 dependent young and 1 = 2 or more dependent young</td>
</tr>
<tr>
<td>bear</td>
<td>Categorical variable representing bear ID</td>
</tr>
</tbody>
</table>
Table 4.2. Models with ΔAICc ≤ 2 for BCI, litter mass of COY, litter mass of yearlings, litter size of COY, and litter size of yearlings. We report the conditional R² for BCI, adjusted R² for litter mass, and Nagelkerke’s R² for litter size.

<table>
<thead>
<tr>
<th>Model</th>
<th>ΔAICc</th>
<th>wi</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>BCI</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>bowhead + ow + ow² + social + cdate</td>
<td>0</td>
<td>0.43</td>
<td>0.73</td>
</tr>
<tr>
<td>bowhead + ow + ow² + social + cdate + bowhead x cdate</td>
<td>0.9</td>
<td>0.28</td>
<td>0.73</td>
</tr>
<tr>
<td>ow + ow² + social + cdate</td>
<td>1.8</td>
<td>0.18</td>
<td>0.73</td>
</tr>
<tr>
<td>Litter mass COY</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lsize + mage + mcondition</td>
<td>0</td>
<td>0.48</td>
<td>0.37</td>
</tr>
<tr>
<td>ow + lsize + mage + mcondition</td>
<td>0.88</td>
<td>0.31</td>
<td>0.39</td>
</tr>
<tr>
<td>Litter mass yearlings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lsize + mage + mcondition</td>
<td>0</td>
<td>0.63</td>
<td>0.70</td>
</tr>
<tr>
<td>Litter size COY</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mage + mcondition</td>
<td>0</td>
<td>0.44</td>
<td>0.15</td>
</tr>
<tr>
<td>bowhead + mage + mcondition</td>
<td>0.73</td>
<td>0.30</td>
<td>0.22</td>
</tr>
<tr>
<td>Litter size yearlings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mage + mcondition</td>
<td>0</td>
<td>0.53</td>
<td>0.29</td>
</tr>
<tr>
<td>ow + mage + mcondition</td>
<td>1.55</td>
<td>0.24</td>
<td>0.33</td>
</tr>
</tbody>
</table>
Table 4.3. Parameter estimates from the top-ranked model for BCI, litter mass of COY, litter mass of yearlings, litter size of COY, and litter size of yearlings, with standard errors and $P$-values, for polar bears in the SB subpopulation.

<table>
<thead>
<tr>
<th>Effect</th>
<th>$\beta$</th>
<th>SE</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>BCI</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>bowhead</td>
<td>0.4965</td>
<td>0.2498</td>
<td>0.048</td>
</tr>
<tr>
<td>ow</td>
<td>3.5202</td>
<td>0.9574</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$ow^2$</td>
<td>-2.2554</td>
<td>0.9736</td>
<td>0.021</td>
</tr>
<tr>
<td>social - adult males</td>
<td>2.0369</td>
<td>0.1338</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>social - subadults</td>
<td>0.1068</td>
<td>0.1467</td>
<td>0.467</td>
</tr>
<tr>
<td>social - solitary females</td>
<td>0.1261</td>
<td>0.1477</td>
<td>0.394</td>
</tr>
<tr>
<td>social - yearlings</td>
<td>-0.1145</td>
<td>0.1938</td>
<td>0.555</td>
</tr>
<tr>
<td>cdate</td>
<td>0.0023</td>
<td>0.0031</td>
<td>0.468</td>
</tr>
<tr>
<td>Litter mass COY</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lsize - 2 or more cubs</td>
<td>6.2671</td>
<td>2.1959</td>
<td>0.008</td>
</tr>
<tr>
<td>mage</td>
<td>0.7546</td>
<td>0.3853</td>
<td>0.060</td>
</tr>
<tr>
<td>mcondition</td>
<td>2.7263</td>
<td>1.5454</td>
<td>0.089</td>
</tr>
<tr>
<td>Litter mass yearlings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lsize - 2 or more cubs</td>
<td>104.3310</td>
<td>14.8130</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>mage</td>
<td>1.7120</td>
<td>1.7130</td>
<td>0.329</td>
</tr>
<tr>
<td>mcondition</td>
<td>12.5930</td>
<td>11.2060</td>
<td>0.273</td>
</tr>
<tr>
<td>Litter size COY</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mage</td>
<td>0.2600</td>
<td>0.1520</td>
<td>0.087</td>
</tr>
<tr>
<td>mcondition</td>
<td>-0.6476</td>
<td>0.5244</td>
<td>0.217</td>
</tr>
<tr>
<td>Litter size yearlings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mage</td>
<td>0.1684</td>
<td>0.1086</td>
<td>0.121</td>
</tr>
<tr>
<td>mcondition</td>
<td>-1.8017</td>
<td>0.9064</td>
<td>0.047</td>
</tr>
</tbody>
</table>
Fig. 4.1. Predicted BCI for adult males (black line) and other bears (dashed line; including female with cubs, solitary adult females, subadults, and yearlings) and the proportion of bowhead whale in the diet generated from the top-ranked model for polar bears of the SB, while holding all other variables constant at their mean values. Filled circles represent observed BCI values for adult males while open circles represent other bears.
Fig. 4.2. Predicted BCI for adult males (black line) and other bears (dashed line; including female with cubs, solitary adult females, subadults, and yearlings) and the prior year open-water season generated from the top-ranked model for polar bears of the SB, while holding all other variables constant at their mean values. Filled circles represent observed BCI values for adult males while open circles represent other bears.
Discussion

Climate change is having substantial impacts on polar bears due to declining sea ice (Durner et al. 2009). Sea ice is expected to continue declining and become seasonally ice-free before the end of the 21st century (Stroeve et al. 2012). Polar bears of the SB subpopulation appeared to be responding to declining sea ice by coming onshore in greater numbers when sea ice retracts to its annual minima since the early 2000s (Atwood et al. 2016). Prior studies indicated bears that come onshore feed at subsistence-harvested bowhead whale carcasses (i.e., bone piles), which are deposited along coastal regions by indigenous hunters (Rogers et al. 2015; Atwood et al. 2016; McKinney et al. 2017). Thus, it is important to understand the development and fitness consequences for polar bears feeding at bone piles as sea ice continues to decline.

In chapter 2, I found that mother-offspring social learning was the primary mechanism for the development of onshore behavior. Other bear species have been shown to socially learn behaviors from their mother (Hopkins 2013; Nielsen et al. 2013; Morehouse et al. 2016). For instance, researchers on grizzly bears in Alberta, Canada used a combination of behavioral and genetic data to investigate the development of conflict behavior (e.g., property damage, obtaining anthropogenic food, killing or attempting to kill livestock) in bears. The researchers concluded that the development of conflict behavior was primarily driven by mother-offspring social learning. We suspect polar bears of the SB subpopulation will come onshore in greater numbers as sea ice
continues to decline. Thus, there is a potential for human-bear conflict, and it will be important to properly manage mother-offspring pairs, when feasible.

In chapter 3, I estimated that as many as 146 (SE = 21) polar bears (sexes combined) visited the bone pile near Kaktovik, Alaska in 2012. Thus, ~ 16% of the SB subpopulation fed at the bone pile using the most recent subpopulation estimate of ~ 900 bears. I found similar proportions of males and females used the bone pile, which implied that both sexes made use of this marine food subsidy. I interpreted my estimate for the number of polar bears using the bone pile as a conservative estimate in regards to the entire subpopulation, because whale carcasses are deposited at other locations along the coast of Alaska. Diet analysis on the SB subpopulation reported that many polar bears have been shown to feed on bowhead whale carcasses (Rogers et al. 2015; McKinney et al. 2017). Therefore, I speculated that more SB polar bears made use of whale carcasses than I estimated. I found male annual rates of apparent site fidelity to the bone pile ranged from 0.60 (SE = 0.07) for the interval 2012-13 to 0.61 for the interval 2011-12 and 2013-14 (SE = 0.07, SE = 0.08, respectively). Rates of apparent site fidelity for female bears were slightly higher than males and estimated at 0.69 (SE = 0.19) for all time intervals.

In chapter 4, I found that spring-sampled polar bears that fed on whale carcasses in the previous fall were in better condition (based on the body condition index; Cattet et al. 2002) than bears that fed primarily on prey hunted from the sea ice. I concluded that polar bears that came onshore and fed at an energy-rich marine food subsidy achieved better body condition than bears that remained on the sea ice year-round, which likely experienced energy deficits and limited access to prey. Additionally, I found a concave
association between body condition and the length of the prior year open-water season. Overall, I concluded that SB polar bears had increased body condition associated with feeding at a marine food subsidy. However, I hypothesize that the SB subpopulation will likely experience declines in body condition as subsistence-harvested whale carcasses will not sustain the entire subpopulation.

My results revealed onshore behavior developed via mother-offspring social learning for SB polar bears. Therefore, it will be important to properly manage mother-offspring bears to mitigate human-bear conflicts for onshore bears as more bears are expected to come onshore. I also showed that as many as many as 146 polar bears visited the bone pile near Kaktovik, Alaska, which represents ~ 16% of the SB subpopulation. However, likely more bears used the whale carcasses than I estimated since bone piles occur at another location in Alaska (i.e., Cross Island). Lastly, I found evidence for higher body condition for polar bears associated with feeding at bone piles, whereas bears that primarily fed on prey hunted from the sea ice had lower body condition. I hypothesize that the entire subpopulation will eventually experience declines in body condition since whale carcasses will not sustain the entire subpopulation. The north coast of Alaska has a large industrial footprint due to oil exploration and extraction activities. Thus, human-bear interactions and conflicts may increase as more polar bears come onshore and feed at the bone piles, and it will be important to monitor for human-bear interactions and conflicts along the north coast of Alaska. If human-bear conflicts increase and appear to be associated with polar bears using bone piles, I suggest evaluating the advantages and disadvantages of providing polar bears with access to the bone pile and/or dispersing whale remains over a broader area away from human
settlements. Managing human-bear conflict resulting from polar bears visiting bone piles will require collaboration between resource managers and the community, along with monitoring for the potential of adverse population-level effects.

References


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