Anthropogenic influence on the autumn migration of polar bears (*Ursus maritimus*) in Hudson Bay

by

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Abstract

Migratory species may shift established spatiotemporal patterns in response to anthropogenic impacts, so understanding the energetic consequences of behavioural plasticity may provide insight into how effectively migratory species respond to climate change. I used satellite telemetry to examine individual variation and trends in the autumn migration of 151 adult female polar bears (*Ursus maritimus*) in western Hudson Bay, Canada from 1991 to 2020. I used regressions and time-to-event models to assess biological and environmental factors that influence migration phenology at the end of the terrestrial fasting period. To quantify vulnerability to an increasing fasting period, I examined the energetics of 136 females with offspring. I found that the timing of on-ice departure was delayed in older bears and, not unexpectedly, in years with later sea ice freeze-up. I also found temporal trends in past sea ice dynamics, a northward shift in the distribution of on-ice departure of 2 km/year, and declining energetic stores for females with first-year cubs, with an estimated 67% of females with offspring that would likely have to cease lactation before their on-ice departure date or risk starvation while 20% still risk starvation having ceased lactation. The analysis of migration phenology, however, does not permit insights into the influence of direct human interactions on the spatiotemporal patterns of bears. Therefore, I used satellite eartag telemetry deployed on 50 polar bears in 2016 – 2020 that were caught by Manitoba Conservation Offices as part of the Polar Bear Alert Program near Churchill, Canada and relocated upon release. This methodology allowed for the analysis of movement patterns and recidivism rates to improve our understanding of human-bear conflict mitigation. I found sex differences in the on-ice departure date, with females departing a mean 12 days earlier in the season than males. I found that bears involved in conflict changed their spatial migratory patterns, departing a mean of 104 km further north than non-conflict bears.

Multinomial logistic models revealed that bears released later during the migratory period were less likely to re-enter a community at a rate of 8% per day. Polar bears exhibit complex patterns in migration due to the interplay between individual attributes, individual behaviour, and seasonally dynamic sea ice habitat, which are further complicated by the effects of climate change and human-wildlife conflict. As such, the management and conservation of polar bears will require a holistic approach that considers these factors.

Preface

This thesis is an original work by Erin Miller. Some of the research conducted for this thesis forms part of a national research collaboration, led by Professor Andrew Derocher at the University of Alberta. Polar bear movement data used in this research was obtained by satellite-linked collars deployed by Dr. A. E. Derocher and Dr. N. J. Lunn at the University of Alberta and Environment and Climate Change Canada and satellite-linked eartags deployed by Manitoba wildlife officers at the Government of Manitoba.

Animal handling protocols that were followed received research ethics approval from the University of Alberta Animal Care and Use Committee for Biosciences, Project Name "Polar bears and Climate Change: Habitat Use and Trophic Interactions", No. AUP00000033.

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Chapter 1

1 | Introduction

Migratory behavior occurs across many taxa and usually correlates to predictable, periodic changes in resource availability and environmental conditions (Woodbury 1941, Avgar et al. 2013, Dingle 2014). Migratory species generally move toward energetically positive habitats with temporarily high resource abundance and away from energetically negative habitats with unfavourable conditions on a seasonal cycle (Blem 1980, Fryxell and Sinclair 1988). As anthropogenic-induced climate forcing continues to lead to changes in once predictable spatiotemporal patterns in habitat resources (Kwon et al. 2019), migrant species may be forced to change their behaviour to more energetically expensive strategies or they may lose access to times of peak resource abundance entirely (Moller et al. 2008, Monteith et al. 2011). Due to its relationship to resources availability and energetics, migration phenology influences most other aspects of a species' life history, and disruptions to this behaviour can have cascading effects on the timing of other biological events that may impact individual fitness and population abundance (Roff 1988, Gienapp and Bregnballe 2012, Shaw 2016). While climate change can lead to gradual and permanent changes in migration phenology (Cohen et al. 2018), abrupt disruptions during migration, including human development and human-wildlife interactions, may lead to rapid, temporary shifts in behaviour or migratory patterns (Mahoney and Schaefer 2002), which may have negative effects on individual fitness (Madsen 2008). The study of changing migration phenology in the face of anthropogenic influence at varying temporal scales is critical to understanding the vulnerability of at-risk populations to future human activity.

Although migratory behaviour has enabled animals to exploit highly seasonal landscapes, they are vulnerable to directional changes in climate over time due to inflexible life strategies resulting from a reliance on multiple discrete home ranges (Laidre et al. 2008, Studds et al. 2017, Wauchope et al. 2017). Global increases in temperature may affect the quantity, quality, and spatiotemporal patterns of resources in habitats at asynchronous rates, which may result in the timing of resource abundance in one habitat becoming less correlated over time to the internal or environmental cue triggering migratory movement (Cohen et al. 2014, Shaw 2016, Saalfeld et al. 2019). This ecological mismatch may lead to reduced individual fitness if migratory movement no longer aligns with peaks in resource abundance (Gilg et al. 2012, Lameris et al. 2017, Kwon et al. 2019). Individuals may respond to short-term change by changing the spatiotemporal patterns of their migratory movement, but this requires a level of behavioural plasticity that may be unavailable for some populations due to the rapid rate of changing conditions or limitations related to energetic requirements and landscape connectivity (Miller et al. 2005, Anderson et al. 2013, Mallory and Boyce 2018). Phenological changes in migration are expected to be the most extreme at high latitudes, where the Arctic climate is changing at a higher rate than the global average (Serreze and Barry 2011).

The circumpolar Arctic is characterized by extreme seasonal variation in temperature and precipitation (Parkinson et al. 1999, Polyakov et al. 1999, Kushner et al. 2018) as well as increasing trends in temperature as a result of climate forcing (Cohen et al. 2014, Landrum and Holland 2020). This Arctic amplification has had an effect on both terrestrial and marine habitats (Box et al. 2019) by disrupting predictable patterns of resource abundance for many species (Daase et al. 2013) as precipitation and vegetation have changed spatially and temporally (Bintanja and Selten 2014, Bhatt et al. 2017) and sea ice extent and duration of cover have decreased over recent decades (Maslanik et al. 2011, Parkinson 2014, Stern and Laidre 2016). As a seasonally dynamic landscape, the Arctic is inhabited by animals that have adapted to extreme variation in resource abundance and environmental conditions (Johnson and Herter 1990, Moore and Huntington 2008) with many having evolved migratory patterns correlated to seasonal pulses in resource availability (Tulp and Schekkerman 2008, McKinnon et al. 2016, Nicholson et al. 2016). The seasonal cycle of sea ice is associated with the migratory behaviour and overall fitness of many Arctic migrants. Many cetaceans, such as bowhead whales (*Balaena mysticetus*) and narwhals (*Monodon monoceros),* rely on the melt of seasonal sea ice to inhabit highly productive Arctic seas in summer (Laidre et al. 2008). Alternatively, other migrants rely on the presence of sea ice, such as caribou (*Rangifer tarandus*), which use sea ice to travel between discrete home ranges (Mallory and Boyce 2018) and many pinniped species, including ringed seals (*Phoca hispida*), bearded seals (*Erignathus barbatus*), which use sea ice as breeding habitat (Smith and Stirling 1975, Lunn et al. 1997b). Polar bears (*Ursus maritimus)* are once such Arctic migrant that relies on the presence of sea ice to access resources (DeMaster and Stirling 1981).

Polar bears inhabit the circumpolar Arctic, where sea ice persists for most of the year (Durner et al. 2009, Hamilton and Derocher 2019). Polar bears are characterized by low reproductive rates, with females demonstrating inter-birth intervals of two to four years (Ramsay and Stirling 1988), giving birth in maternal dens to up to three cubs, and lactating for up to two years (Owen 2021). During their first two years of life, juvenile bears are dependent on and learn from their mothers (Stirling and Latour 1978). While wild polar bears live approximately 25 years (Rode and Stirling 2018), females demonstrate late sexual maturity (4-5 years) and declines in reproductive output as early as 14 years of age (Ramsay and Stirling 1986, Derocher and Stirling 1994). Polar bears are large-bodied carnivores for which critical stages of their life history are dependent on availability of sea ice as a platform from which to hunt seals (Stirling and Archibald 1977, Smith 1980), to mate (Ramsay and Stirling 1986), and to travel between hunting and maternity denning habitat (Pagano et al. 2012, Pilfold et al. 2017). Polar bears experience seasonal cycles of environmental conditions and prey availability, the most extreme of which are seen by those inhabiting seasonal sea ice ecoregions (Amstrup et al. 2008, Durner et al. 2009).

The Western Hudson (WH) subpopulation of polar bears is near the southern extent of the species' range, along the western region of Hudson Bay, Canada (PBSG 2018). Hudson Bay is ice-free in summer but ice-covered during the winter, which forces WH polar bears to migrate onshore and offshore each year, respectively (Stirling et al. 1977, Vongraven et al. 2012, Castro de la Guardia et al. 2017). WH bears spend 4-5 months on land during the ice-free period until freeze-up (Cherry et al. 2013). Prior to freeze-up, bears move northward to the coast to intercept forming sea ice (Latour 1981). The on-land distribution of WH bears differs by sex, with adult males remaining near the coast while adult females move further inland (Derocher and Stirling 1990), and by age, with subadults of both sex inhabiting both coastal and inland areas while avoiding older conspecifics (Towns et al. 2010). Pregnant females remain further inland in maternity dens until the following spring, migrating onto the sea ice with first-year cubs after up to 8 months of fasting (Yee et al. 2017). During the fasting period, polar bears may forage, but this diet is inadequate to prevent body mass loss while seals are unavailable (Russell 1975, Rode et al. 2015, Pilfold et al. 2016, Hamilton and Derocher 2019). Upon the autumn formation of sea ice, polar bears migrate back onto the Bay, upon which they resume hunting seals and subsequently end their fasting period (Castro de la Guardia et al. 2017). While it is known that migration is tied to sea ice dynamics, polar bears demonstrate high individual variation in movement and behaviour that may be explained by other factors interacting within this dynamic habitat.

The timing of migration of WH polar bears onto sea ice is correlated to freeze-up and typically occurs less than 5 days following freeze-up (Cherry et al. 2013, Castro de la Guardia et al. 2017). Temporal trends in autumn migration toward delayed departure onto the sea ice were correlated with declines in sea ice extent over a twenty year period (Cherry et al. 2013). Large-scale atmospheric patterns of the North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) drive variation in sea ice drift and autumn freeze-up (Wang and Ikeda 2000, Qian et al. 2008) and thus it may be possible to use these indices to predict the present and future migration phenology of polar bears. Polar bears demonstrated high inter-individual variation in spring migratory movement (Cherry et al. 2016), but it is unknown what factors affect individual variation in autumn migration. Similarly, while reduced sea ice extent was correlated with declining bear body condition at the population level (Lunn and Stirling 1985, Stirling and Derocher 2012, Sciullo et al. 2016), the factors driving individual vulnerability to increased fasting is unknown.

Quantifying the effects of climate change on the movement and energetics of polar bears during the autumn migration will provide needed insight on individual variation in behavioural plasticity to change and vulnerability to sea ice loss during this critical stage in their life history. In Chapter 2, I sought to examine the spatiotemporal and inter-individual variation in movement and behaviour of WH polar bears during the autumn migration onto the sea ice in relation to biological variables and environmental conditions. I examined migration phenology over a 30-year period using a Cox proportional hazard model to determine the effects of changing climate on trends and individual variation in the timing of on-ice departure. During this same period, I examined individual vulnerability to an extended fasting period to provide context to the effect of these changes on individual fitness and population levels. This chapter aims to provide context toward the spatiotemporal patterns and individual variation of WH polar bears during migration to then, in Chapter 3, examine the more abrupt influence that human-wildlife conflict has on the movement and behaviour of migrating bears.

Most human-polar bear conflicts occur during the time that polar bears move north from inland and toward the coast in preparation for autumn freeze-up (Towns et al. 2009, Laforge et al. 2017, Wilder et al. 2017). While on land, polar bears are in an energetically negative state as well as being physically closer to human communities (Stenhouse et al. 1988, Dyck 2006). Polar bears, similarly to black (*U. americanus*; Spencer et al. 2007) and grizzly bears (*U. arctos*; Can et al. 2014), can become habituated to human communities due to food conditioning, leading to conflict (e.g. garbage dumps; Lunn and Stirling 1985, Hopkins et al. 2010). Bears in low body condition are more likely to enter human communities (Wilder et al. 2017), which has resulted in a high proportion of subadult male bears, which are more likely to be in poor condition (Towns et al. 2009), being involved in conflict (Gjertz et al. 1993, Dyck 2006). Once autumn freeze-up occurs in November, the number of conflicts declines until the following summer (Towns et al. 2009, Laforge et al. 2017). While the factors affecting human-polar bear conflict have been studied, the effect that conflict has on the subsequent movement and behaviour of the individuals involved is unknown.

To protect both the residents of Churchill, Manitoba and the polar bears that may enter the town, the Government of Manitoba created the Polar Bear Alert Program (Kearney 1989). While emphasis is placed on deterring bears from town, those that are not successfully deterred are captured and relocated onto the sea ice or onto coastland away from town (Derocher et al. 2013). The relocation of conflict bears has been used to successfully reduce conflict-related mortality of black bears (Bauder et al. 2021) and was one of the earliest management practices used in Manitoba that led to a noticeable reduction in the number of polar bears returning to town each year (Struzik 2014). Management practices of polar bears have developed over time in efforts to reduce the same-year conflict of individuals. For example, adjusting the relocation of bears to northeast of Churchill after their relocation south resulted in high return rates (Struzik 2014). While the post-conflict outcome is known for bears that re-enter Churchill or are killed in the Nunavut subsistence harvest, the movement patterns and behaviour demonstrated by polar bears post-conflict is unknown due to a lack of telemetry data for these bears. Increasing reports of bears in proximity to Arviat, Nunavut (Tyrrell 2009, Peacock et al. 2010) have been attributed to the movement of Churchill conflict bears northwest along the coast, facilitating their movement into northern communities. Thus, an examination of the post-release movement of these bears is needed to understand the factors influencing recidivism rates of polar bears into Churchill and Arviat and to improve the management of WH polar bears through the identification of high-risk individuals and management practices used by Manitoba wildlife officers that are effective at reducing conflict.

Understanding the influence and efficacy of conflict management practices on the movement and behaviour of polar bears is important to improve management efficiency and reduce recidivism rates as conflict rates are expected to increase due to climate change and human expansion. In Chapter 3, I used eartag telemetry data obtained from the Government of Manitoba to examine the migratory movement of polar bears in response to post-conflict holding and relocation. The use of eartag telemetry to examine the movement of relocated conflict polar bears is a novel application and can provide important insight into the efficacy of current conflict management strategies. Using this data, I examined recidivism rates using multinomial logistic models to determine the effectiveness of management practices and to identify high-risk individuals. In Chapter 4, I predicted future spatiotemporal patterns in autumn migration and conflict of WH bears and discuss the implications of my findings regarding the management of this subpopulation and of human-bear conflicts, including suggestions regarding effective management strategies and future practices to consider. By examining both abrupt and gradual anthropogenic disruptions on the WH subpopulation's autumn migration onto the sea ice, my objective was to provide insight toward the multifaceted impact that human activities have on a vulnerable population during the critical life history stage of the on-ice departure, and the cascading effects on individual fitness and behaviour resulting from this impact.

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Chapter 2

2 | Autumn migration phenology of polar bears (*Ursus maritimus*) in Hudson Bay, Canada

2.1 | Introduction

Migratory behaviour occurs in predictable cycles (McKinnon et al. 2016) as animals move between energetically negative and positive locations that result from spatiotemporal variation in resource abundance (Fryxell and Sinclair 1988, Dingle 2014). The timing of migratory events is usually correlated with resource availability, which may be influenced by a species' ability to move through a seasonally dynamic landscape (McIntyre and Wiens 1999, Mueller et al. 2011). The Arctic, characterized by extreme seasonal variation in temperature and precipitation (Parkinson et al. 1999, Polyakov et al. 1999), is inhabited by seasonal occupants (Johnson and Herter 1990, Curk et al. 2020) and endemic migratory species (Fancy et al. 1989, Moore and Huntington 2008). These migrations have been influenced by trends in environmental conditions resulting from anthropogenic-induced climate change (Laidre et al. 2008, Cohen et al. 2018).

Human-induced climate forcing has led to a global increase in temperature, the largest of which has occurred at high latitudes (Landrum and Holland 2020), and resulted in Arctic sea ice decline in extent and duration of cover (Parkinson 2014, Stern and Laidre 2016). Such changes are associated with large-scale atmospheric patterns reflected by the North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) indices (Wang and Ikeda 2001, Hochheim et al. 2010). In Hudson Bay, both the NAO and AO are correlated with sea temperatures (Singh et al. 2013) and sea ice concentration (Liu et al. 2004) with a positive index value indicating cooler autumn temperatures and increased sea ice cover (Hochheim and Barber 2010). In Arctic marine ecosystems, the presence of sea ice is a dominant feature and the seasonal sea ice cycle is associated with the migratory behaviour and overall fitness of many Arctic marine mammals (Laidre et al. 2008), including the polar bear (*Ursus maritimus*; Stirling et al. 1999, Cherry et al. 2016, Pilfold et al. 2017).

Polar bears are distributed widely where sea ice persists for most of the year (DeMaster and Stirling 1981). The Western Hudson Bay (WH) polar bear subpopulation occurs near the southern extent of the species' range and inhabits a seasonal sea ice ecosystem with extensive sea ice cover most of the year and an ice-free period in summer-autumn that has increased in duration (Castro de la Guardia et al. 2017). Polar bears rely on sea-ice habitat to hunt seals, which are their main prey (Stirling and Archibald 1977, Thiemann et al. 2008). After being forced ashore due to the complete melt of seasonal sea ice, WH polar bears lose access to prey and, due to limited feeding opportunities, lose mass (Rode et al. 2015, Pilfold et al. 2016). Females with offspring lactate during this period, losing mass at a higher rate than solitary females (Arnould and Ramsay 1994, Pilfold et al. 2016). Non-pregnant bears migrate back to the sea ice when it reforms in late autumn and resume hunting (Castro de la Guardia et al. 2017).

Temporal trends in autumn migration of WH polar bears were correlated with declines in Hudson Bay sea ice cover (Cherry et al. 2013), but the factors affecting individual variation in migration are unknown. Reduced sea ice extent was correlated with declining bear body condition at the population level (Stirling and Derocher 1993, Stirling et al. 1999, Sciullo et al. 2016), but how individual condition may be affected by changing phenology is unclear. Polar bear behaviour is affected by reproductive status (Ramsay and Stirling 1988), age (Stirling and Latour 1978, Derocher and Stirling 1994), sex (Derocher and Stirling 1990), and body condition (Galicia et al. 2019) and these factors may affect individual variation in migration. Bears in lower body condition and those rearing offspring may be energetically stressed (Stirling et al. 1999, Molnár et al. 2009) and may depart onto newly formed sea ice to resume hunting. However, these bears may face higher energetic costs when travelling on newly formed sea ice due to habitat fragmentation, sea ice drift, and long-distance swims (Biddlecombe et al. 2021, Pagano and Williams 2021) while bears in better condition may delay migration until habitat conditions improve. Further, females with cubs born in spring had less time on-ice to prepare for the fasting period (Ramsay and Stirling 1988) and may return to the ice sooner. Polar bear maternal behaviour during the 2.5 years of offspring dependency may also influence individual behaviour post-weaning (Derocher and Stirling 1990, Zeyl et al. 2010) and could thus affect the migratory behaviour of adults.

My objective was to examine the phenology of the autumn migration of WH female polar bears relative to past and present sea ice dynamics, climate indices, and individual metrics using satellite telemetry data collected over 30 years. I examined temporal trends in the on-ice departure latitude, date, and sea ice concentration of migrating bears. I also examined individual variation in migration phenology and vulnerability to extended fasting. I predicted that: 1) migration would be delayed over time due to the delayed freeze-up, 2) bears would migrate further north over time to access sea ice earlier; 3) younger individuals and females with offspring would depart earlier in the season; 4) the on-ice departure date would be delayed in years with negative NAO and AO phases; 5) migratory behaviour is learned by the behaviour of mothers responding to the sea ice conditions experienced over an individual's first two juvenile years; and 6) individual variation in body condition and starvation threshold may vary due to an increased fasting period.

2.2 | Methods

2.2.1 | Study area

I studied polar bear migration along the western coast of Hudson Bay, Canada during September to December from 1991 to 2020 (Figure 2.1). Hudson Bay is characterized by high seasonal variation in sea ice, ranging from >90% concentration in winter to ice-free summers (Prinsenberg 1988). Sea ice initially forms mid-October along the northwest coast, due to colder temperatures and freshwater runoff, and spreads southward and eventually eastward across the bay (Gagnon and Gough 2005).

2.2.2 | Capture and handling

Adult females (≥ 5 years old) were located by helicopter and temporarily immobilized via remote injection of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil, Laboratories Virbac, Carros, France; Stirling et al. 1989) from August to September. Capture and handling protocols were approved by the Environment and Climate Change Canada, Prairie and Northern Region Animal Care Committee and the University of Alberta Animal Policy and Welfare Committee, in accordance with the Canadian Council on Animal Care guidelines (https://ccac.ca). Bears were classified by reproductive status at capture as solitary, with cub(s)-of-the-year (CUBs), with yearling(s) (YRLGs), or with 2-year-old(s) (2YRs). A premolar was extracted from bears ≥ 2 years old to estimate age (Calvert and Ramsay 1995). CUBs and YRLGs were aged based on physical size and tooth emergence. Body length (cm), the straight line from tip of the nose to the end of the last tail vertebra, and axillary girth (cm), the circumference around the thorax at the axilla, were measured.

From 1991 to 1997, females were fitted with Doppler shift Argos satellite-linked collars (Telonics, Mesa, AZ) programmed to obtain one location/day. From 2004 to 2019, females were fitted with global positioning system (GPS) satellite-linked collars (Telonics, Mesa, AZ) programmed to obtain one location every four hours. From 1991 to 2006, bears were recaptured to remove collars; from 2007 onwards, collars were fitted with a programmable release mechanism that opened on a predefined date allowing it to fall off. Only adult females were fitted with collars due to risk of injury to growing subadults and the neck diameter of adult males exceeding that of their head.

2.2.3 | Bear movement metrics

To examine trends and inter-individual variation in polar bear migration, I tracked individual movement over the autumn migratory period from September to December using satellite telemetry. All locations were standardized by subsampling to one location/day using the R-package *amt* (Signer et al. 2019). Telemetry locations 3 d post-handling were removed to allow bears to return to normal activity (Thiemann et al. 2013) and were restricted to those after the latest collar deployment. Duplicate timestamps and relocations where the movement rate was >10 km/h, and thus biologically implausible (Parks et al. 2006), were removed using the R-package *argosfilter* (Freitas 2012). The date and location of on-ice departure for each bear was determined visually using ArcGIS (Environmental Systems Research Institute, Redlands, CA) and defined as the first location off-shore not followed by a location on-land until the following spring. Bears with gaps between their last on-shore location and first on-ice location > 10 d were removed.

To determine if polar bear migration has changed over the last 30 years, I examined temporal trends in the departure latitude date, and sea ice concentration from 1991 to 2020 using robustly-fitted simple linear regression or autoregression. I also examined trends in the capture latitude and date using robustly-fitted simple linear regression or autoregression to assess for possible changes in capture methodology over time. . For each regression model, normality was tested using the Shapiro-Wilks and homoscedasticity tested using the Studentized Breusch-Pagan tests with $p \leq 0.05$. The residuals of the regressions of departure latitude, capture latitude, and sea ice concentration were non-normal despite transformations, so I used robust regressions. I used the Durbin-Watson test for autocorrelation in the model residuals ($p \leq 0.05$). The regression residuals of departure date and capture date were positively autocorrelated by year, which was accounted for by the use of a first-order autoregressive models using the R-package *forecast* (Hyndman et al. 2021). Statistical analyses were performed using R version 3.6.2 (R Core Team 2019). A standard significance level ($\alpha = 0.05$) was used.

A time-to-event model to describe migration phenology (e.g., Bauer et al. 2008, Rivrud et al. 2015) was applied to evaluate whether an individual's departure onto the sea ice differed by individual characteristics and both static and dynamic environmental conditions. I used a mixed-effects Cox proportional hazards model with time varying covariates estimated at a daily interval to avoid baseline hazard shape assumptions (Kleinbaum and Klein 1996). I used a 365 d, recurrent time scale with September 29 as the origin (t=0). Censoring was not required as every individual had a migration event. I included a random effect for individual to account for the lack of independence from the inclusion of multiple departures for some individuals. In the Cox proportional hazards model, I assessed the influence of individual characteristics on inter-individual variation in migration departure, I included age, reproductive status, and daily conservative condition in the models. I included age as both first and second order polynomial covariates in separate global models due to the nonlinear relationship between age and body mass (Derocher and Stirling 1994). Annual freeze-up date, juvenile freeze-up date, the best-fitting oscillation index, and the time-varying daily mean temperature were included to assess the effect of environmental conditions. I included the individual's daily distance to the coast, calculated using ArcGIS 10.7.1 as the straight-line-distance from an individual's location to the coast, as a time-varying covariate to determine if departure date was influenced by variation in the summering areas used before migration. Finally, I included departure year to examine temporal trends in migration. Covariates were tested for proportional hazards using a goodness-of-fit test of scaled Schoenfeld residuals ($p \leq 0.05$) and for linearity through visual inspection of Martingale residual plots. I excluded daily condition prior to model selection as it violated the proportional hazards assumptions (Figure A2.1). Model selection was performed on all candidate models using the Akaike Information Criterion corrected for small samples (AIC_c). When multiple models had $\Delta AIC_c < 2$, I chose the most parsimonious model, the one with the fewest parameters, to avoid overfitting with uninformative covariates (Arnold 2010). I used the Bonferroni corrected level of significance ($\alpha = 0.025$) due to the inclusion of the best-fitting NAO covariate.

2.2.4 | Environmental conditions

Daily sea ice concentration was obtained from the National Snow and Ice Data Center (https://nsidc.org/data) following Cavalieri (1997) to produce mean daily sea ice concentration measurements. Sea ice at departure was defined as the % concentration of sea ice cover over the 25 x 25 km area that overlapped with a bear's departure location. Daily mean sea ice concentration was calculated for the area inside the WH population boundary (Lunn et al. 1997a) to determine the annual freeze-up date, defined as the first date at which sea ice concentration was >10% for three consecutive days. I calculated the mean freeze-up date for the birth year and the following year of all adult females collared for the study to examine the sea ice conditions experienced by the bears while accompanying their mothers (juvenile freeze-up). Daily mean temperature was measured at the Churchill, Manitoba airport (from Environment and Climate Change Canada, https://climatedata.ca). Monthly mean values for NAO and AO were obtained from the National Weather Service (https://www.cpc.ncep.noaa.gov).

I examined the influence of NAO and AO phases on sea ice dynamics from 1978 to 2020 using linear regressions. I grouped monthly NAO and AO into three four-month means as covariates to determine the best fitting seasonal index for further analysis. Due to high collinearity (VIF > 4) between the NAO and AO indices, I separated the covariates into two global models. I performed model selection on all possible candidate models using AIC_c. To determine significance, I used a Bonferroni correction ($\alpha = 0.025$) due to the lack of independence from selecting a best-fitting covariate from two global models. I also examined temporal trends in the annual freeze-up date and best-fitting seasonal index over 1991 to 2020 and in the juvenile freeze-up date over the bear birth years of 1978 to 2013 using simple linear regressions. All regression residuals were tested for normality, homoscedasticity, and autocorrelation.

2.2.5 | Vulnerability indices

Body condition (kg/cm^2) was estimated using equations based on girth and body length (Thiemann et al. 2011, Sciullo et al. 2016). I used both a conservative mean daily mass loss rate for all adult females of 0.85 kg/day (Derocher and Stirling 1995b) and a variable daily mass loss rate including the cost of lactation for females with CUBs (1.3 kg/day) and YRLGs (1.0 kg/day; Pilfold et al. 2016). Using a range of mass loss rates allowed me to bound body condition at on-ice departure as I could not monitor post-capture reproductive status. I estimated each bear's condition on two dates: 1) standardized to September 29 to account for latest collar deployment, and 2) variable to the individual's departure date. Using these two dates allowed me to distinguish between condition trends at the population-level and those associated with variation in an individual's fasting period.

I also estimated the starvation threshold, defined as the number of days of stored energy remaining for adult females with CUBs and YRLGs at the time of on-ice departure before experiencing increased risk of mortality due to starvation. This threshold indicates a transition from the controlled physiological state of fasting to the final stage of starvation, a gradual process of damage ending in death or recovery upon refeeding (Nelson et al. 1983, Harlow 2012). I excluded solitary females and females with 2YRs due to sample size (n = 2; n = 1). I estimated body energy content (MJ) at capture based on mass and straight-line body length and the rate of energy loss (MJ/day) based on the energetic costs of somatic maintenance, maintaining posture, movement, and lactation following Molnár et al. (2020) to produce the number of days of stored energy available at capture. I compared this estimate of fasting days to the number of days from the capture date to the individual's departure date to determine the number of days of stored energy remaining at departure. Due to uncertainty in the timing of cessation of lactation in fasting polar bears due to low mass (Derocher et al. 1993, Arnould and Ramsay 1994), I produced two estimates of the starvation threshold by assuming that females would continue lactating until starvation or that they would have ceased lactating while fasting (i.e., no reproductive energetic cost) to assess the range of individual mortality risk associated with starvation. Because returning to the sea ice may not immediately result in re-feeding, I consider the starvation threshold as an index of risk. For bears whose departure date exceeded the starvation threshold (i.e., no remaining energetic stores), I calculated the starvation risk at departure, the probability of mortality due to starvation, using an additive mortality rate of 0.4%/day for all females when assuming ceased lactation and 0.7%/day for females with CUBs or 0.8%/day for females with YRLGs when assuming unimpaired lactation following Molnár et al. (2020).

To compare indices of vulnerability to extended fasting, I examined temporal trends and individual variation in both the condition and starvation threshold of migrating bears using multiple linear regression. I examined condition indices using the conservative and reproductive cost mass loss rates in separate models. I also examined the starvation threshold indices assuming lactation cessation while fasting and unimpaired lactation in separate models. I included age as both first and second order polynomial covariates in separate global models and reproductive status. An interaction term between reproductive status and year was included to test my prediction of the higher vulnerability of females with CUBs to an extended fasting period. Covariates were tested for collinearity using the variance inflation factor (VIF > 4). I found collinearity between reproductive status and the interaction term of reproduction and year in the condition and starvation threshold linear regressions, which I removed by scaling (using 2 SD) and centering all quantitative covariates within reproductive status. All regression residuals were tested for normality, homoscedasticity, and autocorrelation. Model selection was performed on all candidate models using AIC_c. A standard significance level ($\alpha = 0.05$) was used.

2.3 | Results

From 1991 to 1997 and from 2004 to 2019, 88 and 203 collars were deployed, respectively. Due to gaps in transmitted locational data, I recorded 168 on-ice departures from 151 individuals. For years in which departures occurred, a mean of 7.6 departures/y (SE 0.8, range 1 to 15) were recorded, but in two years (1993 and 2009) no departures were recorded. The mean age of females was 14.5 years (SE 0.4, range 5 to 27) and the mean condition at capture was 0.53 kg/cm^2 (SE 0.01, range 0.39 to 0.77). Most females (98.7%) were accompanied by offspring at capture (96 CUBs, 54 YRLGs, 3 2YRs) and only two solitary females were included. The distance to coast on September 29 (t=0) ranged from 0.3 to 69.1 km (mean = 27.7, SE 2.6). The mean latitude at capture was 58.0° (SE 0.04, range 56.9 to 59.8) and mean capture date was September 11 (SE 0.5 days, range August 25 to September 26). Neither the capture latitude nor date changed over time (Table 2.1; robust regression, $F_{1,136} = 0.30$, $p = 0.59$, $R^2 = 0.006$; autoregression model, $ß_{Year} = 0.22$, 95% CI -0.06 to 0.51) suggesting the data were not affected by sampling.

The top model predicting the annual freeze-up date (Table 2.2) included the four-month mean NAO from May to August (summer NAO) and September to December (winter NAO). Summer NAO had a negative effect on annual freeze-up date (Table 2.3; ß = -3.995, 97.5% CI -7.578 to -0.413) while winter NAO did not have a significant effect (ß = -3.852, 97.5% CI -8.105 to 0.401). When restricted to the period with telemetry data (1991 to 2020), neither freeze-up nor the summer NAO changed significantly over time (linear regression, $F_{1,28} = 1.86$, $p = 0.184$, $R^2 = 0.10$; $F_{1,28} = 3.03$, $p = 0.093$, $R^2 = 0.06$); however, juvenile freeze-up changed significantly from 1978 to 2013 (linear regression, $F_{1,29} = 33.44$, $p < 0.001$, $R^2 = 0.54$) with a mean delay of 0.4 days/year (SE 1.5; Figure 2.2).

Simple linear regressions of migratory behaviour indicated a spatial shift in migration from 1991 to 2020. Over the study period, WH polar bears departed at a mean latitude of 58.9° (SE 0.1). Within a year, bears departed a mean difference of 2.0° latitude (SE 0.3, range 0.1 to 4.7) between the northernmost and southernmost locations (Figure 2.3). The location of on-ice departure shifted further north over time (Table 2.1; linear regression, $F_{1,166} = 7.20$, $p = 0.008$, $R^2 = 0.039$) with bears departing farther north by 0.07° latitude/year (SE 0.11) or approximately 2 km/year. Over the study period, bears departed on the mean date of November 23 (SE 0.6, range October 21 to December 18). Within a year, bears departed a mean difference of 15.4 days (SE 2.1) between the earliest and latest departure (Figure 2.3). Departure date did not change over time (Table 2.1; autoregression model, $ß_{\text{Year}} = 0.08$, 95% CI -0.19 to 0.34). Over the study period, bears departed onto a mean sea ice concentration of 32% (SE 2, range 2 to 94). Within a year bears departed a mean difference of 49% (SE 6) between the lowest and highest sea ice concentration (Figure 2.3). Sea ice concentration at departure did not change over time (Table 2.1; linear regression, $F_{1,157} = 2.83$, $p = 0.09$, $R^2 = 0.009$).

The time-to-event model included 4,487 locations from 145 departure events, with a mean of 31 (SE 0.8) daily locations per event. Six top models best explained the variation in the on-ice departure date out of 256 candidate models (Table 2.4), with the most parsimonious model including the individual’s age and the annual freeze-up date (Table 2.5). Bears departed earlier in the migratory period during years with earlier freeze-up. Older individuals departed a mean 0.5

days later per year of age (SE 0.3). Although the summer NAO index and the juvenile freeze-up date were included in the top models, their inclusion did not improve model fit, suggesting that the formation of sea ice within the WH zone, rather than larger-scale seasonal trends in the NAO or past sea ice conditions, was the better predictor of variation in migration timing. Bears departed a mean 2.5 days (SE 0.5) after freeze-up. Similarly, while year was included in the subset of top models, it's absence in some top models suggests that the on-ice departure date has not changed significantly over time.

Before examining variation in bear body condition, I evaluated whether the date at which condition was estimated influenced trends, and it did not. The interaction term between body condition and the date on which individual condition was measured, whether September 29 or on-ice departure, did not have a significant effect on temporal trends from 1991 to 2020 (Table 2.6; Figure 2.4, linear regression, ß (slope) = -0.0004, 95% CI -0.0028 to 0.0020), so I only examined individual variation in condition at departure.

Body condition resulted in two top models for the conservative estimate and one top model for the reproductive estimate out of 20 candidate models each using AICc selection (Table 2.7). The best-fitting, most parsimonious models for both estimates of body condition at departure provided evidence of intra- and inter-annual temporal trends in individual departure condition whether reproductive costs were accounted for in the mass loss rate or not. Condition declined with delayed departure date regardless of reproductive status and declined over the study for females with CUBs (Table 2.8; Figure 2.5). While age was included in one of the top conservative condition models, it's inclusion did not improve model fit. The mean departure condition using a conservative mass loss rate was 0.377 kg/cm^2 (SE 0.006, range 0.200 to 0.593) for all females and using variable mass loss rates by reproductive status was significantly different for the two reproductive groups, with 0.281 kg/cm^2 (SE 0.008, range 0.099 to 0.498) for females with CUBs and 0.356 kg/cm^2 (SE 0.008, range 0.238 to 0.497) for females with YRLGs.

Both estimates of starvation threshold at departure, assuming ceased lactation or unimpaired lactation, resulted in one top model out of 20 candidate models each using AIC$_c$ selection (Table 2.9). The best-fitting models indicated that the number of fasting days of stored energy remaining for migrating bears was lower for older bears and those with delayed departure dates (Table 2.8). The mean starvation threshold at departure assuming ceased lactation while fasting was 7.9 d (SE 1.1, range -26 to 57) and declined over time for females with CUBs while females with YRLGs did not change (Figure 2.5). When assuming ceased lactation, I found that 28 females (20 with CUBs and 8 with YRLGs) out of 136 departed past their estimated starvation threshold, experiencing a mean accumulated starvation risk of 4.4% at on-ice departure (SE 0.6, range 0.4 to 10.4). While not an indication of absolute mortality, these bears had crossed the threshold indicating a transition into the final stage of starvation that increases risk of mortality (Harlow 2012). The mean starvation threshold at departure assuming unimpaired lactation was significantly lower for females with CUBs at -13.8 days (SE 1.4, range -45 to 27) than with YRLGs at 4.7 days (SE 1.8, range -26 to 28) and declined over time for females with CUBs (Table 2.8). When assuming unimpaired lactation, I found that 91 females (74 with CUBs and 17 with YRLGs) departed past their estimated starvation threshold, experiencing a mean accumulated starvation risk of 11.2% at on-ice departure (SE 0.8, range 0.7 to 31.5). An additional 26 bears assuming ceased lactation and 16 assuming unimpaired lactation would have run out of energetic stores with one additional week of fasting.

2.4 | Discussion

I used telemetry and capture data spanning thirty years to examine polar bear migration phenology and individual vulnerability to environmental conditions. While I found evidence of delayed freeze-up along the western coast of Hudson Bay over the bear birth years of 1978 to 2013, I found no significant temporal trends in freeze-up or that the autumn migration of WH polar bears had shifted over the last three decades. However, I did find a northward shift in the location of on-ice departure over time. These results suggest behavioural plasticity through the learned response of juveniles to maternal behaviour. The on-ice departure date was, however, associated with same-year sea ice dynamics, with bears departing earlier during years with earlier freeze-up. I found that both the condition and the starvation threshold of females with CUBs declined over time, while there were no similar trends for females with yearlings.

While polar bear migration phenology did not change over the past 30 years, bears departed further north despite no change in the timing of freeze-up over the same period. I suggest that these bears may instead be responding to the freeze-up dates at the locations they experienced as juveniles while dependent on their mothers, which delayed over this earlier period from 1978 to 2013. Cubs learn where to den (Derocher and Stirling 1990) and how to hunt (Stirling and Latour 1978) from their mother's behaviour. Given evidence of a sudden, marked change in sea ice dynamics from 1988-1989 (Scott and Marshall 2010), it is possible that the bear's mothers may have changed their behaviour by seeking areas with earlier forming sea ice in northwestern Hudson Bay to avoid the increased energetic costs and starvation risk associated with an extended fasting season. Such learned behaviour could lead to the individuals in the study departing further north as cubs and subsequently as adults. Departing further north may increase energetic costs because of the longer distance travelled to these northern departure locations

(Molnár et al. 2010). The lack of trend in the departure date found in this study differed from the results reported by Cherry et al. (2013) who reported delayed departure of WH polar bears; however, that study ended in 2010 and freeze-up in the years following occurred earlier, and this study included the resulting earlier departures. The difference between the studies emphasizes the value of long-term studies.

While the top model for the on-ice departure date included the annual freeze-up date, juvenile freeze-up date, and the summer NAO, annual freeze-up was the best predictor. This finding supports Cherry et al. (2013) who linked the migratory behaviour of polar bears to the formation of sea ice. Over the last 40 years, there has been a trend towards later freeze-up of Hudson Bay (Castro de la Guardia et al. 2017) as a result of increasing surface temperatures (Hochheim and Barber 2010). While bear behaviour is influenced indirectly by variation in climate driven by large-scale pressure systems, individuals respond to local environmental conditions (Cherry et al. 2016). I found that 30% of inter-annual variation in departure date was explained by annual freeze-up date. If freeze-up is further delayed in the future, I expect that polar bear migration will similarly be delayed.

I found that age influenced the behaviour of adult polar bears during migration, with younger bears departing earlier in the season. Studies examining age effects in polar bears have often found differences in behaviour and fitness between subadults (2-4 years) and adults (≥5 years; Derocher and Stirling 1990, Lunn et al. 2016) and I found that age effects continued into adulthood. Polar bear mass increases as they age and only declines in their last years (Derocher and Stirling 1994), and thus younger bears, that are nutritionally stressed, may depart onto newly formed sea ice while older bears, with higher energetic stores, wait for improved sea ice conditions.

I sought to examine the individual vulnerability of adult females to changes in phenology by examining their condition and energetics at the end of the fasting period. I made assumptions when calculating polar bear mass and body composition that may have underestimated variation in my estimates of their condition and starvation threshold at departure. To determine the daily rates of energy and mass loss while fasting, I assumed a constant movement rate for all individuals (Derocher and Stirling 1995b), which may not account for the range of movement costs possible with this study. As well, I calculated the starvation threshold assuming no offspring mortality (Molnár et al. 2020) with all females reaching the Hudson Bay sea ice with their offspring regardless of their condition, which may be unrealistic for individuals in poor condition. I explored this assumption by using a range of individual fasting thresholds reflecting a high and low reproductive cost. Finally, I only included bears that successfully departed onto the sea ice because I could not differentiate between dropped or failed collars and mortality events.

I found that the body condition of females with CUBs declined over the last thirty years whereas females with YRLGs remained stable. The difference by reproductive status is likely explained by females with CUBs leaving their spring dens following a prolonged fasting period and entering the subsequent fasting period after a shorter on-ice season with which to recover mass (Ramsay and Stirling 1988, Yee et al. 2017) together with the higher rate of mass loss experienced over the fasting period resulting from higher energetic costs associated with lactation (Arnould and Ramsay 1994, Molnár et al. 2020). These two factors may make females with CUBs more vulnerable to shifts in behaviour, such as the increased distance traveled over time due to the northward shift in migration. Alternatively, this decline may be explained by mechanisms not explored in this study, such as the advancing spring break-up of sea ice leading to shorter on-ice seasons for females with CUBs to recover body mass before fasting (Cherry et al. 2013, Castro de la Guardia et al. 2017) as well as increasing the length of the fasting period.

Annual decline in condition is one indicator of climate change impacts on the WH polar bear population that has negative demographic consequences (Stirling et al. 1999, Regehr et al. 2007). The rate of decline was similar whether estimating condition early in the fasting period or as a function of when an individual neared the end (on-ice departure), suggesting that females are beginning the fasting period in progressively lower condition and thus that this decline is consistent regardless of individual variation in fasting period length. Declining condition for females with cubs may lower pregnancy and birth rates (Derocher and Stirling 1992, Molnár et al. 2011), cub survival (Derocher and Stirling 1992, Derocher and Stirling 1996), and litter size (Folio et al. 2019). Reduced body condition could also affect adult survival due to increased starvation (Molnár et al. 2010), and, indirectly, due to increased human-bear conflict (Stenhouse et al. 1988, Towns et al. 2009). Population estimates over the last thirty years found a decline of over 30% (Derocher and Stirling 1995a, Lunn et al. 2016, Dyck et al. 2017), suggesting that the ongoing declining condition of females has resulted in reductions in fecundity and survival.

Females with CUBs departed closer to their starvation threshold over the last thirty years. While 67% of females with cubs departed past the lower threshold, that assumes milk production, I estimated that an additional 12% would deplete energetic stores if freeze-up was delayed one additional week and all females would deplete energetic stores if it was delayed one month. Individuals who surpass the threshold assuming unimpaired lactation face reduced reproductive success and gradually increasing mortality risk during the fasting period. These results may explain the low proportion of yearlings (0.03) compared to cubs (0.07) observed in the WH area in late summer (Stapleton et al. 2014). This study suggests a possible explanation for WH population decline through the expectation that, as females increasingly deplete stored energy before departure, cessation of lactation may be occurring earlier in the fasting period, leading to increasing CUB mortality. Early cessation of lactation during the fasting period may influence CUB survival more than that of YRLGs due to rapid CUB growth rates, reflected in the higher milk energy transfer of mothers to CUBs than to YRLGs (Arnould and Ramsay 1994), and insufficient fat stores for CUBs to fast for the remaining ice-free period (Derocher et al. 1993).

WH polar bears exhibit high variability in migratory behaviour due to inter-annual variation in highly dynamic sea ice conditions and individual characteristics. Although freeze-up did not change during the study, it was delayed over the juvenile period of the bears in this study when they were learning from their mothers, which may explain the population's northward shift in migration along the western coast of Hudson Bay. This energetically costly response may have led to the rising vulnerability of food-stressed adult females with first year cubs to an increasing fasting period.

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2.6 | Tables

Table 2.1. Parameters (including 95% confidence intervals) of regression and autoregressive models examining temporal trends in the autumn migration of Western Hudson polar bears (n=168) and capture methodology (n=138) [a, b, c].

Model	Covariates	Coef.	L.CI (95%)	U.CI (95%)
Latitude	Year	0.019	0.004	0.034*
Date [d]	Year	0.076	-0.190	0.342
	Date_{Y-1}	0.512	0.380	0.643*
Sea Ice	Year	0.265	-0.071	0.641
Capture latitude	Year	-0.004	-0.017	0.009
Capture date [d]	Year	0.202	-0.054	0.457
	$\text{Capture date}_{Y-1}$	0.471	0.317	0.625*

[a] Significance of coefficients determined using 95% CI and indicated using *.

[b] Lower (L.CI) and upper (U.CI) limits of the 95% confidence intervals are presented.

[c] Sea ice (% concentration), date, and latitude (decimal degrees) extracted from the departure location to describe migratory behaviour. Departure defined as the first location onto sea-ice from the west Hudson Bay coast in autumn without returning until spring.

[d] Due to autocorrelation of the regression residuals, first-order autoregressive models were used for departure date and capture date.

Table 2.2. Second order information criterion (AIC_c) and Akaike weights (W) resulting from model selection of linear regressions examining the effect of atmospheric oscillation phases during various seasons on the Hudson Bay freeze-up date from 1978 to 2020 (n=43) [a, b, c].

Model	Covariates	AIC_c	ΔAIC_c	W
1	NAO May-Aug + NAO Sept-Dec	297.5	0.00	0.511
2	NAO May-Aug	299.5	2.10	0.179
…				
8	NAO Jan-Apr	306.1	8.66	0.007
1	Null	304.0	0.00	0.349
2	AO Sept-Dec	305.2	1.21	0.191
3	AO Jan-Apr	305.5	1.52	0.164
4	AO May-Aug	306.3	2.29	0.111
…				
8	AO Jan-Apr + AO May-Aug + AO Sept-Dec	310.0	6.00	0.017

[a] Freeze-up date defined as the date at which mean sea ice concentration of the WH population zone is greater than 10% for three consecutive days.

[b] The temporal variation in the influence of the North Atlantic Oscillation (NAO) and the Arctic Oscillation (AO) indices were examined in separate global models due to collinearity.

[c] The best fitting model was used to select an appropriate environmental covariate for predicting the migratory behaviour of Western Hudson polar bears.

Table 2.3. Parameters (including Bonferroni corrected 97.5% confidence intervals) of best-fitting multiple linear regression model examining the effect of atmospheric oscillation phases during various seasons on the Hudson Bay freeze-up date from 1978 to 2020 (n=43) from model selection using second order Akaike information criterion (AIC_c) [a, b].

Covariates	Coef.	L.CI (97.5%)	U.CI (97.5%)
Summer NAO	-3.995	-7.578	-0.413*
Winter NAO	-3.852	-8.105	0.401

[a] Lower (L.CI) and upper (U.CI) limits of the 97.5% confidence intervals were used to determine significance, with significance indicated using *.

[b] Freeze-up date defined as the date at which mean sea ice concentration of the WH population zone is > 10% for three consecutive days.

Table 2.4. Second order information criterion (AICc) and Akaike weights (W) resulting from model selection of mixed-effects Cox proportional hazards models with time-varying covariates examining the autumn departure date of Western Hudson polar bears (n=145).

Model	Covariates	AIC_c	ΔAIC_c	W
1	Age + NAO[a] + Freeze-up[b] + (1|Bear)[c]	1090.6	0.00	0.19
2	Age + Freeze-up + Temp[d] + (1|Bear)	1091.0	0.36	0.16
3	Age + NAO + Freeze-up + Temp + (1|Bear)	1091.2	0.58	0.15
4	Age + NAO + Freeze-up + dCoast[e] + (1|Bear)	1091.4	0.77	0.13
5	Age + Freeze-up + (1|Bear)	1092.3	1.66	0.09
6	Age + NAO + Freeze-up + Temp + dCoast + (1|Bear)	1093.2	2.56	0.05
….				
256	dCoast + Year + (1|Bear)	1187.6	96.97	0.00

[a] Annual mean NAO index from May-August.

[b] Annual Hudson Bay freeze-up date, defined as the date at which sea ice concentration is > 10% for three consecutive days.

[c] Individual was included as a random effect to account for unexplained individual variation and lack of independence associated with the inclusion of multiple departure events for some bears.

[d] Daily mean temperature recorded at the Churchill, Manitoba airport.

[e] The nearest straight-line distance from an individual's daily location to the coast.

Table 2.5. Parameters (including Bonferroni corrected 97.5% confidence intervals) of best-fitting mixed-effects Cox proportional hazards model with time-varying covariates examining the autumn departure date of Western Hudson polar bears (n=145) from 1991 to 2020 from model selection using second order Akaike information criterion ($AIC_c < 2$) [a, b].

Covariates	Coef.	L.CI (97.5%)	U.CI (97.5%)
Age	-0.046	-0.088	-0.005*
Freeze-up [c]	-0.129	-0.170	-0.088*
ID SD	0.100		

[a] Lower (L.CI) and upper (U.CI) limits of the 97.5% confidence intervals were used to determine significance, with significance indicated using *.

[b] All models included individual as a random effect, reported with standard deviation (SD).

[c] Annual Hudson Bay freeze-up, defined as the date at which sea ice concentration of the WH population zone is > 10% for three consecutive days.

Table 2.6. Parameters (including 95% confidence intervals) of linear multiple regression examining the body condition (kg/cm^2) of migrating Western Hudson polar bears (n=136) over time using individual estimates on September 29 and individual departure date [a, b].

Covariates	Coef.	L.CI (95%)	U.CI (95%)
Year	-0.002	-0.004	-0.001*
Date	0.726	-5.594	4.141
Year:Date	-4×10^{-4}	-0.002	0.003

[a] Lower (L.CI) and upper (U.CI) limits of the 95% confidence intervals were used to determine significance, with significance indicated using *.

[b] Body condition (kg/cm^2) of individuals calculated via mass (kg) and length (cm) and applied with a conservative mass loss rate of 0.85 kg/day for all females. Two condition estimates were produced per bear, on September 29 and individual departure date (Date).

Table 2.7. Second order information criterion (AICc) and Akaike weights (W) resulting from model selection of multiple linear regressions examining the effect of year and date as well as demographic characteristics on the body condition (kg/cm2) at departure for migrating Western Hudson polar bears (n=136) estimated using two mass loss rates (MLR) [a, b].

MLR	Model	Covariates	AIC_c	ΔAIC_c	W
Conservative	1	Year + Date + Family [c] + Year:Family	-366.1	0.00	0.61
	2	Year + Date + Family + Year:Family + Age	-364.5	1.61	0.27
	3	Year + Date + Family	-360.1	6.01	0.03
	…				
	20	Age^2 + Age	-350.7	18.86	0.00
Reproductive	1	Year + Date + Family + Year:Family	-356.0	0.00	0.64
	2	Year + Date + Family + Year:Family + Age	-353.9	2.04	0.23
	…				
	20	Age^2 + Age	-302.7	53.22	0.00

[a] Body condition (kg/cm) calculated via mass (kg) and length (cm) and applied with a mass loss rate of 0.85 kg/day (Conservative) and a variable mass loss rate including the cost of lactation of 1.0 kg/day for females with YRLGs and 1.3 kg/day for females with CUBs (Reproductive).

[b] Departure defined as the first location onto sea-ice from the western Hudson Bay coast in autumn without return until the spring. The date and year extracted from the departure location were included to describe intra- and inter-annual variation in body condition.

[c] Females with yearlings are compared to females with cubs-of-year.

Table 2.8. Parameters (including 95% confidence intervals) of best fitting linear multiple regressions examining the influence of spatiotemporal variation in migratory behaviour and individual characteristics on the body condition (kg/cm^2) and starvation threshold (days) at departure for Western Hudson adult female polar bears (n=136) selected using second order Akaike information criterion (AIC$_c$) [a].

Model	Covariates	Coef.	L.CI (95%)	U.CI (95%)
Body condition [b]	Intercept	0.388	0.370	0.405*
(conservative loss rate)	Year	-0.001	-0.015	0.013
	Date	-0.016	-0.027	-0.006*
	Family $_{COY}$ [c]	-0.020	-0.042	0.002
	Year:Family $_{COY}$	-0.031	-0.053	-0.010*
Body condition [b]	Intercept	0.355	0.337	0.373*
(reproductive loss rate)	Year	-0.004	-0.018	0.011
	Date	-0.021	-0.032	-0.010*
	Family $_{COY}$	-0.072	-0.095	-0.050*
	Year:Family $_{COY}$	-0.028	-0.051	-0.006*
Starvation threshold [d]	Intercept	11.650	7.908	15.392*
(ceased lactation)	Year	0.150	-2.874	3.174
	Date	-5.352	-7.644	-3.060*
	Family $_{COY}$	-2.306	-7.007	2.396
	Year:Family $_{COY}$	-6.306	-10.993	-1.619*
	Age	-2.792	-5.066	-0.517*
Starvation threshold [d]	Intercept	4.708	1.461	7.955*

(unimpaired lactation)	Year	0.252	-2.371	2.876
	Date	-5.786	-7.775	-3.955*
	Family $_{COY}$	-17.786	-21.865	-13.707*
	Year:Family $_{COY}$	-5.557	-9.623	-1.490*
	Age	-2.074	-4.048	-0.100*

---

[a] Lower (L.CI) and upper (U.CI) limits of the 95% confidence intervals were used to determine significance, with significance indicated using *.

[b] Calculated via mass (kg) and length (cm) and applied with a conservative mass loss rate of 0.85 kg/day and a mass loss rate by reproduction status of 1.0 kg/day for females with YRLGs and 1.3 kg/day for females with CUBs.

[c] Comparison between females with cubs-of-year and with yearlings.

[d] Number of days worth of stored energy remaining at the time of departure before increased mortality due to starvation, was calculated based on the body composition (MJ) and the daily rate of energy loss (MJ/day) for fasting bears assuming either unimpaired lactation or ceased lactation during the fasting period.

Table 2.9. Second order information criterion (AIC_c) and Akaike weights (W) resulting from model selection of multiple linear regressions examining the effect temporal variation and demographic characteristics on the starvation threshold (days) at departure for migrating Western Hudson polar bears (n=136) assuming ceased lactation and unimpaired lactation [a, b].

	Model	Covariates	AIC_c	ΔAIC_c	W
Unimpaired	1	Year + Date + Family + Age + Year:Family	1056.9	0.00	0.67
	2	Year + Date + Family + Year:Family	1059.1	2.22	0.22
	…				
	20	Null	1139.6	82.64	0.03
Ceased	1	Year + Date + Family + Age + Year:Family	1095.5	0.00	0.65
	2	Year + Date + Age	1099.2	3.65	0.11
	…				
	20	Family	1120.1	24.53	0.04

[a] Starvation threshold (days), defined as the number of days worth of stored energy remaining at the time of departure before death by starvation, was calculated based on the body composition (MJ) and the daily rate of energy loss (MJ/day) for fasting bears assuming either unimpaired lactation or ceased lactating during the fasting period.

[b] Departure defined as the first location onto sea-ice from the western Hudson Bay coast in autumn without return until the spring. Date and year extracted from the departure location and were included to describe intra- and inter-annual variation in body condition.

2.7 | Figures

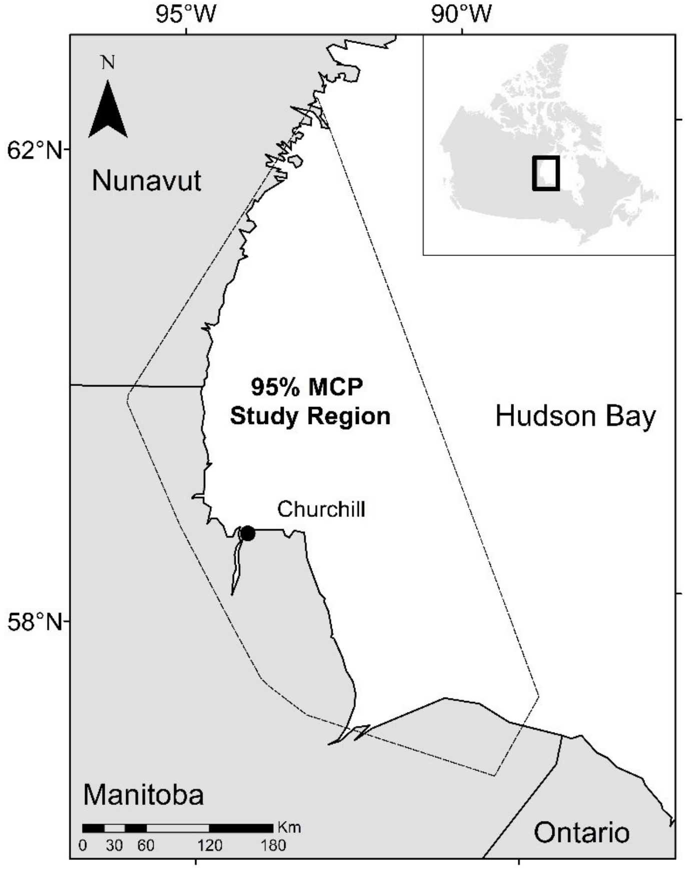

Figure 2.1. Map of Hudson Bay, Canada, showing a 95% minimum convex polygon (dashed line) of all satellite telemetry locations of 151 WH polar bears from September 29 to each individual's departure onto the sea ice over the study from 1991 to 2020. Polar bears were captured on land between Churchill, Manitoba and the Manitoba-Ontario border from August to September and fitted with Argos or Iridium satellite-linked collars.

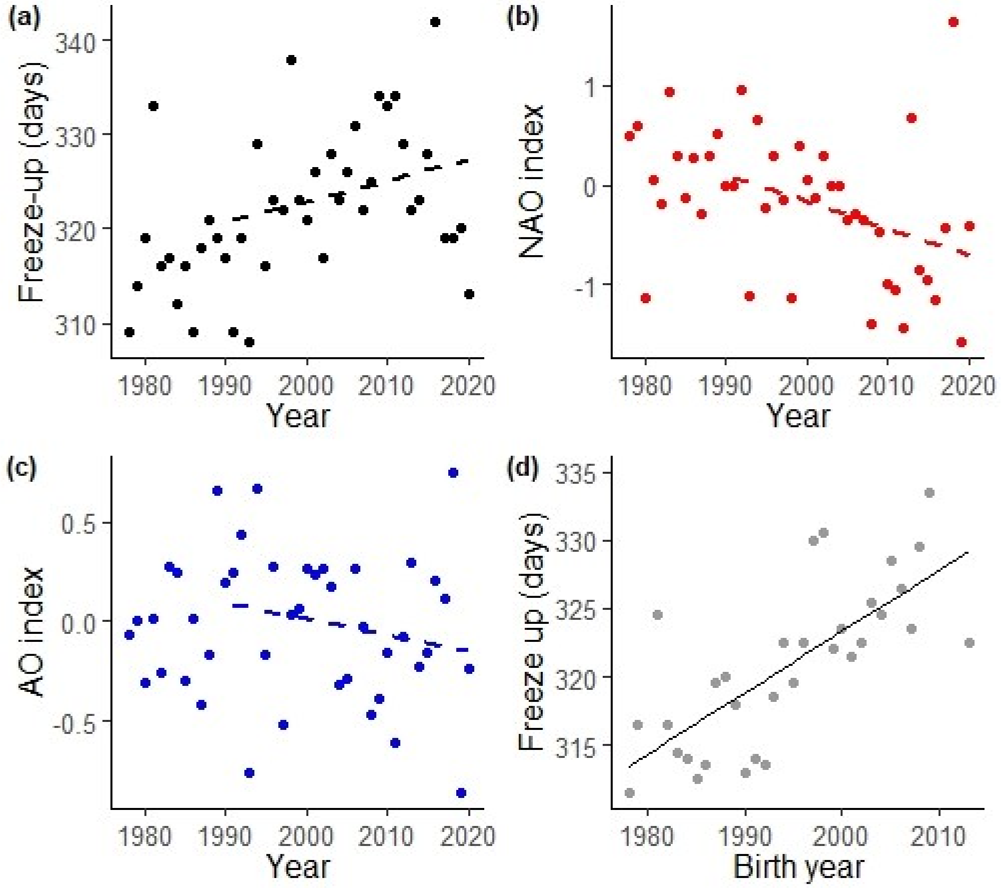

Figure 2.2. Trends in (a) annual freeze-up date for western Hudson Bay, Canada and the mean May to August (b) NAO and (c) AO indices from 1991 to 2020 and in (d) the juvenile freeze-up date from 1978 to 2013. Freeze-up defined as the first date upon which the mean sea ice concentration of the WH population zone > 10% for three consecutive days. Juvenile freeze-up defined as the freeze-up date averaged between a bear's birth year and the following year. All linear regressions were non-significant except for the juvenile freeze-up date (ß = 0.467, 97.5% CI 0.276 to 0.657). Significant linear trends indicated with a solid line.

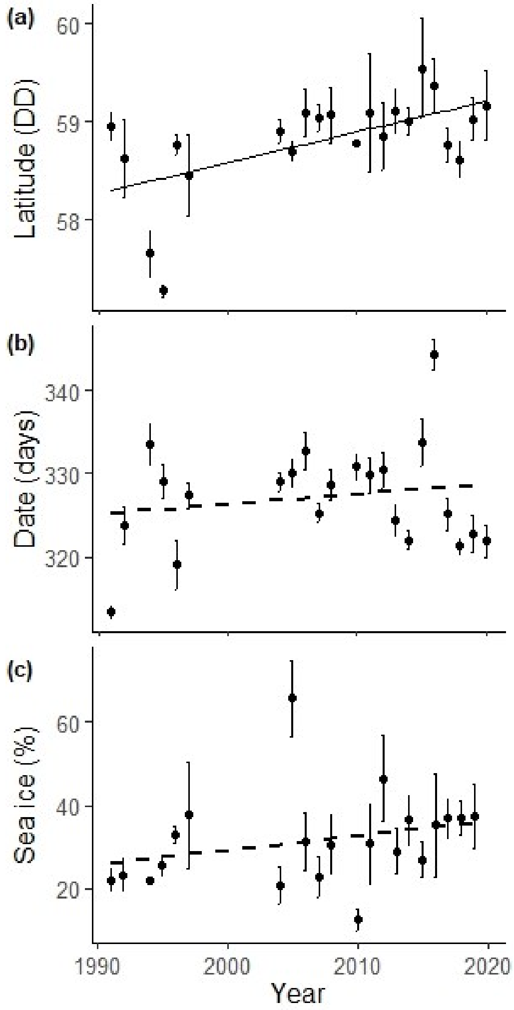

Figure 2.3. Temporal trends in characteristics of autumn departure locations during 168 migrations of 151 Western Hudson Bay female polar bears during the autumn migratory period from 1991 to 2020. Annual mean values (± SE) were extracted from each departure location to examine behaviour plasticity during migration, including (a) the departure latitude (decimal degrees), (b) departure date, and (c) mean daily sea ice concentration (%) over a 25 x 25 km area (d). Departure defined as the first location onto sea-ice from the western Hudson Bay coast in autumn without returning until spring. All linear regressions were non-significant except for the departure latitude (solid; ß (slope) = 0.019, 95% CI 0.004 to 0.034). Significant linear trends indicated with a solid line.

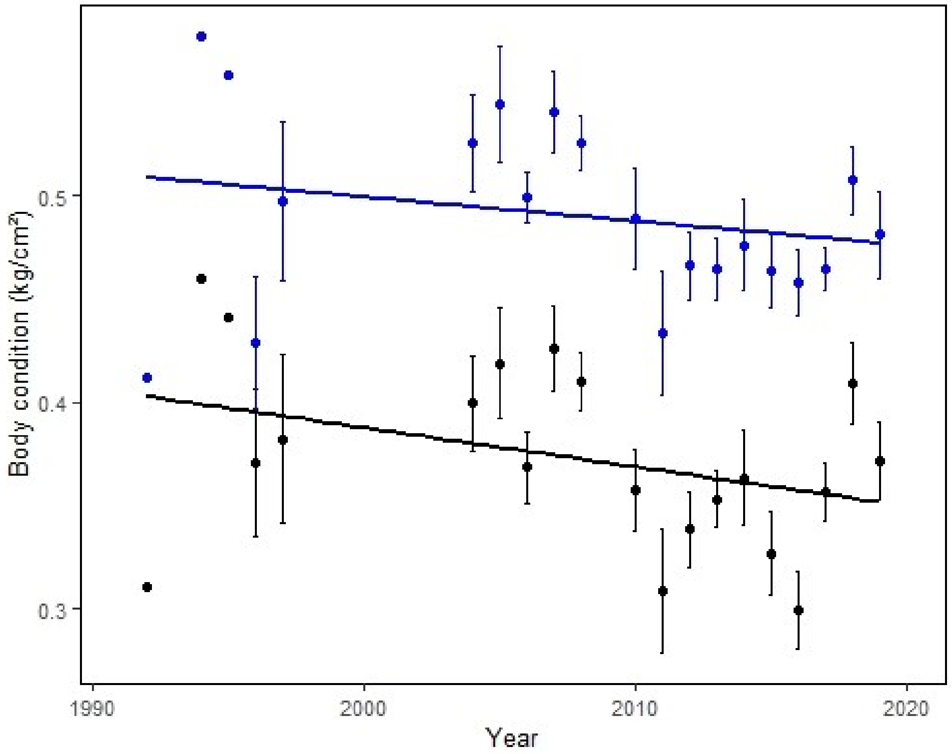

Figure 2.4. Bear body condition (kg/cm^2) on September 29 (blue) and individual departure date (black) for 136 Western Hudson Bay polar bears during the autumn migratory period from 1991 to 2020. Departure defined as the first location onto sea-ice from the west Hudson Bay coast in autumn without return until the spring. The temporal trends of condition estimated on the two dates were not significantly different (linear regression, ß $_{\text{condition:date}}$ (slope) = -4x10^{-4}, 95% CI -0.002 to 0.003).

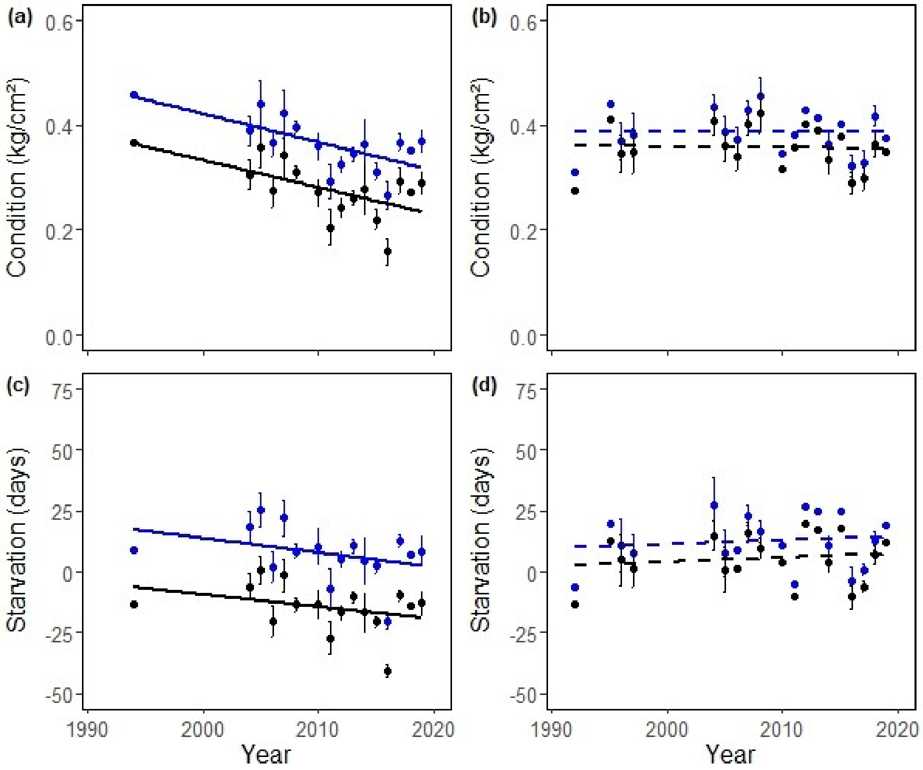

Figure 2.5. Trends in condition and starvation threshold at departure of 136 adult female WH polar bears with offspring during the autumn migratory period from 1991 to 2020. Two rates of energy loss were used: assuming bears had ceased lactating while fasting (blue) and then assuming lactation would continue unimpaired until starvation (black). Two rates of mass loss were calculated for (a) females with cubs-of-year and (b) yearlings using a conservative mass loss of 0.85 kg/day (blue) and 1.3 kg/day for females with cubs and 1.0 kg/day for females with yearlings (black). Starvation threshold, defined as the number of days-worth of stored energy remaining at departure, was calculated for (c) females with cubs-of-year and (d) yearlings based on body composition (MJ) and the daily rate of energy loss (MJ/day). Departure was defined as the first location onto sea-ice from the western Hudson Bay coast in autumn without returning until the spring. Significant linear trends indicated with a solid line.

2.8 | Appendix

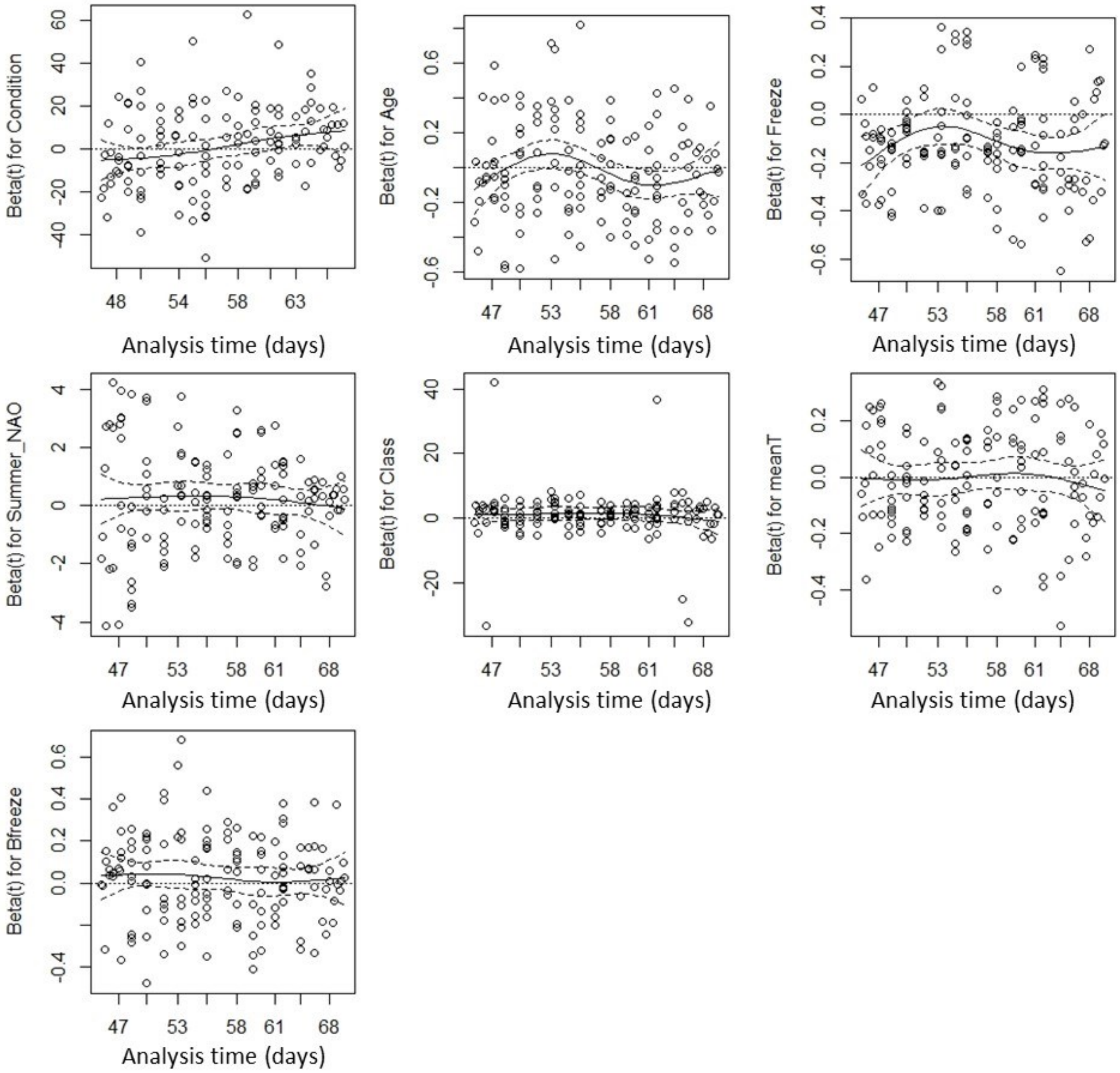

Figure A2.1. Hazard rate over time for all covariates included in the global model of the mixed-effect Cox proportional hazards model with time-varying covariates examining the autumn departure date of Western Hudson polar bears from 1991 to 2020. Using a goodness-of-fit test of scaled Schoenfeld residuals, daily body condition (kg/cm^2) was found to violate the assumption of proportional hazards ($p \leq 0.05$) and was removed from the global model before model selection.

Chapter 3

3 | Human-polar bear conflict during the autumn migratory period in Hudson Bay, Canada

3.1 | Introduction

Conflict between humans and carnivores has increased in frequency and impact on species conservation in association with habitat loss, human expansion, and climate change (Treves and Karanth 2003, Nyhus 2016, Abrahms 2021). Human safety and property are threatened during conflict with carnivores (Loe and Roskaft 2004, Gulati et al. 2021). Thus, conflict involving large-bodied carnivores often results in the mortality of the animal, directly impacting population abundance (Karanth and Chellam 2009). Due to either real or perceived threat, tolerance towards carnivores may decline without appropriate management and result in lethal control, further exacerbating mortality rates (Rabinowitz 1986, Woodroffe 2000). Community support for conservation programs may decline, resulting in the politicization of conservation, which may impact its efficacy (Torres 1996, Clark et al. 2008). One species whose conservation and management has become highly politicized is the polar bear (*Ursus maritimus*; Dowsley and Wenzel 2008, Lokken et al. 2019), due in part to its importance as a symbol of conservation and to Indigenous communities (Kovacs et al. 2011, Peacock et al. 2011).

Polar bears are specialized carnivores distributed across the circumpolar Arctic in association with sea ice (DeMaster and Stirling 1981) that require sea ice to hunt their main source of prey, ringed seals (*Pusa hispida*; Stirling and Archibald 1977, Thiemann et al. 2008). Those that inhabit the seasonal sea ice ecoregion (Amstrup et al. 2008, Durner et al. 2009), including the Western Hudson (WH) subpopulation (Stern and Laidre 2016) in Hudson Bay, Canada, lose access to this prey source during the ice-free period for up to five months, resulting in seasonal mass loss (Rode et al. 2015, Pilfold et al. 2016). At freeze-up, with the exception of females in maternity dens (Yee et al. 2017), WH polar bears migrate from land back onto the sea ice and resume hunting (Castro de la Guardia et al. 2017). It is during their time on land, when prey are unavailable, that most human-polar bear conflicts occur (Towns et al. 2009).

Most human-wildlife conflicts involving WH polar bears occur during the ice-free period of Hudson Bay from August to November, with rates peaking between October and November before freeze-up (Dyck 2006, Laforge et al. 2017, Wilder et al. 2017). Conflict rates involving polar bears have increased from the 1970s to the early 2000s in both Manitoba (Towns et al. 2009) and Nunavut (Tyrrell 2006, Henri et al. 2010, Peacock et al. 2010). A recent study found that conflict rates declined around Churchill, Manitoba after the early 2000s (Heemskerk et al. 2020) and suggested that possible causes may include population decline, lower recruitment, and the efficacy of new management protocols (e.g., preventative hazing, closure of the local landfill). A recent report from the Manitoba government stating increasing occurrence of bears near Churchill from 2009 to 2016 suggests that the decline in conflicts may indeed be attributed to preventative management protocols rather than a reduction of bears found in proximity to communities (Lunn et al. 2018). While residents in local communities are seeing more bears onshore in places and at times not previously observed and report that the polar bear population has increased (Clark et al. 2008, Dowsley and Wenzel 2008, Henri et al. 2010), scientific estimates of abundance suggest that the WH population has declined from approximately 1200 bears in the 1990s (Derocher and Stirling 1995a, Lunn et al. 1997a) to 800 in the 2010s (Lunn et al. 2016, Dyck et al. 2017). Given the association between the timing of freeze-up and conflict rates, the trend toward increasing conflicts up to the 1990s may be explained in part by the lengthening of the Hudson Bay ice-free period (Gagnon and Gough 2005, Parkinson 2014, Laidre et al. 2015), which has resulted in a decline in female body condition (Stirling et al. 1999) and more time spent on land, possibly facilitating more interactions between humans and bears. Food seeking behaviour by several bear species is common, often associated with natural food shortages (Azad et al. 2017) and anthropogenic food availability (Merkle et al. 2013, Hagani et al. 2021).

Most interactions between humans and polar bears appear to result from polar bears seeking alternative food sources within or near human communities (Wilder et al. 2017), but several factors may influence the likelihood of an individual bear being involved in conflict. Polar bears, like all other bears, can become habituated to humans due to food conditioning, (e.g. garbage dumps; Lunn and Stirling 1985, Hopkins et al. 2010). Most polar bears involved in conflict events were classified as being in poor condition (Wilder et al. 2017), with subadult males being both disproportionately represented in conflicts and more likely to be in poor condition (Dyck 2006, Towns et al. 2009). These characteristics may be explained in part by the higher metabolic rates seen in subadults due to growth (Molnár et al. 2009), with male subadults growing at a faster rate than females due to their larger adult size (DeMaster and Stirling 1981), the inefficient hunting practices utilized by subadults as they learn to hunt (Stirling and Latour 1978, Herrero and Fleck 1990), and the higher risk of a kill being stolen by a larger male (Stirling 1974). The management of polar bears should thus consider factors affecting individual variation in conflict rates to develop practices that can more efficiently prevent conflicts.

Polar bear management in Canada falls within the jurisdiction of provinces and territories (Peacock et al. 2011). In Manitoba, the Polar Bear Alert Program based in Churchill, was established in the 1980s with the goals being both the safety of humans and the avoidance of unnecessary bear deaths (Kearney 1989). The Alert Program uses various strategies to mitigate human-bear interactions, including attractant reduction and hazing bears from town as well as the capture, temporary holding, and relocation of bears away from the community (Derocher et al. 2013, Struzik 2014). Bears are captured by wildlife officers and may be held until the sea ice forms along the western coast and then released directly onto the sea ice or released on-land outside of the Alert Program's management perimeter, usually northwest of the Churchill River (Kearney 1989). It has been hypothesized that the placement of habituated bears north of Churchill facilitates the northward movement of bears along the western coast, leading to the increased presence of bears reported in Arviat, Nunavut (Tyrrell 2006), which lies along the migratory path of the bears (Figure 3.1). While conflict rates have increased over time in Arviat (Peacock et al. 2010), conflict-related mortality of bears has declined since the 1980s as non-lethal measures were implemented (Dyck 2006, Lunn et al. 2018).

The goal of this study was to examine the effect of management practices, sea ice conditions, and biological factors on the migratory movement of polar bears involved in conflict after their capture, relocation, and release by Manitoba wildlife officers using satellite telemetry and capture data from 2016 to 2020. I predicted that conflict bears, those captured by Manitoba wildlife officers due to their proximity to Churchill, would depart earlier in the season than non-conflict bears, those collared for research with no recent history of conflict, due to their association of being in poor condition and may thus migrate onto early forming sea ice. I also predicted that conflict bears would depart onto the sea ice further north to intercept early forming sea ice. I examined the directionality of conflict bears post-release and predicted that bears would demonstrate an overall northward movement because of their search for sea ice north of Churchill. Finally, I examined the recidivism rates of conflict bears, defined as those who either re-entered Churchill or entered Arviat post-release, in relation to three hypotheses: Recidivism rates were influenced by 1) management practices, 2) sea ice conditions, and 3) individual characteristics. I predicted that bears were more likely to re-enter Churchill when they were released east of, and close to, Churchill, earlier in the season, and on days with low sea ice concentration along the coast near Churchill. I predicted that bears were more likely to enter Arviat when they were released farther from, and west of, Churchill, earlier in the season, and on days with low sea ice concentration along the western coast near both Churchill and Arviat. Finally, I predicted that bears with lower energetic stores would demonstrate the highest likelihood of recidivism, which would result in a high proportion of subadult male bears re-entering communities.

3.2 | Methods

3.2.1 | Study area

This study was conducted along the western coast of Hudson Bay, Canada during the annual autumn migration from 2016 to 2020 (Figure 3.1). Hudson Bay is characterized by high seasonal variation in sea ice, ranging from >90% sea ice concentration in winter to ice-free summers (Prinsenberg 1988). Sea ice initially forms mid-October along the northwest coast due to colder temperatures and freshwater runoff (Prinsenberg 1988) and is influenced primarily by temperature and wind which combine to form a cyclonic gyre that drives sea ice drift southward (Gagnon and Gough 2005).

3.2.2 | Individual metrics and environmental conditions

I utilized two datasets of polar bear locations, the first comprising “conflict” polar bears. Conflict bears are defined as those that were captured from 2016 to 2020 by Manitoba wildlife officers on land within the high priority management area of the Alert Program, which was approximated as a circle surrounding Churchill, Manitoba with a radius of 6.9 km (Kearney 1989). These bears were fitted with Doppler shift Argos® satellite-linked eartags (Telonics, Mesa, AZ; SirTrack, Hawkes Bay, New Zealand), which were programmed to sample one location every 24 h and to last up to 7 months. The second dataset included “non-conflict” adult female polar bears who were captured between 2016 and 2019 by helicopter and tranquilized from the air via remote injection of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®, Laboratories Virbac, Carros, France; Stirling et al. 1989) on land in the western Hudson Bay coast between Churchill, Manitoba and the Manitoba-Ontario border in August and September. They were fitted with GPS Argos® or Iridium satellite-linked collars (Telonics, Mesa, AZ). Collars were programmed to release after 2.5 years or were removed upon recapture. Capture and handling protocols for the non-conflict bears were approved by the Environment and Climate Change Canada, Prairie and Northern Region Animal Care Committee and the University of Alberta Bio Sciences Animal Policy and Welfare Committee, in accordance with the Canadian Council on Animal Care guidelines.

The sex of each conflict bear was determined at capture. A premolar was extracted from each bear > 1 year old to estimate age based on cementum growth layers (Calvert and Ramsay 1995) and bears <1 year old were aged based on tooth eruption patterns. Bears were grouped into age classes of juvenile (< 2 year), 2-years-old, subadult (3-4 years), and adult (≥ 5 years). Body mass (kg) was measured using a scale and body length (cm), the straight line from tip of the nose to the end of the last tail vertebra, was measured before release from the holding facility. Storage energy (MJ) was estimated separately for each age and sex class using mass and body length from Molnár et al. (2009). Only adult female bears are included in the non-conflict dataset, with sex determined following immobilization and age estimated using Calvert and Ramsay (1995).

Hudson Bay sea ice concentration was obtained from the National Snow and Ice Data Center (NSIDC) archives (https://nsidc.org/data) at a 3 x 3 km resolution (Cavalieri 1997). The mean daily sea ice concentration was calculated for the release-zone, which was defined as the 30 km area from the coast bounded by all release locations of conflict bears between 2016 and 2020, with the exception of one outlier release location south of Churchill, and for the north-zone, defined as the 30 km area from the coast north of all release locations up to Arviat, Nunavut (Figure 3.1). Sea ice concentration was also obtained from NSIDC at a 25 x 25 km resolution and used to calculate the mean daily concentration inside the WH population boundary (Lunn et al. 1997a) to determine the annual freeze-up date for the WH zone, defined as the first date at which sea ice concentration was >10% for three consecutive days.

3.2.3 | Data Analysis

For both conflict and non-conflict bears, duplicate timestamps and all relocations with a speed >10 km/h were removed (Parks et al. 2006). The intervals between polar bear telemetry locations varied from 30 min to 24 h and were standardized by subsampling to 24 h. The telemetry locations of conflict bears were filtered to those with a maximum allowable error of 1.5 km. Initial locations within the high priority Alert Program management area were defined as post-capture holding locations and were removed from analysis. The release date and location of conflict bears was obtained from Government of Manitoba records. On-ice departure was defined for both conflict and non-conflict bears as the first location 10 km offshore that was not followed by a location on-land until the following spring. The date and location of departure for each bear was determined visually using ArcGIS 10.7.1 (Environmental Systems Research Institute, Redlands, CA). Departure events were not included for bears with a gap > 10 days between the last on-land location and the first offshore location. All statistical analyses were performed using R version 3.6.2 (www.rproject.org, accessed 20 Sep 2021). A standard significance level ($\alpha = 0.05$) was used unless adjusted.

I compared the migratory movement of conflict bears to non-conflict bears by examining the date and latitude of on-ice departure from 2016 to 2020. I combined the two datasets and used linear multiple regressions to examine the influence of conflict status, age group, and sex on spatiotemporal variation in migration. The residuals of the regressions of departure latitude and date were non-normal despite transformations, and so I used robustly fitted linear regressions. I performed model selection on all candidate models of the global model using the adjusted R-squared, with the highest adjusted R-squared defining the top model. I determined significance of covariates via 95% confidence intervals. I produced kernel density estimations for the departure locations of conflict and non-conflict bears for visual comparison using ArcGIS 10.7.1.

I examined the directionality of post-release movement of conflict bears via analysis of circular distributions. I performed the Rayleigh Z test to examine the distribution of movement post-release using the R-package *CircStats* (Lund and Agostinelli 2018) to test if bear movement demonstrated unimodal clustering north as hypothesized. Each bear's on-land movement was followed post-release until departure or final transmission. A bear's bearing was computed between each consecutive relocation for all on-land locations. All locations were then pooled to calculate an average angle for on-land movement. I determined significance of the z test statistic via p-value ($\alpha \leq 0.05$).

I used multinomial logistic regressions to examine the influence of management practices, sea ice conditions, and individual characteristics on the recidivism rates of conflict bears using R-package *nnet* (Ripley and Venables 2021). Bears with < 30 post-release locations were not included in analysis unless a post-release conflict was recorded by wildlife officers. Bears with locations < 10 km of Arviat or Churchill post-release were defined as recidivists, which I determined by calculating the shortest straight-line-distance from an individual's daily location to each community in ArcGIS 10.7.1. I produced separate models to examine the probability of a bear re-entering Churchill or entering Arviat post-release when influenced by 1) management practices, including the release location's distance and east-west direction from Churchill, the number of days a bear was held in the holding facility, and the release date, 2) sea ice conditions, including the daily mean release-zone sea ice concentration, daily mean north-zone sea ice concentration, and the annual WH zone freeze-up date and 3) individual characteristics, including the sex, age group, and storage energy at release. All covariates included in analysis were tested for collinearity using the variance inflation factor (VIF > 4), and the assumptions of normality and homoscedasticity using the Shapiro-Wilks and studentized Breusch-Pagan tests, respectively ($p \leq 0.05$). Model selection was performed using the Akaike Information Criterion corrected for small samples (AIC_c). When multiple models had $\Delta AIC_c < 2$, I chose the most parsimonious model to avoid overfitting with uninformative covariates (Arnold 2010). I used the Bonferroni corrected level of significance ($\alpha = 0.017$) to determine significance of covariates via 99.8% confidence intervals.

3.3 | Results

From 2016 to 2020, 50 unique polar bears were captured by wildlife officers between July 17 and December 1 and released 53 times with eartags during the autumn migratory period (Table 3.1). Of these conflict bears 21 were male and 29 were female, with 5 of the females accompanied by cubs. Conflict bears included 2 juveniles (< 2 years), 10 two-year-olds, 10 subadults (3-5 years), and 28 adults (> 5 years). Conflict bear release dates ranged from August 21 to December 2 following a mean holding period of 21 days (SE 2) between a bear's conflict and release dates. Bears were released with mean energy stores of 1060 MJ (SE 121). Mean distance of release from Churchill was 34.1 km (SE 2.7, range 5.5 to 74.3) at a mean latitude of 58.9° (SE 0.05). The percentage of conflict bear releases that resulted in a bear's recapture or proximity to a community before on-ice departure was 36% (n = 53), with 8 bears that re-entered Churchill and 11 that entered Arviat post-release. From 2016 to 2019, 35 non-conflict bears were captured and released with collars and recorded migrating onto the sea ice. I removed 5 of these bears due to their history of conflict near Churchill in previous years.

I recorded 29 on-ice departures from conflict bears and 30 departures from non-conflict bears between 2016 and 2020. Model selection of multiple robust regressions of the latitude at departure resulted in one top model that included conflict status and age group (Table 3.2). The mean departure latitude of conflict bears (mean = 59.8°, SE 0.2) was 104 km further north than non-conflict bears (mean = 58.9°, SE 0.1; Table 3.3; Figure 3.2). Model selection of multiple linear regressions of the date at departure resulted in one top model that included sex and age group (Table 3.4). The mean departure date of male bears (mean = December 7, SE 4 days) was 12 days later than females (mean = November 25, SE 1 day; Table 3.3; Figure 3.3). This effect was consistent when the outlier was removed (Table A3.1; Figure 3.2). A post-hoc, two-sample t-test showed that the mean release dates of female (mean = November 11, SE 3 days) and male (mean = November 15, SE 3 days) conflict bears were not significantly different (t-test, t = -0.832, df = 38, p-value = 0.412), suggesting the data was not affected by variable management procedures.

Analysis of circular distribution included 716 locations from 31 individuals, with a mean of 23 (SE 3) daily on-land locations/bear. The circular distribution of migrating bears post-release clustered significantly around one mode before departure (Rayleigh test, $Z = 43.1$, $n = 716$, $p = 1.9 \times 10^{-19}$), with a mean angle of 345° (SE 2; Figure 3.4), which is nearly parallel to the approximated angle of the coastline immediately north of Churchill (325°). Despite being released on average (58.9°, SE 0.05) at the same latitude where non-conflict bears departed onto the sea ice (58.9°, SE 0.10), conflict bears continue moving northward post-release until on-ice departure.

Thirty-four conflict bear releases were included in the recidivism models. Hypothesis 1 resulted in two competing top models out of fifteen candidate models examining the influence of management practices on the probability of recidivism. The most parsimonious model included the release date (Table 3.5). Examination of the 99.8% confidence intervals suggested that bears released later in the season were less likely to enter Arviat or to re-enter Churchill (Table 3.6). Each additional day later in the season that a bear was released reduced the odds of recidivism by 8.2% for re-entering Churchill and 7.9% for entering Arviat. Hypothesis 2 resulted in one top model out of seven candidate models examining the influence of sea ice conditions on recidivism rates, which included the daily mean sea ice concentration of the north-zone at release (Table 3.7). The 99.8% confidence intervals overlapping zero suggested that sea ice conditions did not influence the likelihood of recidivism (Table 3.6). Hypothesis 3 resulted in two competing top models out of seven candidate models examining the influence of individual characteristics on recidivism rates, which I averaged into a single model due to both models having one covariate. The top model included the bear's sex and storage energy at release (Table 3.8). The 99.8% confidence intervals both overlapping zero suggested that individual characteristics did not influence the likelihood of recidivism (Table 3.6).

3.4 | Discussion

I used telemetry and capture data to examine the migratory movement of WH polar bears involved in human-wildlife conflict after their release by wildlife officers during the autumn migratory period. I found that conflict bear movement differed from that of non-conflict bears and varied by management practices at release. Conflict bears traveled northward post-release until departure, eventually migrating onto the sea ice further north than non-conflict bears. Conflict bear departures clustered near Churchill and Arviat, which may suggest that these bears are habituated to humans and are choosing to wait for autumn sea ice near human communities. Male bears departed later in the season than females, regardless of conflict status. Conflict bears released later in the season were less likely to re-enter a community before on-ice departure, while other management practices had no effect. Over one-third of conflict bears released during the autumn migratory period were found again near human communities before they departed onto the sea ice.

My use of Manitoba wildlife management reports to supplement recidivism of bears in Churchill with fewer than one month of locations was with the aim to reduce bias against recidivism rates in Churchill. These records were used to prevent the possibility of bears being removed from analysis due to a lack of data resulting from their re-entering Churchill within one month of release and having fewer than 30 total locations. This may have resulted in the study underestimating the number of bears involved in conflicts post-release in Arviat, due to a lack of similar reports being available for conflict bears in the area. However, the majority of bears that were found in this study to be in proximity to Arviat were not captured or killed, allowing for over one month of locations regardless of the recidivism date and so I believe that most recidivist bears were identified. To account for this potential bias during data collection, I do not compare Arviat and Churchill recidivism rates.

After release onto the western coast or directly onto the sea ice, polar bears moved northward. These conflict bears migrate farther up the coast than non-conflict bears, with some eventually departing onto the sea ice near Arviat. Despite the mean latitude of the release location being the same as that of the on-ice departure of non-conflict bears at 58.9°, the conflict bears continued to travel north during their post-release migration. Non-conflict bears that were not handled also demonstrate a northward direction in their movement after September and before on-ice departure (Derocher and Stirling 1990), so this may suggest that the bears did not change their behaviour after handling and relocation and instead are responding to environmental stimuli by moving north regardless as other bears did. The northward shift in distribution of migrating conflict bears may be the result of bears being placed geographically ahead of schedule upon release and having more time before freeze-up to move.

An alternative explanation to the northward shift in distribution of conflict bears may be that conflict bears, who are more likely to be in low body condition (Wilder et al. 2017), are migrating further distances in search of earlier forming sea ice and would travel further north than non-conflict bears whether they were handled and released by wildlife management or not. As freeze-up continues to delay (Stern and Laidre 2016), further declines in the condition of WH polar bears are expected that, when combined with more time spent on land, may result in an increase in conflict rates, particularly in Arviat if more bears are traveling north of Churchill in search of early sea ice (Heemskerk et al. 2020).

Female polar bears departed onto the sea ice earlier than males, regardless of conflict status. The results do not appear to be due to the management practice of immediately releasing family groups (Kearney 1989), as female and male conflict bears had similar release dates. My results may instead suggest that females are departing earlier, likely due to low energetic stores (Molnár et al. 2009). While adults of both sexes have demonstrated declining condition over time (Stirling et al. 1999), male polar bears enter the fasting period with higher storage mass than females and have lower thermodynamic requirements than females with cubs (Molnár et al. 2009). These results may suggest that female conflict bears should be released immediately at freeze-up, rather than extending their fasting season.

Conflict bears released later in the autumn migratory period were less likely to re-enter Churchill or to enter Arviat before departure onto the sea ice. Most conflicts occur while polar bears are on land, with rates peaking immediately before freeze-up (Towns et al. 2009, Laforge et al. 2017). Considering that the timing of polar bear migration is correlated to freeze-up, with bears departing a mean of 2.5 days following freeze-up (Cherry et al. 2013), the less time that occurs between release from holding and sea ice freeze-up, the less opportunity available for bears to re-enter communities. Holding conflict bears until freeze-up along the western coast is thus an effective strategy for countering the same-year recidivism of conflict bears.

When considering how to effectively manage conflict bears with a high risk of recidivism, research should examine information associated with the conflict event itself. A bear that obtains anthropogenic foods before capture may be more incentivized to return to the community than a bear that was successfully hazed away or caught before feeding. Food habituation is the leading cause of human-bear conflicts in *U. americanus* and *U. arctos* and will likely factor into recidivism rates of polar bears (Spencer et al. 2007, Can et al. 2014). Another factor that may provide further insight in polar bear recidivism would be to include the specific deterrent strategies used on bears. For example, diversionary feeding has been attempted near Arviat since 2013 (Lunn et al. 2018) but its impact on the migratory movement of polar bears is unclear.

While I examined same-year recidivism, many individuals in this study were recaptured at least one other time in subsequent years. If these bears were to be fitted with eartags over multiple years, research could examine intra-individual variation in post-release movement and may provide further insight into effective strategies to minimize recidivism of bears in the years following their first conflict event. Additional mortality effects may also play a role in the importance of conflict management for the conservation of polar bears. Nearly one quarter of conflict bears released from Churchill were harvested in Nunavut (Towns et al. 2009). Examining the relationship between conflict bears in Churchill to those harvested in Nunavut using their post-release movement could provide necessary insight when considering the management of the WH population as conflict rates increase, given that 20% of the bears released in this study were found near Arviat within the same year.

Due to my findings that conflict bears continued their directional movement north past non-conflict migratory locations and that more conflict bears eventually entered Arviat than re-entered Churchill, I propose that the Alert Program consider examining the efficacy of the past practice of releasing polar bears south of Churchill. I believe that it would be useful to place eartags on these bears to determine if they continue to demonstrate unimodal directionality northward and if this management strategy may lead to similar migration locations to non-conflict bears. While it was known whether these bears eventually ended up Churchill due to Manitoba wildlife officer reports when this strategy was used in the past, the use of telemetry data would allow us to determine if this practice influenced conflict rates in Arviat. I acknowledge that this strategy when used in the past resulted in bears returning to Churchill often within the same season (Struzik 2014), but I propose that the practice may reduce the total number of same-year conflicts along the coast.

Management of polar bear conflicts has been the subject of controversy and discourse as conflict rates have risen (Towns et al. 2009). I found that conflict bears demonstrated migratory movement patterns that differed from those that are not involved in conflict, but that the release location did not affect the likelihood of a bear re-entering a community before on-ice departure. The only effective solution to reduce same-year conflict with a bear may be to release them later in the season, closer to freeze-up. As the ice-free period continues to increase, I expect that human-polar bear conflicts will increase in frequency, and that the management of conflict bears will require greater consideration in the conservation of the WH population.

3.5 | References

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3.6 | Tables

Table 3.1. Sample sizes by age, sex, and conflict status of migrating Western Hudson polar bears from 2016 to 2020.

Conflict	n	Sex	n	Age	n
Yes	50	Female	29	Juvenile *	2
				2-years-old	5
				Subadult	6
				Adult	16
		Male	21	Juvenile	0
				2-years-old	5
				Subadult	4
				Adult	12
No	30	Female	30	Adult	30

* Juvenile defined as independent cub(s)-of-year and yearlings not accompanied by their mothers.

Table 3.2. Adjusted R-squared (R^2), F-statistic (F), and p-value (p) resulting from model selection of linear regressions examining the effect of individual characteristics and conflict status on the latitude at departure of migrating Western Hudson polar bears from 2016 to 2020 (n=59) [a, b].

Model	Covariates	R^2	F	p
1	Conflict + Age	0.239	6.200	0.001
2	Conflict + Age + Sex	0.230	4.824	0.002
3	Conflict	0.211	16.75	0.0001
4	Conflict + Sex	0.208	8.367	0.0007
5	Sex	0.091	4.025	0.050
6	Age + Sex	0.071	3.426	0.023
7	Age	0.0006	0.032	0.291

[a] Departure defined as the first location onto sea-ice 10 km from the western Hudson Bay coast in autumn without returning until spring.

[b] Conflict status refers to whether bears had a history of being captured within the Polar Bear Alert management area or not during the autumn migratory period.

Table 3.3. Parameters (including 95% confidence intervals) of best-fitting robust multiple linear regressions examining the influence of individual characteristics and conflict status on the timing and location of the on-ice departure of Western Hudson polar bears (n = 59) selected using the adjusted R-squared [a, b].

Model	Covariates	Coef.	L.CI (95%)	U.CI (95%)
Latitude [c]	Intercept	58.230	57.311	59.149*
	Conflict	1.224	0.525	1.922*
	Age Group $_{\text{subadult}}$	0.428	-0.249	1.532
	Age Group $_{\text{adult}}$	0.642	-0.653	1.508
Date [c]	Intercept	328.815	320.212	337.420*
	Sex $_{\text{male}}$	10.826	2.781	18.870*
	Age Group $_{\text{subadult}}$	12.654	-3.591	28.900
	Age Group $_{\text{adult}}$	-0.572	-9.173	8.030

[a] Lower (L.CI) and upper (U.CI) limits of the 95% confidence intervals were used to determine significance, with significance indicated using *.

[b] Conflict bears were defined as those captured by wildlife officers near Churchill, Manitoba due to their proximity to the high priority management area of the Polar Bear Alert Program.

[c] Date and latitude (decimal degrees) extracted from the departure location to describe migratory behaviour. On-ice departure defined as the first location 10 km offshore from the west Hudson Bay coast in autumn without returning until spring.

Table 3.4. Adjusted R-squared (R^2), F-statistic (F), and p-value (p) resulting from model selection of linear regressions examining the effect of individual characteristics and conflict status on the date at departure of migrating Western Hudson polar bears from 2016 to 2020 (n=59) [a, b].

Model	Covariates	R^2	F	p
1	Age + Sex	0.213	3.267	0.028
2	Age + Sex + Conflict	0.199	2.537	0.050
3	Sex	0.155	7.472	0.008
4	Conflict + Sex	0.146	4.052	0.023
5	Conflict + Age	0.129	2.224	0.095
6	Age	0.117	2.230	0.117
7	Conflict	0.057	4.594	0.036

[a] Departure defined as the first location onto sea-ice 10 km from the western Hudson Bay coast in autumn without returning until spring.

[b] Conflict status refers to whether bears had a history of being captured within the Polar Bear Alert management area or not during the autumn migratory period.

Table 3.5. Second order information criterion (AIC_c) and Akaike weights (W) resulting from model selection of multinomial logistic regressions examining the effect of management practices (H1) on the likelihood of a Western Hudson conflict bear re-entering a community during the autumn migratory period from 2016 to 2020 (n=34).

Model	Covariates	AIC_c	ΔAIC_c	W
1	Date + East-west direction	62.887	0	0.359
2	Date	63.672	0.785	0.243
3	Distance to Churchill	65.407	2.520	0.102
…				
15	Date + East-west direction + Distance to Churchill + Days held	74.257	11.370	0.001

Table 3.6. Parameters (including 99.8% confidence intervals) of best-fitting multinomial logistic regressions examining the influence of management practices (H1), sea ice conditions (H2), and individual characteristics (H3) on the probability of a Western Hudson Bay conflict polar bear (n = 34) re-entering a community during the autumn migratory period selected using second order Akaike information criterion (AICc < 2) [a, b].

Model	Response	Covariates	Coef.	L.CI (99.8%)	U.CI (99.8%)
H1	Arviat	Intercept	24.444	15.122	33.766*
		Release date	-0.082	-0.114	-0.050*
	Churchill	Intercept	25.003	16.235	33.773*
		Release date	-0.086	-0.117	-0.054*
H2	Arviat	Intercept	2.932	-0.817	6.681
		North-zone sea ice [c]	-1.621	-3.635	0.394
	Churchill	Intercept	1.663	-1.983	5.308
		North-zone sea ice	-0.948	-2.458	0.562
H3	Arviat	Intercept	-0.326	-2.426	1.774
		Sex $_{\text{female}}$	-0.343	-2.505	1.819
		Storage energy [d]	0.091	-8.879	9.061
	Churchill	Intercept	-1.058	-3.675	1.559
		Sex $_{\text{female}}$	-0.185	-2.595	2.225
		Storage energy	0.935	-10.161	12.030

[a] Lower (L.CI) and upper (U.CI) limits of the 99.8% confidence intervals were used to determine significance, with significance indicated using *.

[b] Conflict polar bears defined as re-entering either Arviat, Nunavut or Churchill, Manitoba when located within 10 km during the same migratory period as the initial conflict and release. Bears that do not move near either community before on-ice departure as defined as having no conflict post-release.

[c] North-zone sea ice calculated as the mean daily sea ice concentration for the north-zone, the 30 km area from the coast north of all release locations of conflict bears up to Arviat, Nunavut.

[d] Storage energy (MJ) calculated via mass (kg) and straight-line body length (cm).

Table 3.7. Second order information criterion (AIC_c) and Akaike weights (W) resulting from model selection of multinomial logistic regressions examining the effect of sea ice conditions (H2) on the likelihood of a Western Hudson conflict bear re-entering a community during the autumn migratory period from 2016 to 2020 (n=34).

Model	Covariates	AIC_c	ΔAIC_c	W
1	North-zone sea ice [a]	49.986	0	0.817
2	Release sea ice [b] + North sea ice	54.124	4.138	0.103
3	North-zone sea ice + Freeze date [c]	54.827	4.841	0.073
4	North-zone sea ice + Release-zone sea ice + Freeze date	59.974	9.988	0.006
5	Release-zone sea ice	62.231	12.245	0.002
6	Release-zone sea ice + Freeze date	67.807	17.821	0.000
7	Freeze-date	76.318	26.332	0.000

[a] North-zone sea ice calculated as the mean daily sea ice concentration for the north-zone, the 30 km area from the coast north of all release locations of conflict bears up to Arviat, Nunavut.

[b] Release-zone sea ice calculated as the mean daily sea ice concentration for the release-zone, the 30 km area from the coast bounded by all release locations of conflict bears.

[c] Freeze-up date defined as the date at which mean sea ice concentration of the WH population zone is greater than 10% for three consecutive days.

Table 3.8. Second order information criterion (AIC_c) and Akaike weights (W) resulting from model selection of multinomial logistic regressions examining the effect of individual characteristics (H3) on the likelihood of a Western Hudson conflict bear re-entering a community during the autumn migratory period from 2016 to 2020 (n=34) [a, b].

Model	Covariates	AIC_c	ΔAIC_c	W
1	Sex	78.191	0	0.510
2	Storage energy	78.591	0.400	0.418
3	Sex + Storage energy	83.472	5.281	0.036
4	Age	83.675	5.484	0.033
5	Age + Storage energy	90.249	12.058	0.001
6	Sex + Age	90.571	12.380	0.001
7	Sex + Storage energy + Age	98.057	19.866	0.000

3.7 | Figures

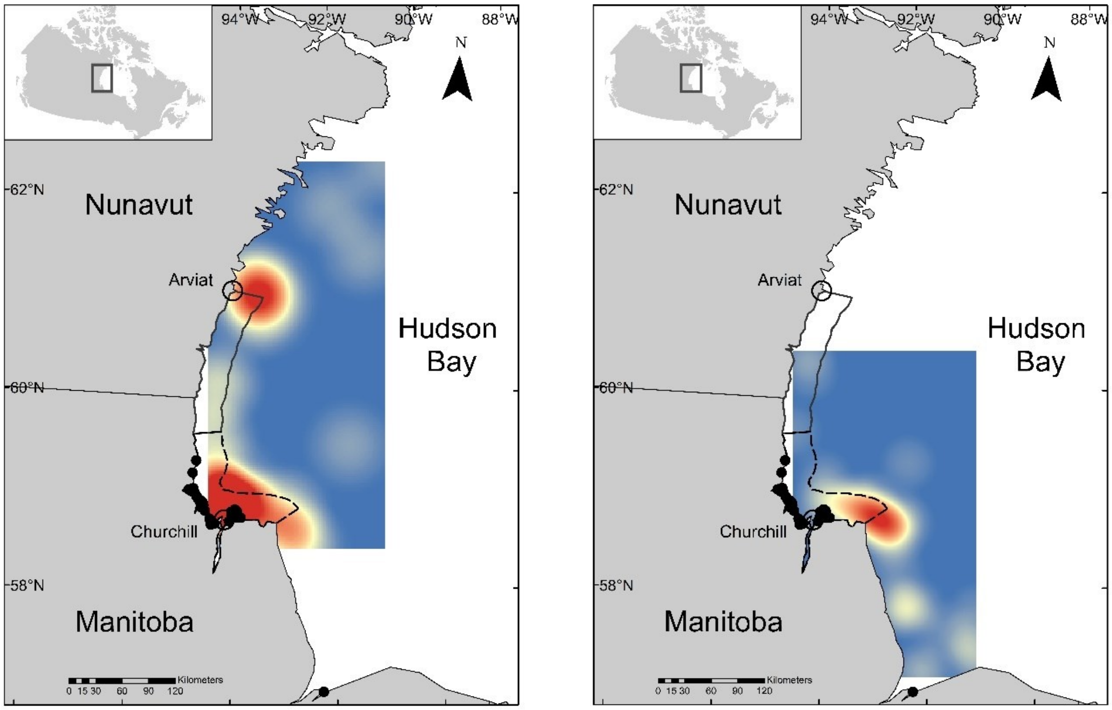

Figure 3.1. Map of Hudson Bay, Canada, showing the Kernel Density Estimations of the autumn departures of 29 problem bears (left) and 30 non-problem bears (right) from 2016 to 2020. Problem bears were captured near Churchill, Manitoba from July to December through the Polar Bear Alert Program and were fitted with Argos satellite-linked eartags prior to release. Non-problem bears were captured on land between Churchill, Manitoba and the Manitoba-Ontario border from August to September and fitted with Argos or Iridium satellite-linked collars. On-ice departure was defined as the first location 10 km offshore that was not followed by a location on land until the following spring. Mean daily sea ice concentration was calculated within the release-zone (dashed line), defined as the 30 km area from the coast bounded by 53 release locations of problem bears between 2016 and 2020 (one southern outlier release location was not

included), and the north-zone (solid line), defined as the area 30 km from the coast bounded between the northernmost release location and Arviat, Nunavut.

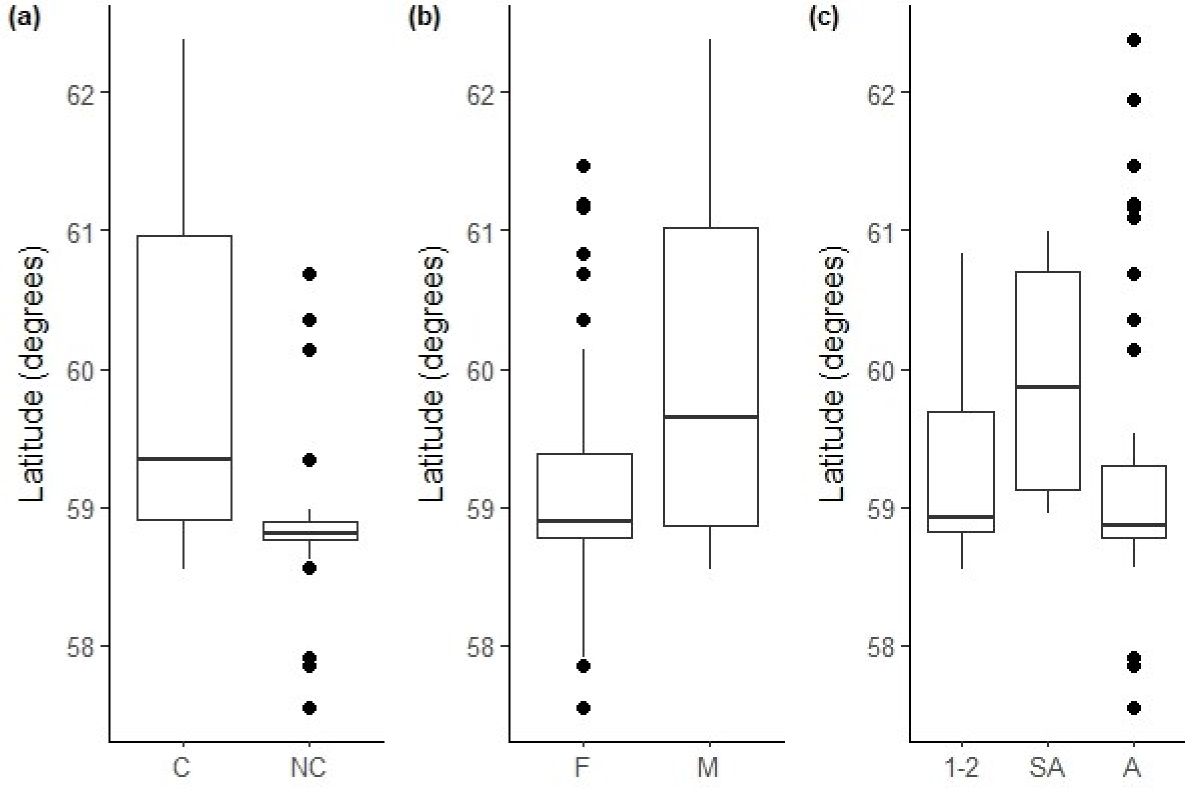

Figure 3.2. Comparison of the on-ice departure latitude between (a) conflict bears, defined as those who were captured near Churchill, Manitoba and released through the Polar Bear Alert Program, and non-conflict bears, defined as those with no history of human-wildlife conflict, (b) female and male bears, and (c) 1-2-year-olds, subadults (3-4 years), and adults (≥ 5 years). Each comparison included the combined datasets of conflict and non-conflict bears belonging to the Western Hudson Bay subpopulation (n = 59). On-ice departure was defined as the first location 10 km offshore that was not followed by a location on land until the following spring.

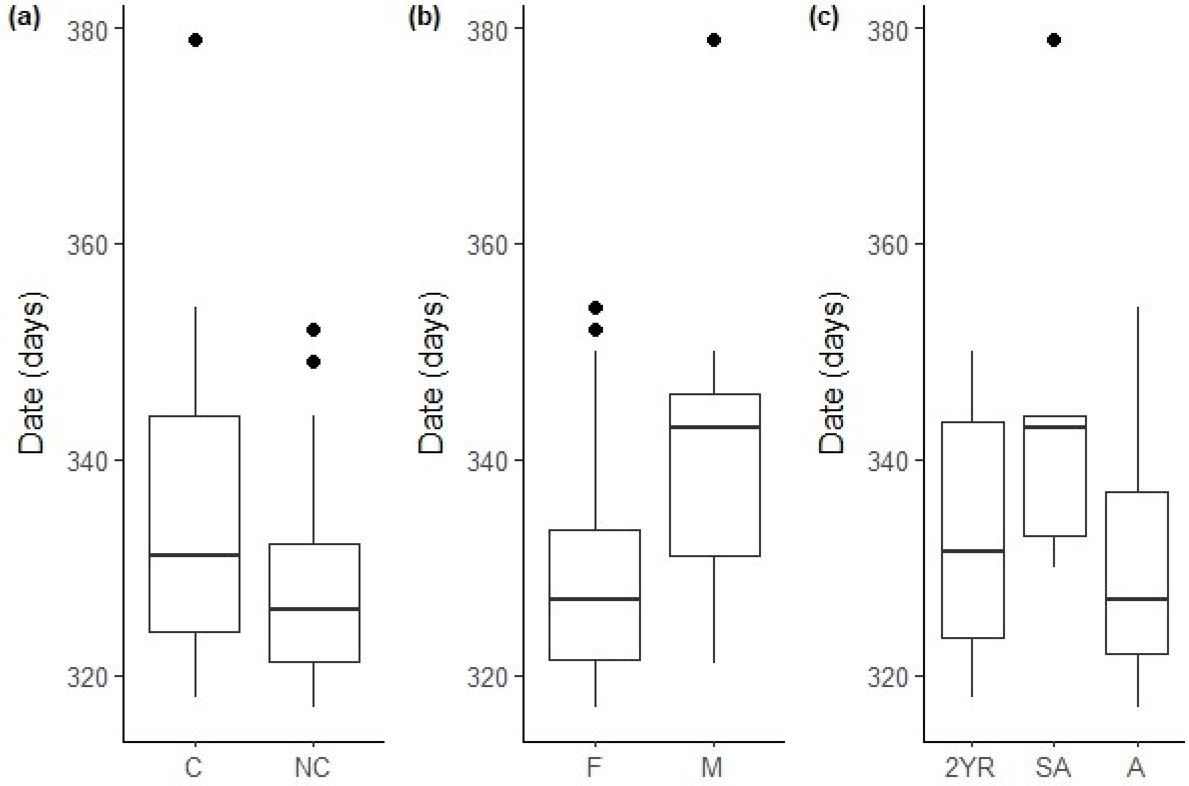

Figure 3.3. Comparison of the on-ice departure date between (a) conflict bears, defined as those who were captured near Churchill, Manitoba and released through the Polar Bear Alert Program, and non-conflict bears, defined as those with no history of human-wildlife conflict, (b) Female and male bears, and (c) 2-year-olds, subadults (3-4 years), and adults (≥ 5 years). Each comparison included the combined datasets of conflict and non-conflict bears belonging to the Western Hudson Bay subpopulation (n = 59). On-ice departure was defined as the first location 10 km offshore that was not followed by a location on land until the following spring.

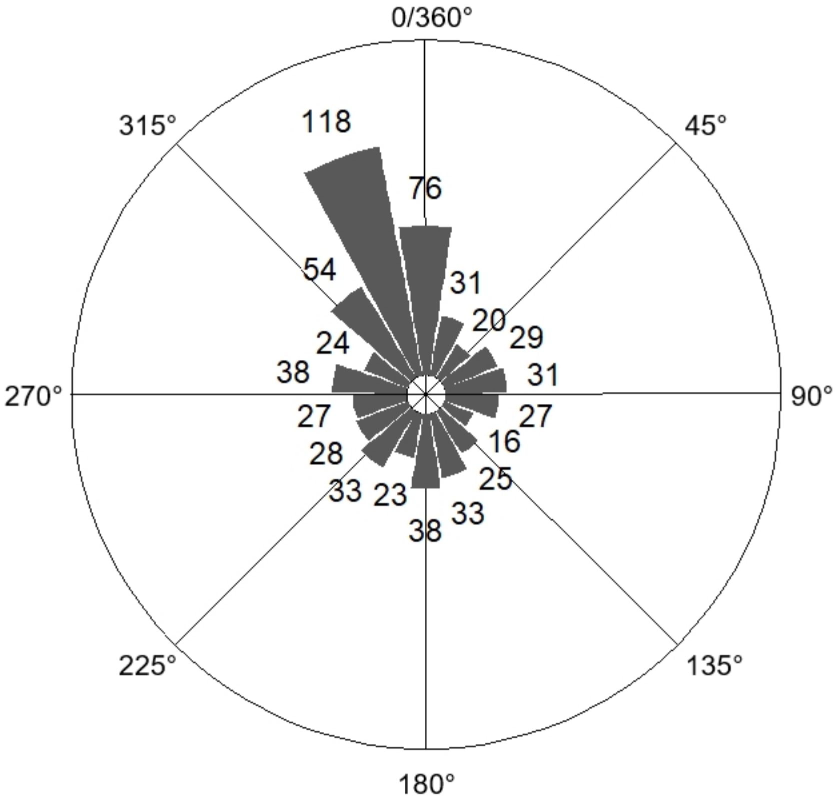

Figure 3.4. Circular histogram of the post-release movement of 31 Western Hudson Bay polar bears. Problem bears were captured near Churchill, Manitoba from July to December through the Polar Bear Alert Program and were fitted with Argos satellite-linked eartags before release. Their movement was followed until on-ice departure or final transmission, for a minimum of 10 locations with the bearing calculated between all consecutive locations. The number of locations per 20° binned angle is reported above each bar.

3.8 | Appendix

Table A3.1. Parameters (including 95% confidence intervals) of best-fitting robust multiple linear regressions examining the influence of individual characteristics and conflict status on the on-ice departure date of conflict (n=28) and non-conflict (n=30) Western Hudson polar bears with outlier removed selected using the adjusted R-squared [a, b, c].

Model	Covariates	Coef.	L.CI (95%)	U.CI (95%)
Date [d]	Sex $_{male}$	8.486	1.597	15.374*
	Age Group $_{juvenile}$	-1.093	-9.748	7.563
	Age Group $_{subadult}$	5.686	-4.164	15.536

[a] Significance of coefficients determined using 95% CI and indicated using *.

[b] Lower (L.CI) and upper (U.CI) limits of the 95% confidence intervals are presented.

[c] Conflict bears were defined as those captured by wildlife officers near Churchill, Manitoba due to their proximity to the high priority management area of the Polar Bear Alert Program.

[d] Date extracted from the departure location to describe migratory behaviour. On-ice departure defined as the first location 10 km offshore from the west Hudson Bay coast in autumn without returning until spring.

Chapter 4

4 | Conclusion

Many of the predictable patterns once exhibited by migratory species have become increasingly disrupted by environmental change associated with anthropogenic activities (Cohen et al. 2018). Polar bear (*Ursus maritimus)* migration emerged soon after the species diverged from the terrestrial *U. arctos* at the end of a period of glacial maximum, approximately 125,000 years ago as the some bears followed the northward retreat of the sea ice southern boundary (Kurtén 1964). As the multiyear ice sheet in Hudson Bay transitioned to seasonal sea ice, polar bears inhabiting the area developed predictable patterns of movement on and off the Bay timed to annual sea ice freeze-up and break-up (Shilts 1986, Cherry et al. 2013). I sought to examine the effects of climate change and the more abrupt effects of human-wildlife disturbance on established movement patterns during the autumn migration of Western Hudson (WH) polar bears onto Hudson Bay sea ice. I found sex and age differences in the on-ice departure date, with females and younger adult bears departing onto the sea ice earlier than males and older bears, and reproductive differences in 30-year energetic trends, with females with first-year cubs growing more vulnerable to extended fasting. I found 30-year trends in the spatial distribution of on-ice departure, with bears moving north over time. I also found that the abrupt disturbance of human handling influenced the spatial distribution of migration, with bears involved in human-wildlife conflict migrating further north than undisturbed, non-conflict bears. My results may suggest that spatial patterns of polar bear migration may be more plastic than temporal ones, with polar bears responding to both gradual and abrupt disturbances by shifting the location of on-ice departure rather than the timing of migration.

Polar bears appear to preferentially respond to delayed sea ice freeze-up by shifting migratory patterns spatially rather than temporally, but they may be forced to delay on-ice departure due to future sea ice decline (Cherry et al. 2013). Future delays in freeze-up along the western coast may initially result in further northward movement along the coast as bears search for earlier forming sea ice to avoid extending the fasting period, but bears may eventually lose access to early sea ice regardless of their spatial distribution, leading to delays in on-ice departure date. Past sea ice decline in Hudson Bay has been demonstrated to occur in a step-change, with large declines over relatively short periods (Scott and Marshall 2010), so future sea ice change may cause abrupt changes to migration phenology over as few as two years. This delay will likely occur first in females, who migrate earlier in autumn and are most vulnerable to an extended fasting period, which will exacerbate trends of declining energetic stores.

If the declining trend in the energetics of females with CUBs continues due to climate change, the WH subpopulation may face further population decline. Females with CUBs are the most vulnerable class to extended fasting due to their lower energetic stores from a shorter on-ice period (Ramsay and Stirling 1988) and higher energetic requirements over the fasting period (Molnár et al. 2009). With most females in this study departing past their estimated stores assuming maintained lactation, I suggest that female recruitment rate in the WH population may be declining at a more rapid rate than the decline first demonstrated in the late 1980s (Derocher and Stirling 1995b) due to increasing cub mortality late in the fasting period. If future reductions in sea ice extent forces bears further north and eventually into an extended fasting season, offspring survival will continue to decline followed closely by the survival of adult females.

I suggest that future research examine the temporal relationship between the surpassing of a bear's starvation threshold and the eventual endpoint of mortality due to a lack of refeeding. I found that females with CUBs increasingly surpassed their starvation threshold regardless of reproductive output, suggesting that adult female survival may have declined over the last 30 years; however, it is not known how long after this threshold has been crossed that mortality will occur. Starvation is a unique process in bears that involves a gradual transition from a controlled state that minimizes deterioration to exhaustion and eventual death due to the prolonged absence of energetic stores (Harlow 2012). Further insight is needed to understand the impact that surpassing this starvation threshold has on the reproductive output and survival of adult females. By quantifying the effect of fasting period length on offspring and adult mortality rates, this research will provide necessary insight to reassess the sustainability of current harvest quotas, given that the conflict-related mortality of adult females may also increase due to the association between bear body condition and conflict frequency (Wilder et al. 2017).

Both the frequency and demographic structure of human-polar bear conflicts may change due to future spatial and energetic trends in WH polar bear migration. As sea ice extent declines, spring break up will occur earlier, leading to less time for bears on the Bay ice to regain mass, and autumn freeze-up will be delayed, leading to bears spending more time in a food-deprived state (Castro de la Guardia et al. 2013). Bears spending more time on land, where they are in closer proximity to communities and in lower condition, may lead to increasing conflict rates (Towns et al. 2009). Given the association of bears in poor condition entering human communities (Wilder et al. 2017) and the declining condition of females with CUBs, family groups and solitary females who recently lost their CUBs may increasingly be involved in human-wildlife conflict. Cubs appear to learn site fidelity of landfills from their mothers (Lunn and Stirling 1985), so a demographic shift toward more females entering communities could lead to population-level increases in habituated bears and conflict-related mortality. The northward shift in on-ice departure exhibited by WH bears may lead to the increased presence of bears in proximity to Arviat, Nunavut and other Nunavut communities farther north. These communities may not be prepared to handle large numbers of conflict bears, which may result in increases in conflict-related mortality before management can respond with effective, non-lethal methods.

Given predictions of the increasing presence of bears in proximity to communities along the western coast as the ice-free period extends, the management of conflict bears should emphasize the use of deterrents, reduction of attractants, and public education to prevent bears from becoming involved in conflict. Despite observations of increasing bears near communities over recent decades (Tyrrell 2006), the number of conflicts with bears in Churchill has declined over time (Heemskerk et al. 2020), which may be the result of a transition in management protocol toward conflict prevention and deterrence (e.g., hazing). Conflict rates have been shown to decline following the removal of attractants, such as town landfills (Struzik 2014). I suggest that future research regarding Churchill conflict bears focus on the effect of deterrent strategies, with the aim of avoiding conflict altogether, given that the efficacy of current post-conflict management practices may become limited by depleting energetic stores in bears held progressively later in the fasting period.

While this study provided insight as to the effect of various management protocols in reducing same-year recidivism of conflict bears, the delayed formation of sea ice may limit the success of current practices. Bears that were released later in the fasting period were less likely to re-enter a community before on-ice departure. Given predictions of increasing conflict frequency due to sea ice delay, I suggest an expansion to the current Alert Program's holding facility capacity (Kearney 1989); however, this solution may lead to management holding bears past the depletion of their energetic stores due to delayed freeze-up, resulting in increasing starvation-related mortality risk before release. While this risk could be reduced by supplemental feeding, it is not recommended due to the expected effect of incentivizing bears to return to town each year (Lunn and Stirling 1985), leading to annual increases in conflict.

My research found that sea ice conditions, individual attributes, and human-wildlife interaction influenced the spatiotemporal variation and trends in the autumn migration of polar bears onto the Hudson Bay sea ice. With continued declines in sea ice extent due to climate change (Castro de la Guardia et al. 2013), my results suggest that the WH population will migrate progressively further north until they are eventually forced to delay on-ice departure, which may have negative consequences on bear energetics and conflict management. My research highlights the interplay between highly individualistic polar bear behaviour, a seasonally dynamic sea ice habitat, and the multi-faceted impact of anthropogenic disturbance during this critical stage in the life history of an Arctic top predator.

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