

**Individual variation in on-ice movement dynamics and site fidelity of western Hudson Bay
polar bears**

by

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Abstract

Individual variation affects fundamental aspects of ecology and behaviour in many species. Individuals vary in sex, age, reproductive status, and personality, which can be compared between individuals (inter-individual) or within individuals (intra-individual). In this dissertation, I tested whether individual variation affected various aspects of movement in polar bears (*Ursus maritimus*) of the western Hudson Bay subpopulation during the first and second halves of the ice season. In my first chapter, I examined whether intra-individual variation in age and reproductive status, as well as individual identity affected fidelity to on-ice areas in Hudson Bay. To this intent, I analysed differences in pairwise seasonal range centroid distance (as a proxy for broad-scale fidelity) and percent seasonal range overlap (as a proxy for fine-scale fidelity) of 87 collared adult females recaptured over multiple ice seasons in 2004-2021. Pairs of seasonal ranges had a mean centroid distance of 183 km (range 12 – 630 km, SE = 7 km), and overlapped on average by 12 %, (range 0 – 74 %, SE=0.01%), with 25% of pairs having zero overlap. Model selection revealed that broad-scale on-ice fidelity varied mainly by individual, suggesting possible differences in exploratory tendency between bears; however, there was no evidence of fine-scale fidelity in the western Hudson Bay population. In my second chapter, I investigated whether speed, path tortuosity, seasonal range size, and migration dates (i.e., on-ice departure and on-land arrival) differ as a function of sex and age, and individual identity. To do so, I used a combination of doppler-shift ear tag and GPS collar data from 110 bears, consisting of adult females with and without cubs, adult males and subadults captured in 2016-2021. Mean speed was 1.00 km/h (range 0.48 - 1.90 km/h, SE = 0.056 km/h) over all bears and was lower in

adult males and females with offspring. My index of path tortuosity averaged 0.36 over all bears (range 0.042-0.90, SE=0.05; an index of 0 indicates an extremely tortuous path and an index of 1 indicates a perfectly straight path). Path tortuosity was lower in females with cubs-of-the-year and 2-year-olds. Overall mean seasonal range size was 22 000 km² (range 1500 – 87 000 km², SE=6400 km²), with males and subadults having significantly smaller seasonal ranges. Finally, bears departed onto the ice on average 7 days after sea ice freeze-up (range 1-20 days, SE=4.6 days) and arrived on land on average 38 days after sea ice break-up (range 14-55 days, SE=14.4 days). Migration dates did not differ by sex, age, or reproductive status. Each movement metric except for on-land arrival date also varied by individual bear, suggestive of differences in boldness levels, foraging strategies or physiology that possibly influenced individual movement. Each of my data chapters provides insights on how individual variation affects polar bear movement in western Hudson Bay and highlights the importance of including individual factors in polar bear movement research.

Preface

This thesis is an original work by Camille Anne Marielle Jodouin. Global positioning system collars deployed by Dr. A. E. Derocher and Dr. N. J. Lunn at the University of Alberta and Environment and Climate Change Canada, respectively, provided data on polar bear movements for this research. I acknowledge the use of imagery from the NASA Worldview application (<https://worldview.earthdata.nasa.gov/>), part of the NASA Earth Observing System Data and Information System (EOSDIS).

To date, manuscripts derived from my two data chapters have not been submitted to peer-reviewed journals.

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Chapter 1: Introduction

Movement and space use are fundamental processes in animal ecology, enabling animals to access resources, change their landscape use, migrate, and respond to threats by escaping (Johnson et al. 1992, Chapman et al. 2011, Neumann et al. 2015, Shaw 2020). Environmental factors and individual variation including sex, reproductive status, age, personality and social status can affect movement (Ruckstuhl 1998, McLoughlin et al. 2000). For example, differences in body size between sexes can result in larger home range sizes in males (Cederlund & Sand 1994, Herfindal et al. 2005, Harvey et al. 2008), females with offspring often select different habitat patches (Fontaine et al. 2006, Viejou et al. 2018), younger animals may move less efficiently due to lack of experience (Fagan et al. 2013, Harel et al. 2016), and bolder individuals may travel longer distances when dispersing (Fraser et al. 2001, Dingemanse et al. 2003, Chapman et al. 2010, Schirmer et al. 2019).

Studying how individual variation affects movement can increase our understanding of habitat selection and resource requirements (Hutchings & Gerber 2002, Harrison et al. 2019). Further, by including individual variation as a variable in energetics or space use models, we can increase their accuracy and improve predictions of how environmental change may affect a species (Dodd et al. 1998, Merrick & Koprowski 2017, Klappstein et al. 2022). However, despite progress in research on individual variation in ecology (Bergmüller et al. 2010, Dall et al. 2012, Metcalfe et al. 2016, Burgan et al. 2019), the effects of individual variation on animal movement remains understudied (Holyoak et al. 2008, Shaw 2020).

To address this gap, I suggest that researchers focus on animal groups (e.g., populations, species, communities) possessing the following three elements:

- 1. High energetic costs of movement.** Movement is an important form of energy output in animals (Halsey 2016) and is used to access essential resources (Fahrig 2007). Therefore, individual variation in movement may be an important determinant of individual fitness or survival, especially for animals that require long and sustained movements to access resources such as migrators (Alerstam et al. 2003, Alerstam & Bäckman 2018).
- 2. Strong inter-individual differences that may influence movement.** These differences may include pronounced sexual dimorphism or high costs of reproduction in females, which can affect their energetics or resource requirements and therefore their movement (Madsen et al. 1993, Forsyth et al. 2005, Norquay et al. 2013, Lima-Santos et al. 2021). Further, groups where individuals show variation in personality traits, such as boldness and exploratory tendency, may display more differences in movement patterns than groups with limited variation in personality among individuals (Spiegel et al. 2017, Schirmer et al. 2019).
- 3. Rapidly declining or highly dynamic habitats.** Understanding the role of individual variation in movement patterns may provide insights on how animal groups adapt to changing environments. For example, animals with high site fidelity may be more affected by environmental change (Laidre et al. 2008, Merkle et al. 2022) or species may show sex-specific responses to change (Anadón et al. 2012).

One animal group that possesses these three elements is the subpopulation of polar bears (*Ursus maritimus*) inhabiting western Hudson Bay, Manitoba, Canada. First, Polar bears in western Hudson Bay are seasonal migrators that spend 7-8 months per year hunting seals and mating on annual sea ice, and then fast on land during the ice-free season (Lunn & Stirling 1985, Stirling &

Derocher 1993, Castro de la Guardia et al. 2017). Second, polar bears possess many inter-individual differences which may lead to variation in movement, including pronounced sexual dimorphism (Derocher et al. 2005), high energetic costs of reproduction (Atkinson & Ramsay 1995, Ramsay & Stirling 1988), and individual or age-related differences in behaviour and movement patterns (Zeyl et al. 2009, Johnson et al. 2017, Miller et al. 2022). Third, Hudson Bay has undergone significant warming over the past 30 years, leading to a shortening of the ice season (Gagnon & Gough 2005a, Hochheim et al. 2010, Stern and Laidre 2016) and therefore of the bears' hunting season (Stirling & Parkinson 2006, Cherry et al. 2013). The resulting increase in the terrestrial fasting period of polar bears in western Hudson Bay was linked to declines in body condition (Stirling et al. 1999, Lunn et al. 2016) and survival (Regehr et al. 2007, Lunn et al. 2016). Further, climate change is increasing sea ice drift (Olason & Notz 2014) and polar bears may experience increased energy costs moving across this dynamic environment (Sahanatien & Derocher 2012, Durner et al. 2017, Pagano & Williams 2021).

Individual variation in polar bear movement has already been investigated; for example, on-land arrival dates during migration and home range size differ by individual in western Hudson Bay (McCall et al. 2015, Cherry et al. 2016). Additionally, habitat selection and path tortuosity vary by sex and age class in other subpopulations (Laidre et al. 2013, Johnson et al. 2020). However, due to the high costs of studying polar bears and limited data for most subpopulations (Hamilton et al. 2018, Vongraven et al. 2018), aspects of individual variation in polar bear movements remain poorly understood, especially those related to intra-individual variation. Further, research on polar bear sex and age class differences has been limited as adult male polar bears cannot be fitted with telemetry collars due to the diameter of their necks exceeding that of their heads, and subadults cannot be collared due to their rapid growth

(Amstrup et al. 2001). These gaps can be addressed in the Western Hudson Bay subpopulation; first, movement data gathered for this subpopulation includes data for the same individuals in different years, enabling studies of intra-individual variation. Second, researchers and conservation agencies focusing on the Western Hudson Bay subpopulation have deployed Doppler-shift ear tags transmitters on all ages and sex classes in addition to geographic positioning system collars on adult females, allowing us to study all classes of bears.

In the following two chapters I examine how individual variation may affect movement dynamics in Western Hudson Bay polar bears during the first and second halves of the ice season. In my first chapter, I determine whether individual identity, age or reproductive status affect broad-scale and fine-scale on-ice-fidelity. To do so, I analyse within-individual overlap and centroid distance between seasonal ranges from adult females collared between 2004 and 2019. The results of this chapter provide insight into the influence of individual identity on polar bear site fidelity. In my second chapter, I examine whether on-ice movement and space use metrics (i.e., speed, path straightness, migration dates, and seasonal range size) are affected by sex, age, individual identity and reproductive status using a combination of collar and ear tag satellite telemetry data gathered in 2017-2021. To this end, I tested whether sex, age class, reproductive status and individual identity are better predictors of those movement metrics in comparison to select environmental variables. This chapter's findings highlight the importance of including biological covariates when analysing polar bear movement dynamics and suggest that migration data from adult females cannot be generalized to other bears in the western Hudson Bay subpopulation.

Chapter 2: Factors influencing polar bear on-ice fidelity in western Hudson Bay

Introduction

Animal behaviour research has rapidly expanded over the last decades (Sumpter 2006, Dingemanse & Wolf 2013, Hertel et al. 2020) with repeatability of behaviour emerging as an area of focus (Bell et al. 2009). Individuals can show predictability in a range of behaviours including foraging techniques (Estes et al. 2003, Potier et al. 2015), mate preference (Lehtonen & Lindström 2008, Folwer-Finn & Rodrigez 2013), and predator avoidance (Van Oers et al. 2004, Ropper 2005). Repeatability of behaviour is often due to a combination of heritable and individual factors such as sex, age, personality, and memory (Nakagawa et al. 2007, Zandberg et al. 2014, Thompson et al. 2022), and their impacts on individual fitness can be detected at the population or species level (Tibblin et al. 2016, Bubac et al. 2018). Studying repeatability of behaviour has applications in ecology and conservation, as it can improve our understanding of habitat selection (Merrick & Koprowski 2017, Hertel et al. 2020), mating success (Kelleher et al. 2018), and resilience to change (Killen et al. 2016).

One repeated behaviour of particular interest is site fidelity, defined as the tendency of an animal to return to the same location overtime (Greenwood 1980, Switzer 1993). Site fidelity ranges from general fidelity to broad areas (Laidre et al. 2005, Vos et al. 2005, Heide Jørgensen et al. 2015, O’Corry-Crowe 2020) to selection of specific habitat features (Kelly et al. 2010) and is common in many taxa, including birds (e.g., Oring & Lank 1982, Schlossberg 2009, Byrne et al. 2022), amphibians (Matthews & Preisler 2010), fish (e.g., Topping et al. 2006, Marnane 2000, Compaire et al. 2022), and mammals (e.g., Chilvers & Wilkinson 2008, Kozakai et al. 2017, Morrison et al. 2021). Individuals may display site fidelity for reasons including breeding

(Blancher & Robertson 1985, Matthiopoulos et al. 2005), denning (Monetti et al. 2005, Sorum et al. 2019), foraging (Hillien et al. 2009, Carrol et al. 2018), and avoidance of predators or conspecifics (Bangs et al. 2005, Wood et al. 2022). Additionally, the degree of site fidelity within a species can vary at the individual level due to personality, sex, or age-related factors (Cameron et al. 2007, Harris et al. 2020, Pfannerstill et al. 2022). For example, site fidelity may be higher for pregnant females returning to the same denning areas (Monetti et al. 2005, Kozakai et al. 2017), but can be lower in dispersing subadults (Smereka et al. 2021) or in bolder individuals with higher exploratory tendencies (Schirmer et al. 2019).

Determining factors that influence site fidelity is useful for understanding the ecology of migratory species (Phillips et al. 2009, Lehnert et al. 2018) and for species inhabiting resource-scarce environments (Edwards et al. 2009, Krištín & Kaňuch 2017). For these animal groups, returning to the same locations overtime may increase survival and reproductive success (Cantos & Telleria 1994, Iverson & Esler 2006). As such, varying degrees of site fidelity have been observed in many Arctic species (Laidre et al. 2008). One of these species is the polar bear (*Ursus maritimus*), an obligate carnivore that specializes on hunting seals on the sea ice (Stirling & Archibald 1977). Site fidelity in polar bears is well documented; for example, individuals may return to permanent ice features with high seal densities like polynyas (Born et al. 1997, Henderson et al. 2021), or consistently select either landfast or pelagic ice (Mauritzen et al. 2001, Brun et al. 2021). Many adult polar bears remain in the same area with little dispersal (Lone et al. 2013, Sahanatien et al. 2015). Finally, female polar bears show high fidelity to denning areas across the species' range (Derocher & Stirling 1990, Amstrup et al. 1994, Zeyl et al. 2009).

Many studies have examined the effect of environmental or biological factors on polar bear site fidelity (e.g., sex and age, kinship, year, season). However, there are few examples of

research comparing how these factors affect polar bear site fidelity relative to each other, preventing a systemic understanding of fidelity. Further, due to the challenges surrounding tracking the same individuals over multiple years, intra-individual variability in polar bear site fidelity is seldom estimated. Because of this, the effects of intra-individual factors (e.g., age, reproductive status, body condition) on site fidelity are poorly understood. Intra-individual variation forms an important part of overall variation in behaviour within species (Bell et al. 2009); additionally, shifts in individual factors - such as changes in reproductive status associated with dependent offspring - are often accompanied by differing resource requirements, which may affect space use (Schaefer et al. 2000, Michelot et al. 2021). Including intra-individual factors can therefore provide insights on the biological mechanisms underlying site fidelity in polar bears.

Research on polar bear site fidelity has mostly occurred in arctic regions with year-round sea ice, leaving areas with seasonal ice largely unstudied. Polar bears inhabiting areas with seasonal ice have adopted a migration strategy where individuals travel to the sea ice after freeze-up and return to land during the ice-free season (Lunn & Stirling 1985, Stirling & Derocher 1993, Castro de la Guardia et al. 2017). As polar bears require an ice platform on which to hunt seals, they fast outside of the ice season save for opportunistic feedings (Derocher et al. 1995, Gormezano & Rockwell 2013). The sea ice dynamics and polar bear behaviour in seasonal ice regions may lead to differences in on-ice fidelity compared to other areas of the bears' range, which may help us further understand the factors affecting their site fidelity.

This study examines within-individual on-ice fidelity for polar bears in western Hudson Bay (Manitoba, Canada). Our objectives were: 1) To quantify on-ice site fidelity in individual polar bears over the first and second halves of the ice season, and 2) To assess the effect of intra-

individual factors (i.e., age, individual identity, and reproductive status), environmental factors that may affect polar bear movement (i.e., sea ice freeze-up date, break-up date, year), and large-scale climatic indices (i.e., the Arctic and North Atlantic Oscillation indices) on polar bear on-ice fidelity. To fulfil these objectives, we used satellite telemetry data from female polar bears collared between 2004 and 2021. We examined on-ice site fidelity on two levels: first, fidelity to broad areas, which we quantified through centroid distance (i.e., distance between the arithmetic means of seasonal range polygons), and second, fidelity to specific areas, which we determined via seasonal range overlap.

Methods

Study area and population

Hudson Bay is a shallow inland sea with an average depth of 150 m that covers an area of approximately 800,000 km² (Jones & Anderson 1994; Figure 2.1), and undergoes an annual freeze-thaw cycle (Maxwell 1986, Castro de la Guardia et al. 2017). Freeze-up typically occurs between October and December, with sea ice forming in the northwest and progressing southwards (Prinsenber 1988, Saucier et al. 2004). Ice cover peaks in mid-January and begins declining in May (Saucier et al. 2004). Hudson Bay becomes fully ice-free in July-August (Wang et al. 1994).

Hudson Bay is used by 3 subpopulations of polar bears: Western Hudson Bay, Southern Hudson Bay, and Foxe Basin (Bethke et al. 1996, Peacock et al. 2010). Our study focuses on the Western Hudson Bay subpopulation, which numbers approximately 620 individuals (Atkinson et al. 2022). Bears from this subpopulation migrate offshore shortly after freeze-up to hunt their primary prey, ringed seals (*Pusa hispida*) (Stirling and Archibald 1977, Thiemann et al. 2008)

and return to land at the end of the ice season (Derocher & Stirling 1990). Mating occurs on the sea ice between March and May (Ramsay & Stirling 1986, Ramsay & Stirling 1988), and coincides with peak hunting season when ringed seal and bearded seal pups are also born, resulting in increased vulnerability to predation (Ferguson et al. 2005). Pregnant female polar bears remain on land after freeze-up to den and undergo parturition (Ramsay & Stirling 1986) and migrate onto the sea ice in late February to early March when their cubs are large enough to follow their mothers (Ramsay & Stirling 1986). As a result of their later on-ice departure, females with cubs-of-the-year will fast up to four months longer than other bears (Derocher & Stirling 1994, Robbins et al. 2012). Offspring typically remain with their mothers for two and a half years (Ramsay & Stirling 1988).

Telemetry data

Polar bear captures occurred on land in western Hudson Bay, in September of 2004-2019. We located and immobilized solitary females and family groups from a helicopter, using a combination of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil[®], Laboratoires Virbac, Carros, France; Stirling et al. 1989). Captured bears were equipped with Argos[®] or Iridium satellite-linked collars (Telonics, Mesa, AZ) that provided six GPS locations per day at 4-hour intervals, with a predetermined release mechanism set to open 1-2 years after capture. Bears were tattooed with an individual number on the inside of their upper lip and given numbered ear tags for identification upon recapture. We determined bear age from counts of cementum growth layers in an extracted vestigial premolar in adults, and used size and tooth eruption patterns to determine age in offspring (Calvert and Ramsay 1998). Capture and handling protocols followed the Canadian Council on Animal Care guidelines (www.ccac.ca) and were

approved by the University of Alberta BioSciences Animal Care and Use Committee (Animal Use Protocols 00000033 and 00003667).

We processed polar bear locations by first removing all on-land locations. Using the *argosfilter* package in R (Freitas 2012), we then deleted locations showing deviations from the path >25 km or >50 km or with turning angles of $>165^\circ$ or $>155^\circ$, respectively (Freitas et al. 2008), to remove spurious locations. Data from dropped collars or from collars with mortality signals was removed from analysis (Togunov et al. 2020).

We defined freeze-up as the first date when sea ice concentration was $\geq 10\%$ within the management boundary of the Western Hudson Bay subpopulation for three consecutive days between October and December (Etkin 1991, Gagnon and Gough 2005). Similarly, break-up was defined as the first date when sea ice concentration was $\leq 50\%$ within the management boundary of western Hudson Bay for three consecutive days between May and July (Gagnon and Gough 2005, Cherry et al. 2013). Freeze-up and breakup dates were calculated using 25 x 25 km resolution passive microwave satellite raster imagery of daily sea ice concentrations from the National Snow and Ice Data Center in Boulder, Colorado, USA (nsidc.org). Because the ice season straddles two calendar years, we separated each bear's data into "ice years", which began on a bear's departure onto the ice in late autumn and ended on the day of breakup the following year. Departure dates were defined as the date of the first on-ice telemetry location that occurred after freeze-up that was not followed by an on-land location until after breakup. To examine seasonal on-ice fidelity, we divided each ice year in half: "Early Season" and "Late Season". For most bears, the Early Season lasted until early March, encompassing the period of increase and peaking in Hudson Bay's ice cover (Saucier et al. 2004). The Late Season included biologically

important events such as the bears' peak hunting and mating season, as well as the migration of previously denning females with their cubs onto the sea ice (Ramsay and Stirling 1986).

The reproductive status of each bear was determined using its status upon capture, as well as its on-ice departure date. For example, bears captured with cubs (< 1 year old) were reclassified as bears with yearlings (1-2 years old) in the following Late Season, and then as bears with two-year olds (> 2 years old) in the next Late Season. Bears departing the den area in February-March were assumed to have given birth to cubs during the Early Season and were classified as such. If a female initially captured with offspring departed in late February to early March over the next two consecutive ice years, she was assumed to have lost her previous cubs. As such, she was reclassified as a female with cubs in the Late Season where the late departure was identified, with all previous seasons reclassified as "Miscellaneous". Finally, solitary females were defined as bears captured without offspring and who did not den during the ice season and departed onto the sea ice between November and January.

Measures of Spatial fidelity

To estimate on-ice fidelity, we first computed each bear's seasonal home ranges (hereafter "seasonal ranges") defined as an individual's home range over the Early Season or Late Season within a given ice year. Seasonal ranges were generated using kernel density estimation (KDE) with plug-in bandwidth selection (Gitzen et al. 2006) using the R package *ks* (Duong 2007). To standardize seasonal ranges and reduce autocorrelation of locations (Otis and White 1999, Blundell et al. 2001), we subset our data by randomly selecting one location per day. We also standardized the number of telemetry fixes by randomly selecting 30 locations per

seasonal range, which is the minimum recommended for generating home ranges (Seaman et al. 1999). Bears were removed from analysis if they had < 2 seasonal ranges.

We used two metrics to estimate on-ice individual site fidelity. Our first metric, distance between seasonal range centroids, was a proxy for broad-scale fidelity (i.e., selection of general areas), whereas our second metric, percent home range overlap, constituted an index of finer-scale fidelity (i.e., selection of specific areas) (Figure 2.2). We then created pairs of seasonal ranges (hereafter “pairs”). Pairs were created regardless of each range’s season (resulting in Early Season – Early Season, Late Season – Late Season and Early Season – Late Season combinations), and ice year (resulting in pairs of seasonal ranges from the same ice year as well as from different ice years). Due to our focus on within-individual variation, pairs were only created from seasonal ranges belonging to the same individual.

We determined distance between seasonal range centroids calculated percent overlap between pairs of seasonal ranges using the functions *gCentroids* and *gIntersection* from the R package *rgeos* (Bivant et al. 2017). Because measures of seasonal range overlap are directional (i.e., percent overlap of seasonal range A on seasonal range B will be different from percent overlap of seasonal range B or seasonal range A), we calculated percent seasonal range overlap using the following equation:

$$I.AB = \frac{O(AB) + O(BA)}{2}$$

Where I=percent overlap between A and B designate two separate seasonal ranges, O=percent overlap, and (AB) or (BA) represents the direction of this overlap (e.g., (AB) is overlap of seasonal range A on seasonal range B). We calculated percent overlap between all possible combinations of seasonal range pairs available for an individual. For example, a bear with 4 seasonal ranges would have 6 overlap values (seasonal ranges 1 and 2, 2 and 3, 3 and 4, 1 and 3,

2 and 4, and 1 and 4), while a bear with two seasonal ranges would have only one overlap value (overlap of seasonal ranges 1 and 2).

Biological and environmental covariates

To investigate the influence of biological and environmental factors on polar bear site fidelity, we created 6 biological covariates and 10 environmental covariates. All covariates were generated within each seasonal range pair apart from the covariate *ID*. Biological covariates included pairwise difference in seasonal range size (*Diff.Size*), mean pairwise bear age (*Mean.Age*), pairwise difference in reproductive status (*Diff.Rep*), and bear identity number (*ID*). *Diff.Size* was determined using the function *gArea* from the R package *rgeos* (Bivand et al. 2017). *Mean.Age* was determined by averaging the age of an individual over both seasonal ranges. *Diff.Rep* was defined as a categorical variable of the reproductive statuses of the individual during each seasonal range in alphabetical order (e.g., “cub– yearling”, “solitary – yearling”, etc).

Environmental covariates included pairwise difference in ice year (*Diff.Ice.Year*), in sea ice breakup date (*Diff.Ice.B*), in sea ice freeze-up date (*Diff.Ice.F*), in North Atlantic Oscillation (*Diff.NAO*), and in Arctic Oscillation (*Diff.AO*), and in season (*Diff.Season*). *Diff.Ice.B* was calculated using the of date of break-up for the ice year of each seasonal range, which we converted into ordinal dates. We used the absolute difference between these numbers as *Diff.Ice.B*. *Diff.Ice.F* was calculated similarly to pairwise difference in breakup date, except we replaced the date of sea ice breakup with the date of sea ice freeze-up. To compute *Diff.NAO* and *Diff.AO*, we first obtained Arctic Oscillation (“AO”) and North Atlantic Oscillation indices (“NAO”) from the National Snow and Ice Data Centre as monthly means. We then obtained

seasonal AO and NAO indices averaging the indices over the months in which each season occurred. The absolute difference between seasonal ranges' AO and NAO indices were calculated to obtain *Diff.NAO* and *Diff.AO*. Finally, *Diff.Season* was defined as a categorical variable showing the seasons of each range within a seasonal range pair in alphabetical order, resulting in three possible variables (“Early Season – Early Season”, “Early Season – Late Season”, and “Late Season – Late Season”).

Statistical analyses

We used AICc model selection to assess the influence of our biological and environmental covariates on site fidelity. After testing for autocorrelation between covariates and only combining covariates that were not correlated (Spearman's correlation coefficient $r \leq 0.6$; Fox 2002), we generated 5 general linear mixed models corresponding to *a priori* ecological hypotheses, with bear identity (covariate *ID*) as a random effect (Table 2.1). We modified the model distribution depending on our response variable, using a zero-inflated beta distribution via the R package *glmmTMB* (Brooks et al. 2017) for percent seasonal range overlap, and a gamma distribution using the R package *lme4* (Vazquez et al. 2010) for centroid distance. For both response variables, we selected the top model using Akaike information criteria corrected for small sample sizes (AICc) and AICc weight (Burnham and Anderson 2004). Finally, to estimate the significance of the random effect, we calculated the log likelihood ratio of the top model and the same model with the random effect removed (Morrell 1998).

Results

Location data was available from 166 female polar bears collared between 2004 and 2021. Of these bears, 87 had sufficient data, yielding 153 seasonal ranges and 255 seasonal range pairs, with a mean of 2.5 pairs/bear. Seasonal ranges were separated by a mean of 1.1 ice years (range 0-13 ice years, SE = 0.06 ice years), with most seasonal ranges occurring within the same ice year (one in the Early Season and one in the Late Season). Overall mean bear age was 13.5 years (range 5-26 years, SE=0.3 years). The reproductive status associated with each seasonal range was 36% “cub”, 37% “yearling”, 17% “two-year-old”, 2% “solitary” and 8% “miscellaneous”. Due to the low sample size of solitary females, seasonal pairs containing any solitary female had their associated *Diff.Repro* covariate relabelled as “miscellaneous”. Mean seasonal range size for the Early Season was 54 445 km² (range: 6825 km² - 186 555 km², SE= 3721 km²) and 20 677 km² for Late Season (range: 2051 km² – 57 219 km², SE= 1134 km²). Early Season ranges were significantly larger than Late Season ranges (t-test: $t_{120} = 9.75$, $p > 0.0001$).

Pairwise centroid distance averaged 183 km over all pairs (range 12 – 630 km, SE = 7 km). The top model for predicting pairwise centroid distance was the climatic model “Clim” (Table 2a). Further examination of this model showed that pairwise centroid distance significantly increased with pairwise difference in breakup date ($p=0.0034$) and pairwise difference in AO index ($p=0.048$) (Table 2.3). Mean percent seasonal range overlap was 12% (range 0 – 74 %, SE=0.01%), with 25% of pairs having no overlap. The top model predicting seasonal range overlap was also the climatic model “Clim” and showed no significant effects of fixed covariates (Table 2.4).

Finally, our likelihood ratio tests were significant for the top model predicting centroid distance ($\chi^2(1) = 11.34$, $p < 0.0001$) suggesting a significant effect of individual bear ID (covariate

ID); however, likelihood tests were not significant for the top models including percent seasonal range overlap as a response variable ($\chi^2(1)=0.98$, $p=0.13$).

Discussion

Site fidelity exists at different scales in animals: while some species or populations display finer-scale fidelity, returning to the same habitat patch or specific location overtime (Lowther et al. 2012, Ferguson et al. 2013), others only show broad fidelity by re-selecting the same general area (Bjørge et al. 2001, Filatova et al. 2022). Our results suggest that polar bears in western Hudson Bay fall into the latter category. All bears displayed general fidelity to Hudson Bay; however, the large variation in percent seasonal range overlap, the large number of range pairs displaying no overlap, and the absence of significant effects of our biological and environmental covariates on overlap all point to a lack of fine-scale fidelity.

Broad-scale fidelity in western Hudson Bay polar bears was influenced by a combination of environmental and biological factors. First, broad-scale fidelity varied by individual, confirming the results of past studies on this subpopulation (McCall et al. 2015). Animals may exhibit personality differences affecting their tendency to select the same general area over different ice years or do so in different seasons of the same ice year (Harris et al. 2020). For example, variation in boldness can affect migration and exploration, with bolder animals showing less site fidelity compared to individuals classified as shy (Chapman et al. 2010, Kudo et al. 2021). Past research on ursids shows varying levels of individual boldness in human-wildlife conflict scenarios (Myers et al. 2018, Hertel et al. 2019, Bombieri et al. 2021). At present, boldness in polar bears has not been directly studied; however, accounts of individuals showing strong exploratory tendencies by covering exceptional distances during migration

(Durner and Amstrup 1995, Johnson et al. 2017) suggests boldness could also affect on-ice fidelity in polar bears.

Broad-scale fidelity also decreased for seasonal ranges occurring in ice years where breakup dates were further apart. Breakup date is directly related to the degree of sea ice concentration in Hudson Bay; for ice years with earlier breakup dates, open-water areas or areas with lower sea ice concentrations appear earlier than in ice years with later breakup (Gough & Cornwell 2004, Cherry et al. 2013). Sea ice patch selection in polar bears is non-random, with bears preferring patches with only 20 - 40% open water (Aars et al. 2017). As a result, polar bears may have avoided areas that they had used in previous seasons if those areas had lower ice concentrations in a given ice year.

Finally, broad-scale fidelity varied by season, with higher levels of fidelity in range pairs that both occurred in the Late Season. Overall lower sea ice concentrations in the Late Season may have restricted polar bears' ability to travel further into Hudson Bay (McCall et al. 2016), resulting in Late Season ranges that were closer together. This explanation is supported by the significantly smaller size of Late Season ranges compared to Early Season ranges.

The lack of fine-scale fidelity in western Hudson Bay polar bears may be due to the widespread availability of high-quality ringed seal habitat in this region. When foraging, ringed seals, polar bears' primary prey, have been shown to prefer shallower waters (Burns & Harbo Jr. 1972, Wathne et al. 2000, Frost et al. 2004). As Hudson Bay is a shallow inland sea (Saucier et al. 2004), seals may be distributed over the whole bay instead of restricted to specific areas, as seen in other populations (Schliebe et al. 2008). Thus, polar bears in western Hudson Bay would have no need to return to the same areas overtime to optimize foraging success. Alternatively, fine-scale fidelity could be impossible to achieve in Hudson Bay due to this area's variable sea

ice and prey dynamics. Ringed seal density in Hudson Bay fluctuates over a decadal cycle, resulting in strong inter-annual variation (Chambellant et al. 2012, Young & Ferguson 2014). This variation may be further increased by inter-seasonal and inter-annual differences in snow-covered sea ice in Hudson Bay, which is necessary for the creation of seal birthing lairs (Iacozza & Ferguson 2014). Thirdly, Hudson Bay's Sea ice varies in cover interannually (Cavalieri & Parkinson 2012) and seasonally (Saucier et al. 2004, Kowal et al. 2017). In combination with increasing rates of sea ice fragmentation due to climate change, the resulting variability in Hudson Bay's ice may affect how polar bears navigate their habitat and make it more difficult for them to return to specific areas (Sahanatien & Derocher 2012, Biddlecombe et al. 2021).

The explanation that lack of fine-scale fidelity is due to higher variability in Hudson Bay's ice is further supported by the fact that higher levels of on-ice fidelity have been reported in polar bears located in northern subpopulations with year-round ice, where environmental conditions are more stable (e.g., Mauritzen et al. 2001, Lone et al. 2013). Moreover, age was not a significant factor influencing polar bear on-ice fidelity in our study. In some species, older individuals display increased levels of site fidelity, suggesting this trait is acquired through experience (Cameron et al. 2007, Votier et al. 2017). Animals use fixed environmental cues or landmarks to return to known habitat patches (Mueller & Fagan 2008, Fagan et al. 2013), but this may not be feasible in highly dynamic habitats (Thompson et al. 2022). Accordingly, polar bears show high fidelity to stable terrestrial areas (Ramsay & Stirling 1990, Zeyl et al. 2010), and may re-select permanent on-ice features like flaw leads and polynyas, which offer high-quality habitat (Henderson et al 2021). Polar bear subpopulations with more stable, year-round ice than western Hudson Bay also display age differences in fidelity, with adults showing higher on-ice fidelity than subadults (Lone et al. 2013); further, the closer proximity between the home ranges of

female bears and their adult offspring compared to unrelated bears suggests that bears learn migration routes from their mothers (Brun et al. 2021). The seasonality of Hudson Bay's sea ice may prevent polar bears from learning migration routes and returning to the same areas in different ice years, resulting in memorization and experience having limited influence on on-ice fidelity in this subpopulation.

While site fidelity often benefits individuals (Lindberg & Sedinger 1997, Robillard et al. 2018, Knox et al. 2018), animals with higher fidelity can also be more affected by rapidly changing environments than those with lower fidelity (Cotton 2003, Forney et al. 2017). The maladaptive aspects of site fidelity can be seen in phenological mismatches, where individuals retain migration routes or fidelity to specific breeding sites despite being out of sync with their food sources or nesting environments (Miller-Rushing et al. 2010, Renner et al. 2018). Animals displaying extreme site fidelity may remain in increasingly unsuitable areas for generations (Pichegru et al. 2010), resulting in declines in survival and reproduction (Matthews et al. 2010, Ekroos et al. 2012, Merkle et al. 2022). Because of warming temperatures, Hudson Bay has experienced declines in sea ice cover and increased ice fragmentation, as well as a shortening of the ice season over the past decades (Gagnon & Gough 2005, Joly et al. 2001, Sahanatien & Derocher 2012). Studies have found evidence of polar bears displaying maladaptive on-ice fidelity by selecting the same areas despite reduced sea ice (Wilson et al. 2016); however, this does not seem to be the case for the western Hudson Bay subpopulation, as we found no extreme fidelity to foraging sites, and broad-scale fidelity varied in large part with environmental factors. Recent northward shifts in the bears' location of on-ice departure, as sea ice forms progressively later in the south of western Hudson Bay, further suggests that polar bears in this region are responding to environmental change, suggesting behavioural plasticity (Miller et al. 2022).

Concerns for maladaptive fidelity in polar bears should mainly be directed towards fidelity to denning sites, which appears much higher than foraging site fidelity in areas with seasonal ice (Derocher et al. 1990, Derocher & Stirling 2004). Shifts in sea ice dynamics resulting from warming temperatures may cause the last remaining ice to drift further south during break-up (Wang et al. 1994, Saucier et al. 2004); this may cause bears to come ashore further away from their denning sites and expend more energy as they travel longer distances to return to them (Cherry et al. 2013). Further, increasing levels of rain in Hudson Bay during the late winter are projected to lead to den collapses, resulting in increased female and cub mortality which may contribute to declines in the western Hudson Bay subpopulation if individuals retain high fidelity to increasingly vulnerable denning areas (Clarkson & Irish 1991, Stirling & Derocher 2012).

Levels of site fidelity can vary by activity in animals; for example, some species display high fidelity to their breeding habitat (Ciarnello et al. 2005, Ng et al. 2018), but not to foraging patches (Edwards et al. 2009, McGuire et al. 2021). Our results show that, in addition to high fidelity to denning areas, polar bears in western Hudson Bay also show broad on-ice fidelity influenced both by personality differences and environmental factors related to sea ice dynamics. Our study also highlights the role of Hudson Bay's seasonal ice in limiting on-ice fidelity, in comparison to other polar bear subpopulations with year-round ice or more permanent ice features. Further comparisons of polar bear fidelity across subpopulations with differing sea ice dynamics may greatly benefit our understanding of polar bear movement ecology.

Chapter 2 Tables

Table 2.1 Models used to predict on-ice fidelity metrics for polar bears in western Hudson Bay, Manitoba. Models predicting pairwise within individual home range overlap were GLMMs with zero-inflated beta distribution, and models predicting pairwise within-individual home range centroid distance were GLMMs with a Gamma distribution. Breakup and freeze-up dates were autocorrelated, and therefore are included in separate models. Random effects are bolded.

Model ID	Model Description	Parameters
Bio	Biological model	<i>Diff.Size + Diff.Ice.Year + Diff.Repro + Diff.Dep + Mean.Age + ID</i>
Clim	Climatic model	<i>Diff.Size + Diff.Ice.Year + Diff.Ice.F + Diff.Ice.B + Diff.NAO + Diff.AO + Diff.Season + ID</i>
Clim.Lag	Climatic model with lagged climatic variables	<i>Diff.Size + Diff.Ice.Year + Lag.Diff.Ice.F + Lag.Diff.Ice.B + Lag.Diff.NAO + Lag.Diff.AO + Diff.Season + ID</i>
Full	Full model without lagged climatic variables	<i>Diff.Size + Diff.Ice.Year + Diff.Ice.F + Diff.Ice.B + Diff.Repro + Mean.Age + Diff.NAO + Diff.AO + Diff.Season + ID</i>
Full.Lag	Full model with lag climatic variables	<i>Diff.Size + Diff.Ice.Year + Diff.Repro + Diff.Dep + Mean.Age + Diff.Lag.AO + Diff.Lag.NAO + Lag.Diff.Ice.F + Diff.Lag.Ice.B + Diff.Season + ID</i>

Table 2.2 Model Rank and Akaike information criteria (AICc) scores for the models used to predict polar bear on-ice fidelity in western Hudson Bay, Manitoba. Metrics used to estimate on-ice fidelity were calculated between pairs of seasonal home ranges belonging to the same individual and included centroid distance (a) and percent overlap (b). AICc = AICc score, Δ AICc = difference in AICc score between a given model and the top model, wAICc = AICc weight. Retained models are bolded.

Response Variable	Model ID	AICc	ΔAICc	wAIC
(a) Centroid Distance	Clim	3026.33	0.00	0.88
	Full	3030.45	4.12	0.11
	Clim.Lag	3038.45	12.12	0.00
	Bio	3038.98	12.65	0.00
	Full.Lag	3048.91	22.58	0.00
(b) Percent Overlap	Clim	-1445.77	0.00	0.83
	Clim.Lag	-1442.57	3.20	0.17
	Bio	-1435.43	10.34	0.00
	Full	-1429.76	16.01	0.00
	Full.Lag	-1425.84	19.93	0.00

Table 2.3 Summary values of fixed effects for the top model used to predict pairwise centroid distance between on-ice seasonal ranges of polar bears in western Hudson Bay, Manitoba. S.E. = Standard error. ES = Early Season and LS = Late Season, referring to the first and second half of the ice season, respectively. Near-significant p-values ($0.1 > p\text{-value} > 0.05$) are shown in italics, and significant p-values (< 0.05) are bolded.

Model ID	Parameter	Estimate	S.E.	P-value
Clim	Diff.Size	0.0016	0.040	0.9700
	Diff.Ice.Year	0.0470	0.049	0.3400
	Diff.Fzp	-0.0540	0.047	0.2500
	Diff.Bkp	0.1400	0.047	0.0034
	Diff.NAO	0.0500	0.037	0.1800
	<i>Diff.AO</i>	<i>-0.0830</i>	<i>0.047</i>	<i>0.0740</i>
	Diff.Season ES-LS	-0.0790	0.110	0.4800
	Diff.SeasonLS-LS	-0.2800	0.140	0.0480

Table 2.4 Summary values of fixed effects for the top model used to predict percent overlap between pairs of on-ice seasonal ranges of polar bears in western Hudson Bay, Manitoba. S.E. = Standard error. ES = Early Season and LS = Late Season, referring to the first and second half of the ice season, respectively. Near-significant p-values ($0.1 > p\text{-value} > 0.05$) are shown in italics, and significant p-values (< 0.05) are bolded.

Model ID	Parameter	Estimate	S.E.	P-value
Clim	Diff.Size	-0.02654	0.06865	0.6991
	Diff.Ice.Year	-0.02148	0.07312	0.7689
	Diff.Fzp	-0.01295	0.07511	0.8631
	<i>Diff.Bkp</i>	<i>-0.13359</i>	<i>0.07613</i>	<i>0.0793</i>
	Diff.NAO	-0.02374	0.06811	0.7274
	Diff.AO	0.02594	0.07335	0.7236
	Diff.Season ES-LS	-0.41308	0.22201	0.0628
	Diff.SeasonLS-LS	-0.28976	0.26911	0.2816

Chapter 2 Figures

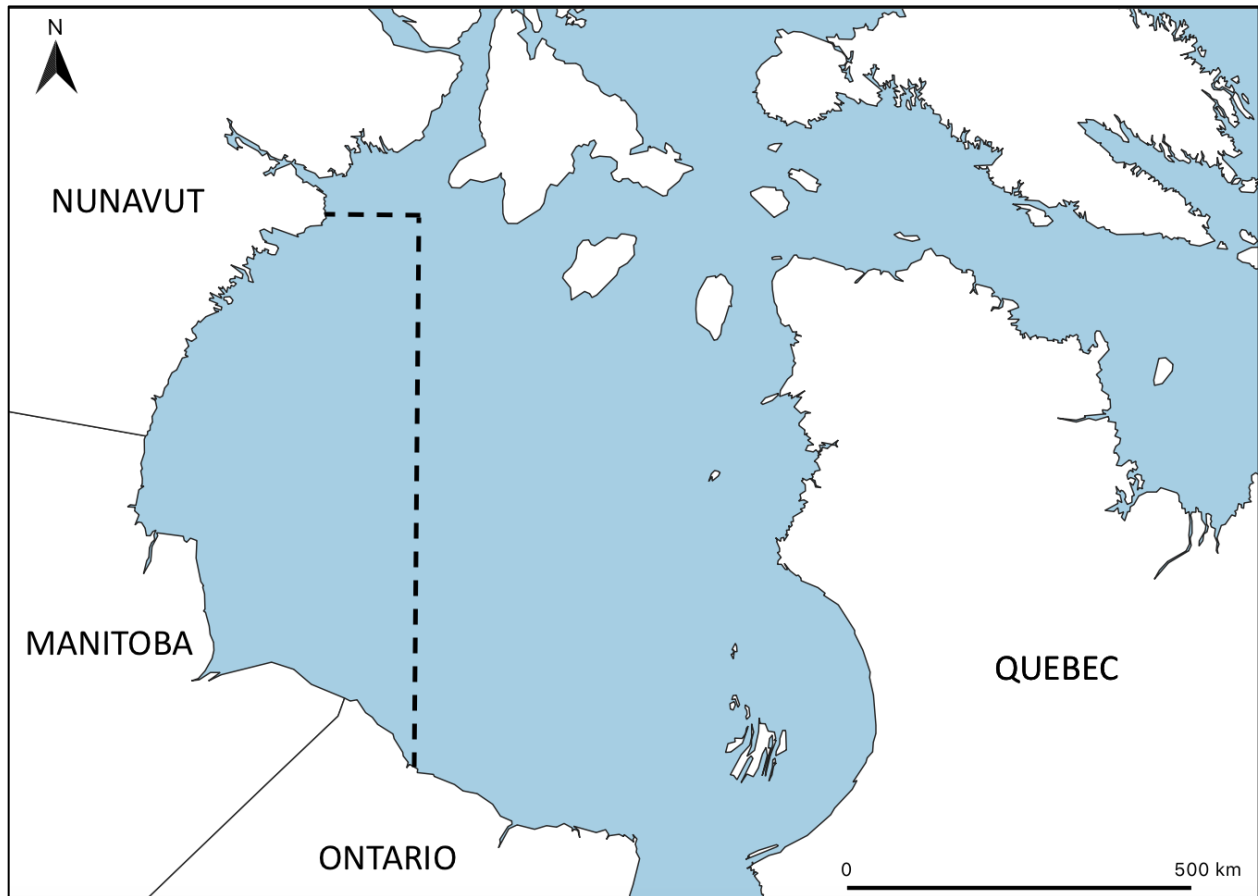


Figure 2.1. Map of the study area, showing Hudson Bay, adjacent provinces, and the western Hudson Bay management boundary. The western Hudson Bay management boundary is shown by the dotted line.

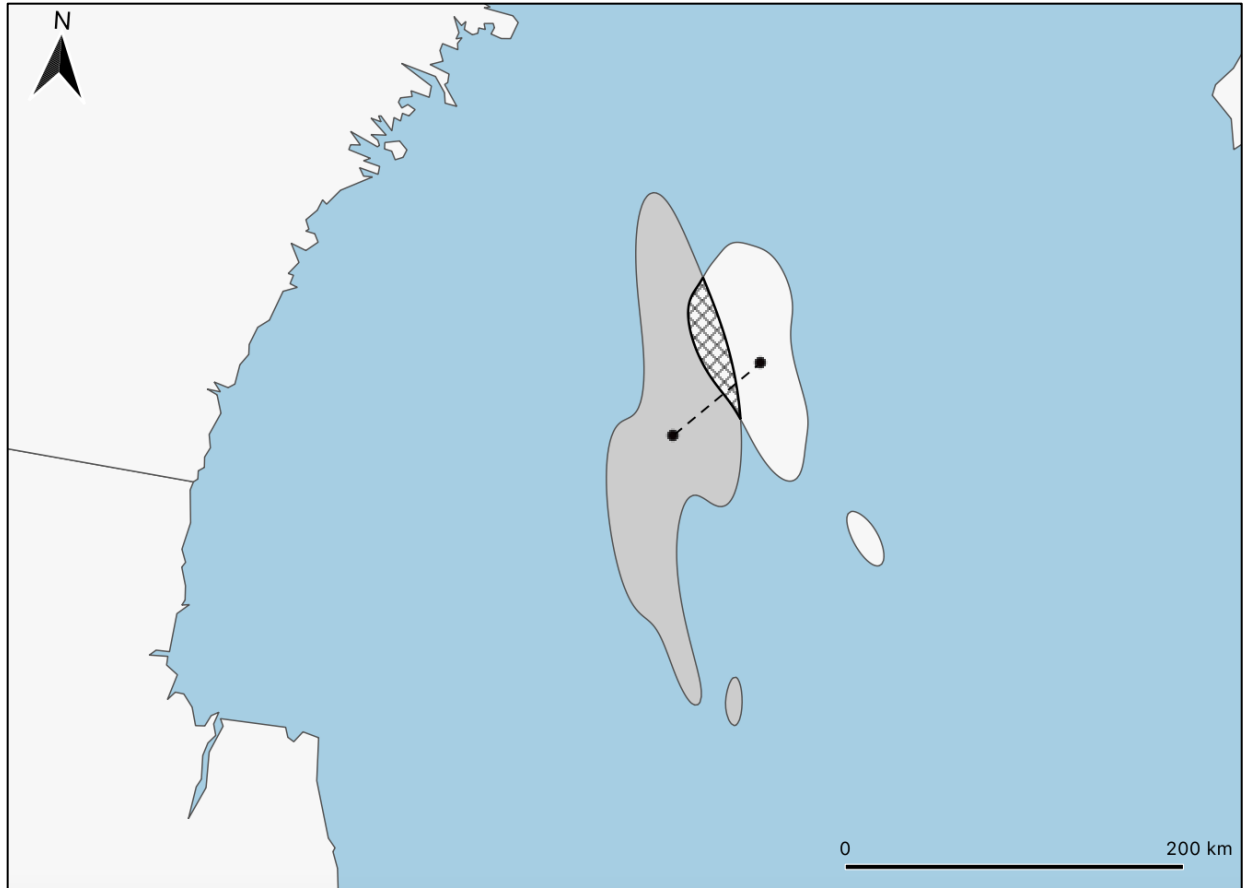


Figure 2.2. Example of home range overlap and centroid distance metrics used to estimate on-ice fidelity for polar bears in western Hudson Bay, Manitoba. Two seasonal ranges are shown in the center of the figure. Centroids are represented by the black points at the center of each seasonal range, and centroid distance is shown by the dashed line between those points. Seasonal range overlap is represented as the dashed area. Seasonal ranges were generated using kernel density estimates (KDE) with solve-the equation plug-in bandwidth.

Chapter 3: Variation in movement and space use of western Hudson Bay polar bears in relation to sex, reproductive status, and age

Introduction

Animal movement is a fundamental ecological process affecting energetics, gene flow, individual survival, and response to environmental change (Fahrig 2007, Hellberg 2009, Tomlinson et al. 2014, Riotte-Lambert & Matthiopoulos 2020). A diversity of environmental factors affect movement (e.g., climate - Duda et al. 1999; landscape features - Shepard et al. 2013; food availability - Stanley et al. 2021), as do intra- and inter-specific interactions (Lima 1998, Brodersen et al. 2008, Tchepmo Djomengi et al. 2018) and factors related to individual variation (Hawkes 2009, Spiegel et al. 2017). Common individual factors that influence movement are sex, age, reproductive status, physiology, and personality (Perrin & Mazalov 2000, Margalida et al. 2016), as they can affect energetic needs (Owen-Smith 1993, Kooijman & Lika 2014), influence resource requirements (Rachlow & Bowyer 1998, Benson and Chamberlain 2007), and affect social status (Ruckstuhl & Festa-Bianchet 2001). For example, inexperienced juveniles may move less efficiently or be more likely to disperse (Dobson 1982, Fagan et al. 2013, Smereka 2021). Moreover, higher energetic demands, predator avoidance, and lower mobility of offspring can affect the movement and habitat selection of females with offspring (Singh and Ericsson 2014). Sex-based differences in movement are also common and males often have larger home ranges that overlap with those of multiple females, presumably to maximize breeding success (Bond & Wolff 1999, Martin & Martin 2007). Finally, individual differences in size and body condition can influence decisions related to habitat selection and timing of migration (Shaw 2020), and individual personality, particularly degrees of boldness, can affect home range size (Ward-Fear et al. 2018).

Understanding the influence of individual factors on movement dynamics allows insights into population ecology, as well as the mechanisms underlying individuals' navigation of their environment (Ogburn et al. 2017, Katzner & Arlettaz 2020). However, while the diverse influence of environmental factors on animal movement has been well documented, the effect of individual factors on movement remains understudied (del Mar Delgado et al. 2018, Melaschenko & Hodges 2020, Shaw 2020).

Given the rapid warming in the Arctic (Polyakov et al. 2010, del Mar Delgado et al. 2018, Landrum & Holland 2020) and diminishing sea ice (Comiso et al. 2008, Serreze & Barry 2011), investigating the energetics and habitat use of Arctic marine mammals has emerged as a conservation priority (Laidre et al. 2008, Johnson et al. 2020, Pagano et al. 2021). For example, habitat alteration and loss for polar bears (*Ursus maritimus*) was identified as the primary threat to the species (Stirling & Derocher 2012, Lunn et al. 2016, Regher et al. 2016). Polar bears are obligate carnivores that specialize in hunting seals on the sea ice (Stirling & Archibald 1977, Smith 1980). In Arctic regions where ice undergoes an annual cycle of freeze and thaw, recent warming temperatures have shortened the ice cover season, reducing the bears' ability to hunt and increasing the time spent fasting in parts of their range (Stirling et al. 1993, Derocher et al. 2004, Castro de la Guardia et al. 2013). Additionally, polar bears may be facing higher locomotor costs due to increases in sea ice drift and open water areas, making them travel longer distances (Durner et al. 2017, Biddlecombe et al. here too), and swim more frequently (Sahanatien & Derocher 2012, Pilfold et al. 2017). The combination of reduced food intake and higher energy expenditure has increased polar bears' risk of starvation (Molnár et al. 2010) and cub mortality (Robbins et al. 2012). Understanding polar bear on-ice ecology and movement is therefore needed to better quantify the effects of climate change on this species' energetics.

The movement ecology of polar bears in western Hudson Bay is well studied in aspects such as environmental and individual factors influencing terrestrial movements (Derocher & Stirling 1990), migration dynamics (Cherry et al. 2013, Cherry et al. 2016, Togunov et al. 2017, Bohart et al. 2021), habitat selection (Lone et al. 2013, McCall et al. 2016), and home range size (McCall et al. 2015). However, a limitation of almost all polar bear movement studies across the Arctic is their focus on adult females (Laidre et al. 2013). This research gap exists mainly because subadults are growing and cannot safely wear tracking collars, and adult males cannot be fitted with telemetry collars as the size of their necks exceeds that of their heads (Amstrup et al. 2001). Moreover, the two studies that examined movements of adult males (Amstrup et al. 2001, Laidre et al. 2013) provide conflicting views on movement patterns. Finally, the movement of subadult polar bears remains mostly unknown. The effects of sex, age, and reproductive status on polar bear movement thus remain poorly understood. Additionally, due to the difficulty in tracking the same individuals over multiple seasons, we currently have limited knowledge on whether individuality can serve as a predictor for polar bear movement.

As a species, polar bears exhibit many physiological and behavioural differences associated with age, sex, reproduction, and individuality. Polar bears have pronounced sexual dimorphism with males weighing up to twice as much as females, which may lead to higher resource requirements for males (Derocher et al. 2005). Further, males can be infanticidal and prey on other bears, possibly leading to avoidance by conspecifics (Taylor et al. 1985, Derocher et al. 1999, Stirling and Ross 2011). In addition, pregnant females have high costs of reproduction as they must fast up to 4 months longer than other bears to den and give birth to cubs, which remain dependent on their mothers for up to 2.5 years with high energetic costs of lactation (Ramsay and Stirling 1988, Arnould and Ramsay 1994, Robbins et al. 2012). Finally,

studies have shown some aspects of polar bear movement vary by individual (McCall et al. 2015, Cherry et al. 2016), and other ursids show evidence of personality (Myers & Young 2018). Due to these differences, individual polar bears may differ in their on-ice movement dynamics, possibly reflecting differences in energetics and foraging strategies.

Here, we examine whether the movement dynamics of western Hudson Bay polar bears during the ice season differed by individual factors. Using satellite telemetry location data from a combination of collar and ear tag transmitters deployed between 2016 and 2021, we test whether age, sex, reproductive status, and individual identity predict polar bear movement when combined with environmental factors known to affect polar bear energetics or sea ice dynamics.

Methods

Study area and population

Hudson Bay is an inland sea bordered in Canada (Figure 3.1), with an area of 800 000 km² and average depth of 150 m (Saucier et al. 2004). As Hudson Bay is in the seasonal sea ice ecoregion, its ice undergoes an annual cycle of freeze and thaw (Amstrup et al. 2008). Sea ice freeze-up typically occurs between mid-October and December starting in the north of the bay and progressing towards the south (Saucier et al. 2004). Sea ice concentration usually reaches its peak in January and remains stable until break-up in June-July, leading to a short ice-free season between August and October (Saucier et al. 2004, Gagnon and Gough 2005). During the ice season, drift occurs mostly counterclockwise, though sea ice is also susceptible to wind forcing (Danielson 1971, Hochheim et al. 2010). Since 1971, warming temperatures have resulted in later sea ice freeze-up and earlier sea ice breakup, resulting in a shortening of the ice season in Hudson Bay at a rate of 6 days/decade (Gagnon and Gough 2005, Gupta et al. 2022), as well as a

decrease in sea ice concentration and thickness (Gagnon and Gough 2005, Stern and Laidre 2016). Further, while the speed and direction of ice drift currently seems unaffected, variability in ice drift speed in Hudson Bay has increased (Klappstein et al. 2020).

Hudson Bay is used by the Western Hudson Bay, Southern Hudson Bay and Foxe Basin polar bear subpopulations (Viengkone et al. 2018) as a platform for hunting seals and mating during the ice season (Stirling & Archibald 1977, Ramsay & Stirling 1986). Bears from these subpopulations migrate annually to the sea ice shortly after freeze-up and return to land on average 21 days after sea ice breakup (Castro de la Guardia 2017). Most polar bear matings occur during the spring (March to May) (Ramsay & Stirling 1986) along with the birth of seal pups, which maximizes prey availability (Ferguson et al. 2005). Bears mainly remain on shore and fast during the ice-free season (Ramsay et al. 1991, Pilfold et al. 2016). Pregnant females den inland before sea ice freeze-up, with parturition usually occurring in December (Derocher et al. 1992) and migrate to the sea ice with their cubs in February and March (Ramsay and Stirling 1986, Yee et al. 2017). Our study focuses on the western Hudson Bay polar bear subpopulation, the second southernmost subpopulation (Amstrup et al. 2008, Viengkone et al. 2018), which is currently estimated at 620 bears (Atkinson et al. 2022).

Telemetry data

We used polar bear telemetry data from satellite collar transmitters deployed on adult females with dependent offspring (i.e., with cubs-of-the-year (“cubs”) <1 year old, yearlings or 2-year-olds) and satellite ear tag transmitters on solitary bears. Family groups were captured on land in September in 2010-2019, between in Manitoba. Solitary bears were either captured in spring (April-May) of 2017-2021 on the sea ice, or near Churchill in autumn (September-November) of

2015-2021 by the Manitoba Department of Conservation (MDOC), who captured conflict bears as part of the community's Polar Bear Alert Program (Miller et al. 2023). Bears were immobilized by remote injection from a helicopter or vehicle, using a combination of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil[®], Laboratoires Virbac, Carros, France) following Stirling *et al.* (1989). All bears were tattooed with an individual number on the inside of their upper lip and given numbered ear tags for identification purposes. Sex was determined at capture, and age was estimated using cementum growth layers in an extracted vestigial premolar in adults (Calvert and Ramsay 1998), or using tooth eruption patterns for dependent offspring. Adult females in family groups were equipped with Argos or Iridium satellite-linked collars (Gen III and IV collars, Telonics, Mesa, AZ) that provided six locations per day at 4-hour intervals, while solitary bears were equipped with Doppler-shift ear tag transmitters (Model ETA-2620, Telonics, Mesa, AZ) linked to the Argos satellite system (CLS America Inc., Lanham, MD) that transmitted up to 16 locations per day during a 2-3-hour window. Capture and handling protocols followed the Canadian Council on Animal Care guidelines (www.ccac.ca) and were approved by the University of Alberta BioSciences Animal Care and Use Committee (Animal Use Protocols 00000033 and 00003667).

We calculated sea ice break-up and freeze-up dates by obtaining daily sea ice concentration in Hudson Bay at 25 km resolution, available as satellite passive microwave data (SMMR/SSMI) from the National Snow and Ice Data Center, Boulder, Colorado, USA (<http://nsidc.org/>). Freeze-up was defined as the first date where sea ice concentration within the western Hudson Bay population management boundary was $\leq 10\%$ for three consecutive days. We defined the date sea ice break-up was defined as the first of three consecutive dates when sea ice concentration date when sea ice concentration within the western Hudson Bay population

management boundary was $\leq 50\%$. We eliminated on-land locations and subset all remaining locations that were within the ice season, which we defined as starting on the date of sea ice freeze-up and ending on the date of breakup. Since the ice season spans across two calendar years, each bear's data was separated into "ice years", beginning on the date of sea ice freeze-up and ending on the date of break-up.

To study the effects of seasonality on the bears' movement, we split the ice season in half, termed "Early Season" and "Late Season". In most cases, the Early Season lasted from November or December to early March, where sea ice concentration increases throughout Hudson Bay bears begin their migration onto the sea ice with the exception of denning females (Ramsay & Stirling 1986). The Late Season included the birth of seal pups and mating season (DeMaster & Stirling 1981, Ramsay & Stirling 1986), as well as the migration of females with their cubs of the year onto the sea ice (Ramsay & Stirling 1986, Yee et al. 2017).

To account for possible effects of immobilization on movement, we removed the first 3 days of transmission for each bear (Thiemann et al. 2013). Using the *argosfilter* package in R (Freitas 2012), we removed locations with biologically improbable speeds (> 4.8 km/h; Amstrup et al. 2000), erroneous locations with deviations from the path >25 km or >50 km with turning angles of $>165^\circ$ or $>155^\circ$, respectively (Freitas et al. 2008), and dropped collars (Togunov et al. 2020). We removed low-quality locations for the ear tag transmitters coded as A, B and Z, and only retained moderate to high quality locations coded as 0, 1, 2 or 3 following Douglas et al. (2012). We standardized the number of daily locations between collar and ear tag transmitters by subsampling to 1 location/day, selecting the highest-quality location available on a given date. If >1 location of the highest quality was available, we randomly selected one location.

Bears were placed into 7 classes by age, sex, and reproductive status: adult males (≥ 5 years old), solitary adult females (≥ 5 years old), subadults (2-4 years old, sexes pooled due to low sample sizes), females with “spring cubs” (≥ 5 years old and accompanied by offspring 3-6 months old), females with “winter cubs” (≥ 5 years old and accompanied by offspring 8-12 months old), females with yearlings (≥ 5 years old and accompanied by offspring 1-2 years old), and females with 2-year olds (≥ 5 years old and accompanied by offspring >2 years old). To determine the reproductive status of females, we first assigned December 1 as the birthdate of offspring (Derocher et al. 1992). We then determined offspring age by taking their initial age determined at capture and adjusting it over the ice season; for example, females captured in September with a cub would be considered a female with winter cubs in the Early Season but would be classified as a female with yearlings in the Late Season as the cub would be over one year old. Females that were solitary in autumn but remained on land until mid-February to late March were classified as females with spring cubs, as this usually means the female had denned, undergone parturition, and migrated to the ice with her 3 to 4-month-old cubs (Ramsay and Stirling 1988). Females reaching the sea ice before mid-February were considered to have lost their cubs while denning and classified as solitary females.

Estimation of movement dynamics

We analysed five movement metrics: mean daily speed, path tortuosity, seasonal range size, on-ice departure, and on-land arrival. Movement metrics were calculated for each season available within each bear. Estimations of animal movement are often sensitive to the time interval between consecutive fixes (Harris et al. 1990, Løkkeborg et al. 2002, Appendix A), which can be affected by missing data (Frair et al. 2010). Our collar data had significantly more

gaps in transmission than our ear tags (mean % locations separated by >24h for ear tags: 1.7%; for collars: 18.2%; t-test: $p < 0.001$), with gaps ranging from 48h to 168h. To avoid missing data from biasing results, we further standardized our two datasets by computing our speed, seasonal range size, and path tortuosity values using groups of 30 consecutive locations that were separated by no more than 48-hour gaps. We chose 48h as our cut-off because the frequency of locations separated by 48 hours did not significantly differ between collars and ear tags (mean for collars: 2.9 %; mean for ear tags: 1.2 %; t-test: $p = 0.07$). We also standardized our data to groups of 30 locations because our speed and path tortuosity values were affected by the number of locations used (Appendix B), and home range sizes in general are known to be sensitive to differences in sample size (Seaman et al. 1999, Boyle et al. 2008). We chose a cut-off of 30 locations to accommodate our ear tag data, as our ear tags transmitted locations for a mean of 47 ± 12 days.

Because drifting sea ice can mask polar bears' true speed and path tortuosity (Auger Methé et al. ref, Appendix C), we removed the effect of drift from our telemetry locations using vector subtraction (Auger-Méthé et al. 2016) before calculating these two metrics. We used Polar Pathfinder Daily 25 km EASE-Grid Sea Ice Motion Vectors (National Snow and Ice Data Centre – CO, USA) converted into *netCDF* format and used R to obtain ice drift vectors. We then subtracted those vectors from the bears' movement vectors to obtain their true step length.

Mean daily speed was calculated from the distance between every two consecutive locations divided by the time between locations, and then averaged across all locations. Path tortuosity was calculated using the equation $T = D/L$, where D was the Euclidean distance between consecutive locations and L was the sum of all step lengths over the interval (Batschelet 1981). This yielded an index between 0 and 1, where paths with scores closer to zero were more tortuous and paths with scores closer to 1 were straighter. Seasonal range size was calculated

using kernel density estimates (KDE) with solve-the equation plug-in bandwidth estimation (Gitzen et al. 2006) using the *ks* package in R Studio (Duong 2007). Our migration dates were calculated by first defining on-ice departure dates as the date associated with the first on-ice location followed by no on-land locations until after sea ice breakup. Conversely, on-land arrival date was defined as the date of the first on-land location occurring after sea ice breakup that was followed by < 3 on-ice locations. To mitigate the effect of missing data on our estimates of migration dates, we only kept dates with cumulative gaps of ≤ 72 h between the first and last locations used to generate our estimates.

Statistical analyses

We analysed the impact of environmental and biological factors on our movement metrics and migration dates using 9 models based on *a priori* ecological hypotheses (Table 2.1). Models used were general linear mixed models with a gamma distribution in the case of all metrics but on-land arrival date, where the model was a general linear model with a gamma distribution. Environmental variables used in all metrics included the ice year in which the metric was measured (*Ice.Year*), the monthly values of Arctic Oscillation (*AO*) and North Atlantic Oscillation (*NAO*) averaged over the season in which a metric was measured, the ordinal dates of sea ice breakup (*Ice.Bkp*) and freeze-up (*Ice.Fzp*), and the lagged effects of those variables (i.e. the values from the previous ice year - *Lag.Ice.Year*, *Lag.AO*, *Lag.NAO*, *Lag.Ice.Bkp*, *Lag.Ice.Fzp*). AO and NAO values were obtained from the NSIDC (nsidc.org) as monthly averages, which were averaged again over the months of the Early and Late seasons to obtain their respective AO and NAO indices. For all models except those with departure or arrival date as the independent variable, we also included the season for which the metric was calculated

(*Season*). Climate variables that were autocorrelated (Spearman's $r \geq 0.6$) were included in separate models (Hefley et al. 2017). In the case of all response variables but on-land arrival date, a large proportion (>30%) of our data was composed of multiple estimates from the same individuals; to account for this, we included individual ID number (*ID*) as a random effect. Before model selection, we defined outliers as values that were 1.5 times the interquartile range (Walfish 2006) and removed them to improve model performance (Hodge & Austin 2004).

We determined the top model for each movement metric using model selection via Akaike's information criterion with correction for small sample sizes ("AICc" – Burnham and Anderson 2004). Models with a difference of AICc that was <2 points more than the top model were also retained, as a difference of <2 still suggested significant support for those models (Burnham and Anderson 2002). The significance of the random effect by calculated the log likelihood ratio between the top model and a reduced version of this model (i.e., with the random effect removed - Morrell 1998). For all tests, we used a significance level of $\alpha=0.05$.

Results

We obtained speed, path tortuosity and seasonal range size from 79 bears collared or ear tagged between 2016 and 2021. Out of those 79 bears, 25 had data for more than one season (19 for two seasons, and 6 for 3 seasons). For 18 out of 25 bears, these multiple seasons were the Early and Late seasons from the same ice year. In total, we analyzed 110 speed, path tortuosity and seasonal range values (19 subadults, 14 adult males, 11 solitary females, 8 females with spring cubs, 24 females with winter cubs, 28 females with yearlings, and 6 females with 2-year-olds), over a total of 3300 telemetry locations. Due to the outlier removal in our model selection analysis, sample sizes per metric varied from 62 to 105.

Over the full ice season, bears walked at a mean daily speed of 1.00 ± 0.056 (1.30 ± 0.07 km/h in the Early Season and 1.00 ± 0.05 km/h in the Late Season; Appendix D). The overall mean path tortuosity index of all bears was 0.36 ± 0.05 (0.33 ± 0.05 in the Early Season and 0.34 ± 0.06 in the Late Season; Appendix E). Seasonal range size averaged $22\,000 \pm 6400$ km² ($38\,000 \pm 8700$ km² in the Early Season and $14\,000 \pm 2300$ km² in the Late Season; Appendix F). The top model retained for mean daily speed was the full model “Full.1” (Table 3.2a), whereas our biological model “Bio” was retained as the top model for both path tortuosity index (Table 3.2b) and seasonal range size (Table 3.2c). All three models showed a significant effect of polar bear class: in comparison to solitary adult females, all classes with the exception of subadults had significantly lower daily speeds (adult males: $p=0.004$, females with spring cubs: $p=0.0011$, females with winter cubs: $p=0.037$, females with yearlings: $p=0.0017$, females with 2-year-olds: $p=0.023$; Table 3.3), females with winter cubs and 2-year-olds had significantly higher path tortuosity indices, ($p=0.032$ and $p=0.015$, respectively; Table 3.4) and subadults and adult males had significantly smaller seasonal ranges ($p=0.03$ and $p=0.04$, respectively; Table 3.5). Additionally, daily speed and seasonal range size both significantly decreased during the Late Season ($p=0.0044$, Table 3.3 and $p<0.0001$, Table 3.5, respectively).

We obtained 129 migration dates over 96 bears, consisting of 61 departure dates and 68 arrival dates. We were able to obtain multiple on-ice departure dates from 9 bears, where 7 had departure dates from two different ice years and 2 had departure dates from three different ice years. 6 bears had two arrival dates available for analysis, with the remaining bears only having one arrival date. Bears departed on average 7 ± 4.5 days after freeze-up and mean on-land arrival date was 38 ± 14 days after break-up (Appendix G). Due to low sample sizes, no females with 2-year-olds were available for summarizing and analysing migration dates. On-ice departure

date was best predicted by our first lag model “Lag.1”, whereas arrival date was best predicted by the models “Lag.1”, “Lag.2” and our second climatic model “Clim.2”. However, none of the fixed effects in those models significantly affected our migration dates (Table 3.6).

Finally, our likelihood ratio tests showed a significant effect of individual identity on all tested metrics (daily speed: $\chi^2(1)=6.78$, $p<0.0001$; path tortuosity: $\chi^2(1)=34.8$, $p<0.0001$; seasonal range size: $\chi^2(1)=28.0$, $p<0.0001$; departure date: $\chi^2(1)=62.8$, $p<0.0001$)

Discussion

Traditionally, most studies on polar bear movement have been limited to adult females. In these studies, only environmental variables were found to influence polar bear movement (e.g., Mauritzen et al. 2001, Cherry et al. 2013, Bohart et al. 2021). When including underrepresented classes like adult males and subadults and accounting for repeated measures from the same individuals, our study found that biological variables affected polar bear movements more than environmental variables.

We first found that most of our polar bear movement metrics varied by individual bear, regardless of sex, age or reproductive status. Individual variation in physiology may affect movement in polar bears; for example, animals often choose to walk at their optimal speed, which can vary depending on size, as an energy conservation strategy (Pyke 1980, Wilson et al. 2015). Differences in body condition could also influence swimming behaviour; swimming is energetically costly, and animals with lower body conditions may instead choose to walk around open water areas, resulting in higher path tortuosity (Pilfold et al. 2017). Habitat selection also varies by individual for polar bears in western Hudson Bay (Chapter 2, McCall et al. 2015). Moreover, due to the dynamic nature of arctic ice, each bear’s immediate environment may

differ depending on individual location (Cherry et al. 2016, Lone et al. 2018), which can affect a bear's path tortuosity (Bohart et al. 2021) or decision to migrate (Cherry et al. 2016). Finally, personality differences in boldness can affect space use, with bolder individuals occupying larger home ranges (Sinn et al. 2014, Johnson et al. 2017, Eccard et al. 2022).

Sex and age class also affected most movement metrics analysed in our study. We first found that solitary adult females and subadults moved significantly faster than adult males and females with offspring of any age. Polar bears show pronounced sexual dimorphism where males can be twice as large as females (Derocher et al. 2005, Derocher et al. 2010). As walking speed can be negatively influenced by size due to higher costs of acceleration (Pagano & Williams 2018, Pagano et al. 2020), the reduced speeds of adult males may help them conserve energy while walking. Moreover, the slower movement rates of females with offspring could be due to offspring limiting their mothers' mobility (Ramsay and Stirling 1986), similar to ungulates (Brook 2010, DeMars et al. 2013), marine mammals (Noren et al. 2008), and primates (Williams et al. 2002). Alternatively, females with offspring may walk at slower speeds and to conserve energy. Energy expenditure is higher in females with offspring than in other polar bear classes due to costs of lactation (Rode et al. 2018). Further, females with spring cubs migrate onto the sea ice closer to their starvation threshold than other bears, due to costs of gestation and longer fasting periods caused by denning on land (Robbins et al. 2012, Miller et al. 2022). As a result, females with winter and spring cubs, yearlings or two-year-olds may be altering their movement dynamics to survive the ice season and provide for their offspring.

We also found that females with 2-year-olds and winter cubs travelled in straighter paths than other bears. Female polar bears with offspring show a tendency to avoid areas with open water while on the sea ice (Stirling et al. 1993, Pilfold et al. 2017, Johnson et al. 2020), because

cubs are vulnerable to hypothermia when immersed (Blix & Lentfer 1979, Aars et al. 2010). Additionally, because some open-water areas like flaw leads are used by other polar bear classes for hunting (Henderson et al. 2021), females with winter cubs or 2-year-olds may also avoid those areas to minimize encounters with conspecifics, especially adult males who may be infanticidal (Taylor et al. 1985, Amstrup et al. 2006). As sea ice areas with more open water are more dynamic and require more turns to navigate effectively (Biddlecombe et al. 2021, Henderson et al. 2021), other classes of polar bears that do travel in these areas will have more tortuous paths.

Our analyses also showed that adult males and subadults had smaller seasonal ranges than solitary adult females and females with offspring. In subadult mammals, larger home range sizes are often due to increased dispersal (Harestad & Funnell 1979, Smereka et al. 2021). As polar bears in western Hudson Bay are migratory, subadults do not disperse, and their smaller range sizes were expected due to their inexperience navigating the sea ice and lower resource requirements compared to other bears (Schoener & Schoener 1982, Carstairs et al. 2019). The smaller seasonal ranges of adult males may be partly explained by their lower walking speeds found in our study, resulting in shorter distances travelled. However, females with offspring, who also had lower speeds, did not show a reduction in range size, invalidating this explanation. Another possibility is that males select areas with different levels of sea ice drift during the ice season. On-ice habitat selection varies by polar bear class in other subpopulations, though data on males is currently lacking (Johnson et al. 2020). Increased levels of drift can either inflate or constrain home range size (McCall et al. 2016, Klappstein et al. 2020). Whether this process influences male seasonal range size in western Hudson Bay remains to be investigated.

Our results regarding seasonal range size and path tortuosity reveal possible differences in mating strategies between different polar bear subpopulations. Adult males have higher path tortuosity in the spring than solitary adult females in the Baffin Bay, East Greenland (Laidre et al. 2013), and Chukchi sea (Wilson et al. 2022) subpopulations. The higher path tortuosity of adult males was interpreted as a mating strategy where they restrict their movement paths to smaller areas, allowing them to avoid other males while optimizing their rate of encounters with females (Ramsay and Stirling 1986, Laidre et al. 2013, Wilson et al. 2022). While this behaviour may also be present in the western Hudson Bay population, we did not find evidence supporting it in our study. First, there were no differences in path tortuosity between males and females; second, while the smaller Late Season ranges of adult males could be interpreted as the males patrolling a specific area in search of females, their seasonal ranges were smaller than other classes during the Early Season, which does not include mating season. Western Hudson Bay is situated further south than the Baffin Bay and East Greenland subpopulations, and therefore differs in sea ice dynamics; for one, it is the only subpopulation of the three that experiences an ice-free season, since sea ice remains year-round in East Greenland (Aagaard and Coachman 1968) and Baffin Bay retains a strip of ice along its coast year-round (Tang et al. 2004). Additionally, the ice in Hudson Bay has become more dynamic and unpredictable over the past decades than more northern arctic areas because of anthropogenic warming (Sahanatien & Derocher 2012, Hocheim et al. 2010). The higher dynamism of western Hudson Bay's sea ice more may be masking possible mating strategies in this subpopulation's bears. Alternatively, male polar bears in western Hudson Bay may be using a different mating strategy altogether, or simply relying on random encounters with females for breeding (Crowley et al. 1991, Stirling et al. 1993, Kokko & Mappes 2013).

We also found no differences in migration dates between our age and sex classes, suggesting that the timing of migration in polar bears not affected by intra-population dynamics. Our findings do not align with anecdotal observations from Rockwell et al. (2009), who reported that subadults arrived on land earlier than other bears. Similarly, Miller et al. (2022) revealed a negative relationship between bear age and departure date, with younger bears departing earlier. While we calculated migration dates as the number of days after breakup or freeze-up, Miller et al. (2022) and Rockwell et al. (2009) used ordinal dates in the calendar year. The fact that we found no differences between sex and age classes suggests that migration is primarily associated with the timing of break-up and freeze-up and associated environmental variables, which falls in line with the results of Cherry et al. (2013) and Bohart et al. (2021); using the calendar date may therefore be masking the effect of sea ice dynamics as the dates of break-up and freeze-up have been changing over the past decades in western Hudson Bay (Gagnon & Gough 2005, Kowal et al. 2017).

The only environmental variable that influenced polar bear migration dynamics in our study was seasonality, as bears moved faster and had larger ranges in the Early Season. Sea ice concentration and thickness increases throughout the Early Season in Hudson Bay but decreases in the Late Season starting in March, with significant increases open water areas occurring in April-May till breakup (Saucier et al. 2004). The resulting increases in sea ice fragmentation during the Late Season may force bears to work against ice drift and navigate against more dynamic sea ice formations, potentially resulting in decreased ranges during this period (Auger-Méthé et al. 2016, Biddlecombe et al. 2021). These conditions may also result in bears having to swim across larger open-water areas (Pilfold et al. 2017), contributing to reductions in speed.

Comparisons between polar bear movement metrics found in our study and those of other subpopulations must be made with caution for two reasons. First, other studies documenting polar bear movement rates and path tortuosity usually do not account for the influence of ice drift in their analyses (e.g., Amstrup et al. 2000, Laidre et al. 2013, Wilson et al. 2022). By using drifting sea ice as a foraging platform, bears move over a dynamic environment that can mask their true movements (Auger-Méthé et al. 2016). Accordingly, removing the effect of ice drift in our study modified our mean speed and path tortuosity values (Appendix C). Patterns of ice drift differ between polar bear subpopulations due to differences in latitude (Hakkinen et al. 2008, Ye et al. 2016), wind forcing (Spren et al. 2011, Liu et al. 2016) and ocean currents (Hibler et al. 1987, Kwok et al. 2013). As a result, we can only make limited conclusions when comparing movements of polar bear subpopulations where the influence of drift is not removed. Second, the interval between telemetry locations used to analyse polar bear movement differs between studies. We found that between-interval differences of even 4 hours result in large differences in polar bear speed and path tortuosity estimate (Appendix A). As such, comparisons between estimates with different intervals is nearly impossible due to those intervals masking the true movement estimates. We recommend using standardized measures whenever possible.

Many studies on polar bear movement that include sex, age and reproductive status have been conducted in other subpopulations (e.g., Amstrup et al. 2001, Laidre et al. 2013, Johnson et al. 2020); however, our study is one of the few to include bears of all sex and age classes. Our findings further confirm the importance of sex, age and reproductive status in polar bear movement ecology, and gives further insights on the effect of individual variation on polar bear movement. Our analyses suggest that movements of adult females with or without offspring, for which telemetry data is abundant, should not be generalized to other bears. We thus recommend

that future research on polar bear movement include subadults and adult males in future studies of polar bear movement to other polar bear subpopulations, especially in those occupying different sea ice ecoregions (Amstrup et al. 2008, Vongraven et al. 2012).

Chapter 3 Tables

Table 3.1 Models used to analyze movement and space use metrics (mean daily speed, path tortuosity index and seasonal home range size) and migration dates (on-ice departure and on-land arrival) for polar bears in western Hudson Bay, Manitoba, during the ice season. All models were generalized linear mixed models with a gamma regression. Random effects are shown as bolded. For migration dates, the “Season” covariate was removed in models containing it. Models were modified for on-land arrival by removing the random effect and converting the models to General Linear Models. The covariates *Ice.Year*, *Ice.Bkp* and *Lag.Ice.Fzp* were autocorrelated to each (Spearman’s $r > 0.6$) and as such, are included in different models. Covariates *Lag.Ice.Bkp* and *Lag.NAO* were also autocorrelated and treated similarly.

Model Description	Model ID	Parameters
Biological model	Bio	<i>Ice.Year</i> + <i>Class</i> + <i>Season</i> + ID
Climatic model 1	Clim.1	<i>Ice.Year</i> + <i>Ice.Fzp</i> + <i>NAO</i> + <i>AO</i> + <i>Season</i> + ID
Climatic model 2	Clim.2	<i>Ice.Bkp</i> + <i>Ice.Fzp</i> + <i>NAO</i> + <i>AO</i> + <i>Season</i> + ID
Full model 1: combination of covariates from the biological and climatic 1 models	Full.1	<i>Ice.Year</i> + <i>Class</i> + <i>Season</i> + <i>Ice.Fzp</i> + <i>NAO</i> + <i>AO</i> + ID
Full model 2: combination of covariates from models “Bio” and “Clim1”	Full.2	<i>Ice.Year</i> + <i>Class</i> + <i>Season</i> + <i>Ice.Bkp</i> + <i>NAO</i> + <i>AO</i> + ID
Lag climatic model 1	Lag.1	<i>Lag.Ice.Fzp</i> + <i>Lag.NAO</i> + <i>Lag.AO</i> + <i>Season</i> + ID
Lag climatic model 2	Lag.2	<i>Lag.Ice.Bkp</i> + <i>Lag.Ice.Fzp</i> + <i>Lag.AO</i> + <i>Season</i> + ID
Full lag model 1: combination of covariates from the biological and lag climatic 1 models	Full.Lag.1	<i>Ice.Year</i> + <i>Class</i> + <i>Season</i> + <i>Fzp</i> + <i>NAO</i> + <i>AO</i> + <i>Lag.Ice.Fzp</i> + <i>Lag.NAO</i> + <i>Lag.AO</i> + ID
Full lag model 2: combination of covariates from the biological and lag climatic 2 models	Full.Lag.2	<i>Ice.Bkp</i> + <i>Class</i> + <i>Season</i> + <i>Ice.Fzp</i> + <i>NAO</i> + <i>AO</i> + <i>Lag.Bkp</i> + <i>Lag.Fzp</i> + <i>Lag.AO</i> + ID

Table 3.2 Model Rank, and AIC scores for the 9 models used to predict on-ice movement and space use metrics for polar bears in western Hudson Bay, Manitoba, during the ice season. AICc = AICc score, Δ AICc = Difference in AICc score between a given model and the top model, w AICc = AICc weight. Top models are bolded.

Movement metric	Model ID	AICc	Δ AICc	w AICc
(a) Mean Daily Speed	Full.1	-42.07	0.00	0.66
	Full.2	-39.84	2.23	0.22
	Lag.1	-35.82	6.25	0.03
	Clim.2	-35.32	6.75	0.02
	Clim.1	-35.27	6.80	0.02
	Full.Lag.2	-34.95	7.12	0.02
	Full.Lag.1	-34.94	7.13	0.02
	Bio	-32.86	9.21	0.01
	Lag.2	-12.56	29.51	0.00
(b) Path Tortuosity Index	Bio	-69.39	0.00	0.74
	Full.2	-65.63	3.76	0.11
	Full.1	-64.08	5.31	0.05
	Clim.2	-63.58	5.81	0.04
	Clim.1	-62.63	6.76	0.03
	Lag.1	-60.68	8.71	0.01
	Lag.2	-60.26	9.13	0.01
	Full.Lag.1	-59.22	10.17	0.00
	Full.Lag.2	-58.30	11.09	0.00
(c) Seasonal Range Size	Bio	2163.85	0.00	0.98
	Clim.2	2173.12	9.27	0.01
	Clim.1	2173.57	9.72	0.01
	Full.2	2178.77	14.92	0.00
	Full.1	2179.11	15.26	0.00
	Full.Lag.1	2185.82	21.97	0.00
	Full.Lag.2	2186.53	22.68	0.00
	Lag.1	2213.89	50.04	0.00
	Lag.2	2222.84	58.99	0.00
(d) On-ice departure date	Lag.1	337.02	0.00	0.57
	Lag.2	339.24	2.22	0.19
	Clim.2	340.22	3.20	0.12
	Clim.1	341.53	4.51	0.06
	Bio	343.80	6.78	0.02
	Full.Lag.1	343.89	6.87	0.02
	Full.Lag.2	343.89	6.87	0.02
	Full.2	346.85	9.83	0.00

	Full.1	348.12	11.10	0.00
(e) On-land arrival date	Lag.2	499.91	0.00	0.30
	Clim.1	500.03	0.12	0.29
	Lag.1	500.08	0.17	0.28
	Clim.2	502.31	2.40	0.09
	Bio	504.32	4.41	0.03
	Full.1	510.68	10.77	0.00
	Full.2	512.64	12.73	0.00
	Full.Lag.1	514.89	14.98	0.00
	Full.Lag.2	516.21	16.30	0.00

Table 3.3 Coefficients (β), standard errors (SE), and p-values (P) of covariates for the top model used to predict the mean daily speed of polar bears in western Hudson Bay, Manitoba, during the ice season. All classes within the “Class” covariate are compared in reference to solitary adult females. The reference point for the “Season” covariate is the Early Season. “Early Season” and “Late Season” refer to the first and second halves of the ice season, respectively. Significant p-values ($p < 0.05$) are bolded.

Top model ID	Covariate	β	SE	P
Full.1	Ice.Year	-0.014	0.036	0.70
	Class: Subadults	-0.12	0.078	0.13
	Class: Adult males	-0.22	0.085	0.004
	Class: Females with spring cubs	-0.32	0.096	0.0011
	Class: Females with winter cubs	-0.21	0.100	0.037
	Class: Females with yearlings	-0.24	0.075	0.0017
	Class: Females with 2-year-olds	-0.28	0.12	0.023
	Season: Late Season	-0.24	0.081	0.0044
	Ice.Fzp	-0.045	0.031	0.15
	NAO	-0.005	0.036	0.88
AO	-0.030	0.030	0.32	

Table 3.4 Coefficients (β), standard errors (SE), and p-values (P) of covariates for the top model used to predict the path tortuosity index of polar bears in western Hudson Bay during the ice season. All classes within the “Class” covariate are compared in reference to solitary adult females. The reference point for the “Season” covariate is the Early Season. “Early Season” and “Late Season” refer to the first and second halves of the ice season, respectively. Significant p-values ($p < 0.05$) are bolded.

Top model ID	Covariate	β	SE	P
Bio	Ice.Year	0.039	0.049	0.41
	Class: Subadults	0.065	0.190	0.73
	Class: Adult Males	-0.220	0.200	0.27
	Class: Females with spring cubs	0.140	0.230	0.55
	Class: Females with winter cubs	0.460	0.210	0.032
	Class: Females with yearlings	0.250	0.180	0.16
	Class: Females with 2-year-olds	0.660	0.270	0.015
	Season: Late Season	-0.049	0.140	0.72

Table 3.5 Coefficients (β), standard errors (SE), and p-values (P) of covariates for the top model predicting seasonal range size for polar bears in western Hudson Bay, Manitoba. All classes within the “Class” covariate are compared in reference to solitary adult females. The reference point for the “Season” covariate is the Early Season. “Early Season” and “Late Season” refer to the first and second halves of the ice season, respectively. Significant p-values (p-value <0.05) are bolded.

Top model ID	Covariate	β	SE	P
Bio	Ice.Year	0.047	0.048	0.33
	Class: Subadults	-0.280	0.190	0.03
	Class: Adult males	-0.420	0.200	0.038
	Class: Females with spring cubs	0.012	0.230	0.96
	Class: Females with winter cubs	0.081	0.220	0.71
	Class: Females with yearlings	-0.180	0.180	0.33
	Class: Females with 2-year-olds	-0.016	0.290	0.96
	Season: Late Season	-0.770	0.140	<0.0001

Table 3.6 Coefficients (β), standard errors (SE), and p-values (P) of covariates for the top model predicting migration dates for polar bears in western Hudson Bay, Manitoba. Significant p-values ($p < 0.05$) are bolded, and near-significant p-values ($0.1 > p > 0.05$) are shown in italics.

Top model ID	Top model ID	Covariate	β	SE	P
On-ice departure date	Lag.1	Ice.Year	0.18	0.27	0.49
		Lag.Ice.Fzp	-0.0013	0.30	0.99
		Lag.NAO	-0.10	0.24	0.67
		Lag.AO	0.19	0.17	0.28
On-land arrival date	Lag.2	Ice.Year	0.072	0.069	0.30
		Lag.Ice.Bkp	0.032	0.036	0.38
		Lag.Ice.Fzp	-0.0059	0.054	0.91
		<i>Lag.AO</i>	<i>-0.11</i>	<i>0.052</i>	<i>0.053</i>
	Clim.1	Ice.Year	0.015	0.040	0.72
		Ice.Fzp	0.078	0.048	0.11
		NAO	0.020	0.037	0.60
		AO	0.021	0.055	0.71
	Lag. 1	Ice.Year	0.060	0.076	0.42
		Lag.Ice.Fzp	-0.0021	0.053	0.97
		Lag.NAO	-0.030	0.038	0.44
		<i>Lag.AO</i>	<i>-0.096</i>	<i>0.055</i>	<i>0.085</i>

Chapter 3 Figures

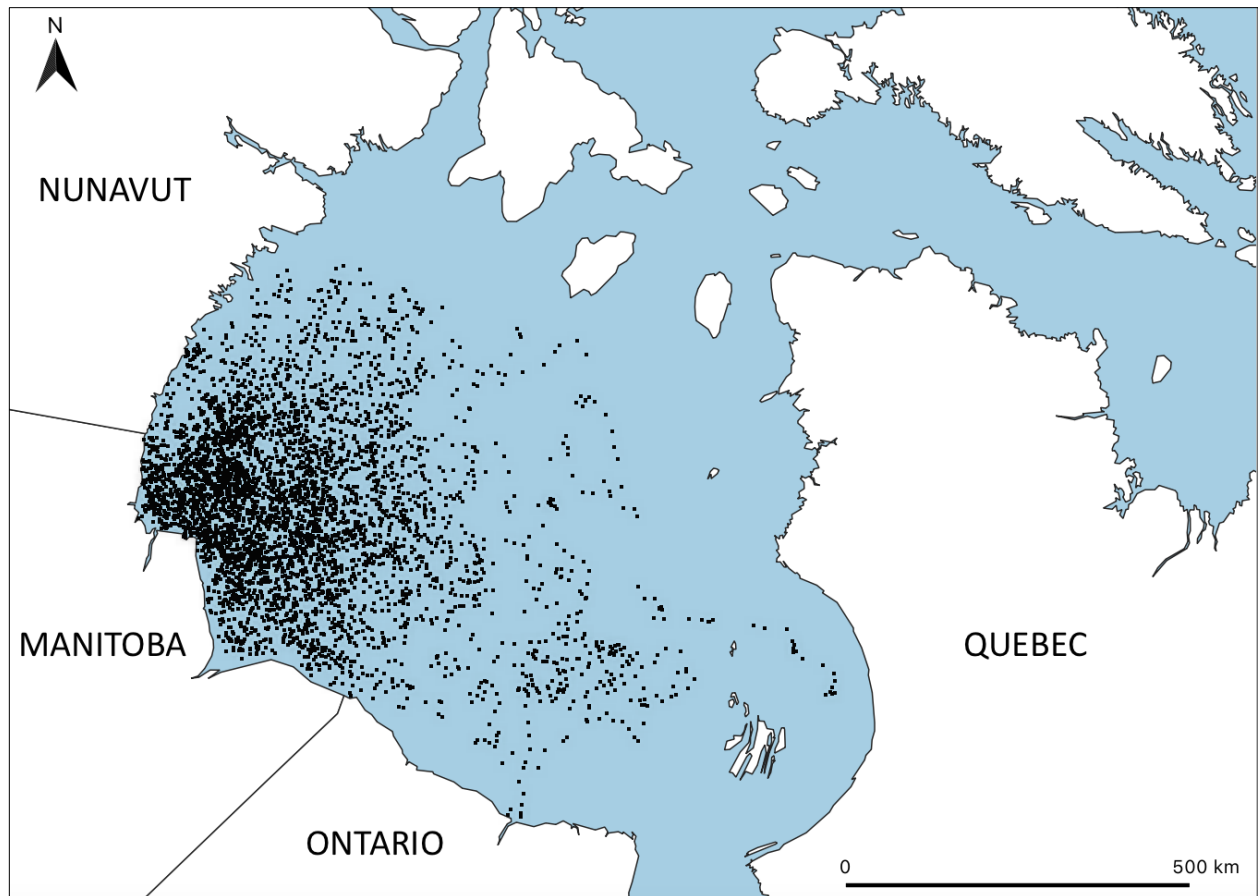


Figure 3.1 Map of study area, showing western Hudson Bay, Manitoba, Canada and adjacent provinces. Black points show the telemetry locations used in our study.

Chapter 4: Conclusion

Individual variation shapes movement dynamics in many species (Merrick & Koprowski 2017, Shaw 2020). However, the relative influence of individual and environmental factors on movement often depends on the stability of a species' environment. For animals in dynamic habitats such as Arctic sea ice, the impact of individual factors can be minimized by all animals having to navigate their environment, causing them to adapt by using similar foraging, habitat selection and energy conservation strategies (Yoshimura & Clark 1991). In some species, however, the effects of individual factors on movement can still be detectable in dynamic environments. These species often have high sexual dimorphism (Rubollini 2004, Saino et al. 2010), sex-specific mating behaviour (Van Dam et al. 2008, Widmann et al. 2015), lack of experience in juveniles (Smereka 2021), alternate space use strategies for parents protecting their offspring (Edwards et al. 2013), and differences in individual personality (e.g., boldness levels – Fraser et al. 2001, Spiegel et al. 2017). Polar bears as a species possess many of the above characteristics (Ramsay and Stirling 1986, Derocher et al. 2005, Pilfold et al. 2017, Johnson et al. 2020). Accordingly, I found that biological factors influenced most aspects of movement examined for polar bears in western Hudson Bay.

I found that movement patterns varied by individual. This result uncovered an understudied aspect of polar bear movement ecology. Within-individual variation is not always included in polar bear movement studies, because their large home ranges and challenges associated with Arctic fieldwork, result in few individuals with repeated. Nonetheless, studying within-individual variation in polar bears may lead to a greater understanding of the species' ecology, especially in subpopulations occupying seasonal ice ecoregions. Because polar bears are a solitary species, their migratory behaviour is more likely to exhibit individual variation

compared to group-living species (Cherry et al. 2016, Westley et al. 2018). My two studies confirm past findings that home range and migration timing of polar bears in western Hudson Bay differed by individual (McCall et al. 2015, Cherry et al. 2016), and show that the including individual identity in movement models can improve measures of site fidelity (Chapter 2), as well as speed and path tortuosity in polar bears (Chapter 3).

I suggest four processes that may underlie the observed movement variation between individuals and merit future research. First, in species with long-term parental care, offspring often learn foraging routes and hunting strategies from their parents (Hoppitt et al. 2008, Thornton & Raihani 2010, Uomini et al. 2020). Polar bear offspring usually stay their mothers for up to 2.5 years in western Hudson Bay (Ramsay & Stirling 1982), and up to three and a half years in other subpopulations (Messier et al. 1994). Studies on ursids have shown that parental transmission of knowledge from mother to offspring influences foraging behaviour in black bears (*U. americanus*) (Breck et al. 2008, Hopkins 2013, Mazur & Seher 2008) and habitat selection in grizzly bears (*U. arctos*) (Morehouse et al. 2016). A few examples of parental transmission of knowledge exist in polar bears, such as the transmission of denning site fidelity from mothers to daughters in the Barents Sea subpopulation (Zeyl et al. 2010), mother-cub transmission of on-shore behaviour in the southern Beaufort Sea subpopulation (Lillie et al. 2018), and mother-daughter transmission of habitat selection in Svalbard (Brun et al. 2021). However, no studies examine whether parental behaviour influences their offspring's degree of on-ice site fidelity or selection of specific sea ice features for hunting. Second, individual size and body condition can influence animal foraging movements and migratory behaviour. For example, animals with a lower body condition may select habitat patches with higher energetic costs of travel or higher levels of predation, but more foraging opportunities (Brodersen et al.

2008, Shaw 2020). Body size also affects the maximum distance travelled during migration in many species (Hein et al. 2012). Body condition had no influence on the swimming frequency and movement dynamics of polar bears (Pilfold et al. 2017, Bohart et al. 2021). However, variation in body condition has been hypothesized to affect timing of migration as polar bears, as lower body conditions could influence individuals' decision to remain longer on the sea ice at break-up (Cherry et al. 2016). Third, differing levels of boldness can affect home range size (Carazo et al. 2014, Ward-Fear et al. 2018), degrees of site fidelity (ZepLin et al. 2007, Harris et al. 2020), and migration timing (Chapman et al. 2011, Hoch et al. 2019). Studies showing evidence of individual differences in boldness have been conducted on black bears (Myers et al. 2018, Hertel et al. 2019) and grizzly bears (Found & St Clair 2018). Boldness studies in polar bears are limited to captive animals (Linder et al. 2020) and human-wildlife conflict situations (Miller et al. 2023). In the Arctic, differences in polar bear boldness are suggested by individual bears covering exceptional distances (Johnson et al. 2017). Further studies quantifying boldness levels in polar bears may offer new insights on the processes underlying polar bear in the movement dynamics of these species. Finally, individual variation between bears could be linked to the adoption of specialized foraging strategies. Sympatric specialization in habitat selection was found in the Svalbard polar bear subpopulation, where groups of polar bears selected either nearshore or pelagic ice (Mauritzen et al. 2001, Lone et al. 2013). Isotopic analyses revealed the two groups of bears occupied different foraging niches (Rogers et al. 2015). Individual differences in polar bear speed, path tortuosity, and seasonal range size for polar bears in western Hudson Bay may be indicative of differences in habitat selection, where bears' movements change as they navigate different areas of the sea ice (Johnson et al. 2019). While the dynamism of western Hudson Bay's sea ice may hinder the development highly specialized habitat

selection as seen in Svalbard, it is possible that individual bears have adopted specific foraging strategies, but this remains to be investigated.

Sex, reproductive status and age class also affected most of the movement dynamics analysed in my second data chapter. Movement differences related to sex, age and reproduction can be caused by a variety of underlying processes. First, differences in size and mass of males, females and subadults can affect movement rates (Heglund & Taylor 1988, Pagano et al. 2018). Second, differences in each class's specific characteristics can lead to variation in habitat selection, which can show up as differences in movement dynamics. For example, females with offspring may have higher resource requirements due to high costs of lactation (Molnár et al. 2010) and increased fasting periods due to denning (Atkinson et al. 1995), leading to them selecting habitat patches with higher prey density (Reimer et al. 2019, Nafus et al. 2022); alternatively, they may show preference for areas with higher sea ice concentrations to limit locomotion costs and avoid open water for the safety of their cubs (Blix & Lenfer 1979, Pilfold et al. 2017). Third, inter-individual interactions can also affect habitat selection: other bears may be avoiding areas frequented by males to prevent possible competition and cannibalizing of cubs, which has been suggested to explain selection patterns in the Beaufort Sea subpopulation (Johnson et al. 2020). Moreover, the focus of males on mating in the second half of the ice season can lead to them change their movement patterns, which has been observed in the Baffin Bay and East Greenland subpopulations (Laidre et al. 2013, Wilson et al. 2022). All three processes can result in differences in speed, path tortuosity, and seasonal range sizes in animals.

My results offer varying support for the first two processes detailed above, and limited evidence for the third. Physiological differences between polar bear classes were primarily shown through their speeds, as larger males were slower and lighter subadults and solitary

females had faster walking speeds. Differences in habitat selection due to differing class characteristics were mainly suggested by the slower walking speed of females with offspring, smaller some range sizes in more inexperienced subadults, and straighter paths exhibited by females with winter cubs and 2-year-olds that suggest different habitat selection patterns for offspring protection. However, this last result needs to be confirmed by further study as cubs of the year and yearlings did not exhibit lower path tortuosity than other bears.

In contrast, I found limited evidence that intra-population dynamics affect polar bear on-ice movement in western Hudson Bay. As polar bears are a solitary species, most interactions between individuals occur during the ice-free season (Latour et al. 1981, Obbard et al. 2016) and mating season (Ramsay & Stirling 1988). The lack of differences in path tortuosity between males, solitary females, and subadults suggest that males do not search smaller areas for females, as seen in the Baffin Bay and East Greenland subpopulations (Laidre et al. 2013, Wilson et al. 2022), and suggests no specific movement strategy aimed at avoiding conspecifics during the rest of the ice season.

My two data chapters offer insights into individual characteristics that affect each bear's decision process in selecting on-ice features for polar bears. I have offered possible physiological and behavioural processes linking those individual characteristics and resulting movement patterns, but due scale of my two studies, the mechanisms involved remain unclear. The environmental variables I used were mainly proxies for more complex sea ice metrics (e.g., the date of sea ice breakup was used as a proxy for changes in overall sea ice concentration – Etkin 1991). I suggest that, in addition to accounting for sex and individual identity (in addition to age and reproductive status, which are more commonly included variables), future studies on polar bear movement couple those variables with finer-scale environmental features, such as sea ice

concentrations around individual telemetry locations. Finally, I recommend expanding the study of individual variation to other polar bear subpopulations. More stable environmental conditions (e.g., lower sea ice drift, more landfast ice or a longer ice season) may lead to individual factors having different impacts on polar bear movement compared to western Hudson Bay. As movement data is still lacking in many polar bear subpopulations (Hamilton et al. 2018), research efforts should be focused on gathering this data in arctic regions with distinct sea ice conditions (Vongraven et al. 2012, 2018).

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Appendices

Appendix A: Effect of interval time between telemetry locations on speed and path tortuosity for polar bears in western Hudson Bay. Line plots (Fig. A1) and linear regressions (Table A1) showing the effect of differing telemetry intervals on bear speed and path tortuosity are shown below. We sampled 4 bears with GPS collars that transmitted locations at 4-hour intervals. We then extracted 132 consecutive locations with no location gaps from each bear, and rarefied this data to locations separated by 8, 12, 24, 48, 72, 96, 120, 144 and 168-hour intervals. We calculated the average speed between consecutive locations and path tortuosity over all locations for the original and rarefied versions of each bear's telemetry data. Values were then averaged by time interval and over all bears.

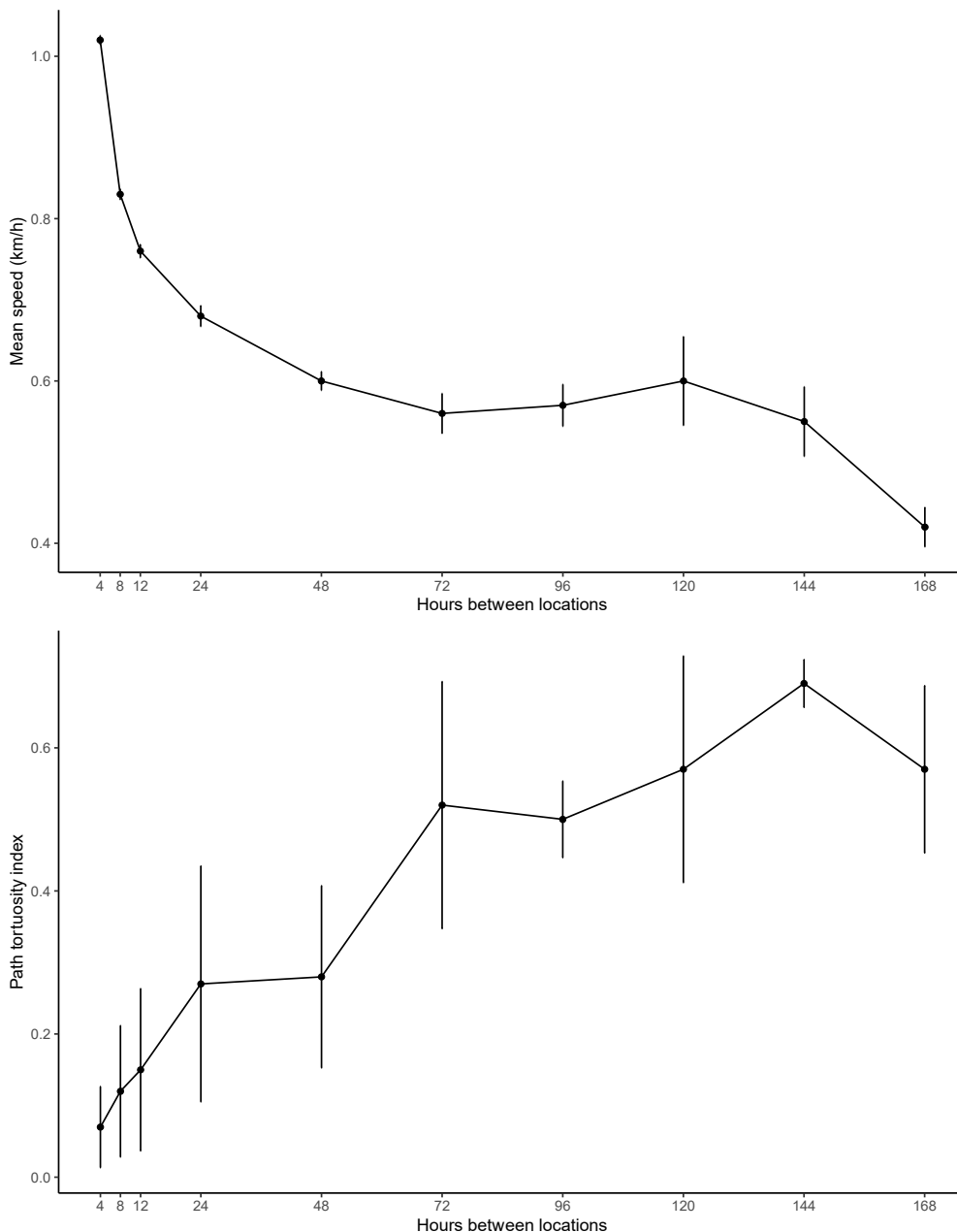


Fig. A1. Line plot showing the effect of differing telemetry intervals on speed between consecutive locations (top) and path tortuosity over all locations (bottom) for polar bears in western Hudson Bay. Each point represents an average over all 4 bears, and vertical lines associated with each point represent the standard error.

Table. A1. Summary of linear regression models showing the effect of differing telemetry location intervals on average speed between locations and path tortuosity index for polar bears in western Hudson Bay.

Metric	Estimate	Standard Error	t-value	p-value
Daily speed	-0.0024	0.00056	-4.23	0.0029
Path tortuosity index	0.0034	0.00047	7.38	<0.0001

Appendix B. Effects of sample size on the mean daily speed and path tortuosity of polar bears in western Hudson Bay. Telemetry data from 176 bears collared between 2004 and 2021 was used for the following tests. We separated our telemetry data into Early Season data and Late Season data depending on the date of the locations (Early Season and Late Season refer to the first and second half of the ice season, respectively). We then extracted the maximum number of consecutive locations separated by no more than 24-hour gaps within each bear per and in each season. For each of those groups of locations, we calculated the mean daily speed (i.e., speed between consecutive locations) and path tortuosity index. We conducted linear regression tests to determine the effect of the number of locations used on these two metrics, revealing a significant negative relationship (Fig. B1, Table B1).

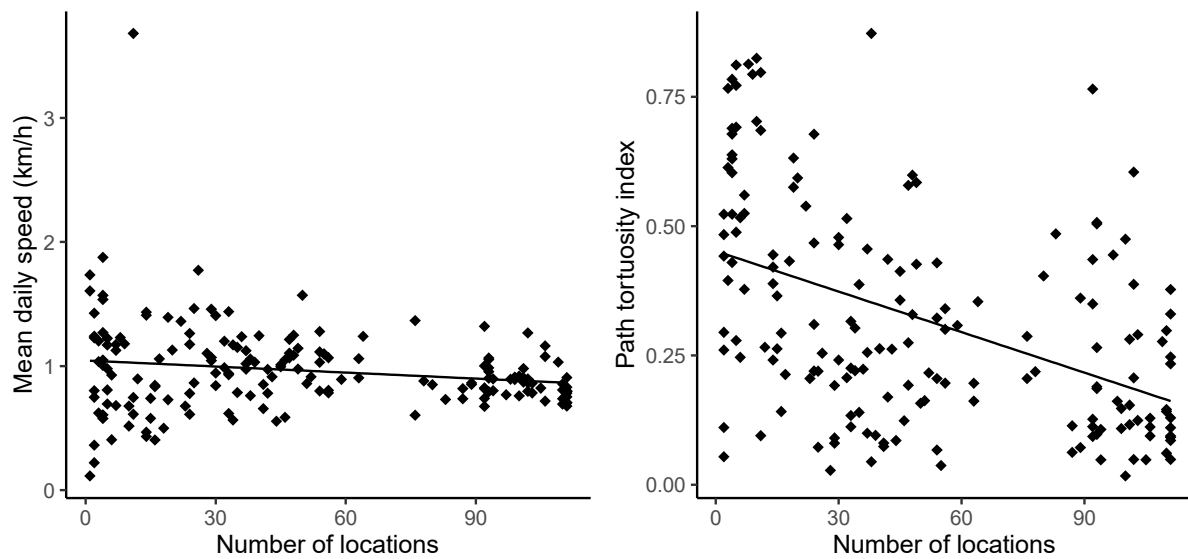


Fig. B1. Scatterplots showing the mean daily speed (left) and path tortuosity index (right) as a function of the number of telemetry locations used per bear. Locations are separated by 24-hour gaps. Each plot represents values for an individual bear within a season.

Table. B1. Summary of linear regressions showing the effect of the number of locations used to compute the average speed and path tortuosity index for polar bears in western Hudson Bay. Significant results are bolded.

Metric	Estimate	Standard Error	t-value	p-value
Daily speed	-0.0016	0.00070	-2.33	0.021
Path tortuosity index	-0.0026	0.00039	-6.77	<0.0001

Appendix C: Effect of sea ice drift on daily speed and path tortuosity for polar bears in western Hudson Bay, Manitoba. Mean daily speed and path tortuosity indices were calculated for all bears used in this chapter with the effect of sea ice drift removed, and a second time with no removal of drift. To remove drift, we obtained daily sea ice drift vectors in Hudson Bay using Polar Pathfinder Daily 25 km EASE-Grid Sea Ice Motion Vectors (National Snow and Ice Data Center – CO, USA) converted into *netCDF* format. We then subtracted those drift vectors from the bears' movement vectors. We compared speed and path tortuosity with drift present vs with drift removed using a paired t-test (Figure C1, Table C1).

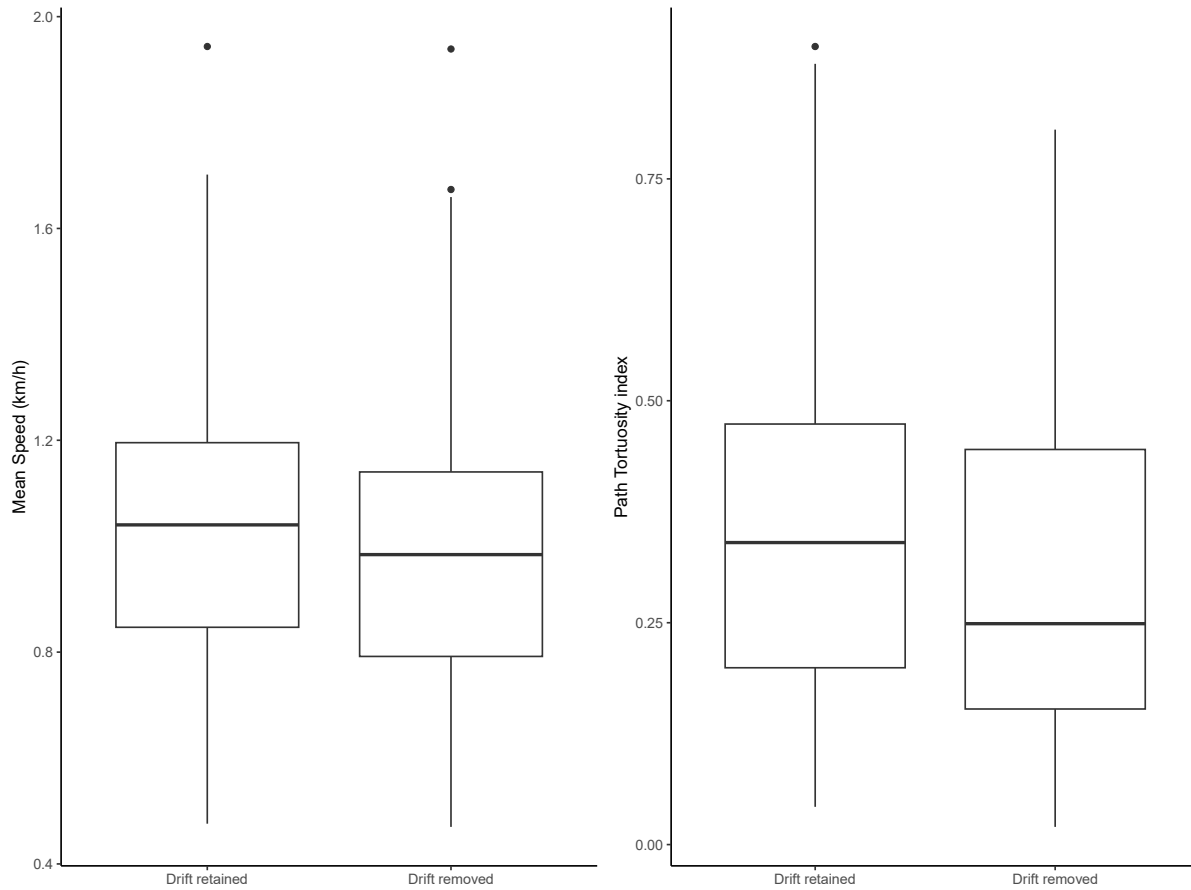


Fig. C1. Boxplot showing the mean daily speed (left) and path tortuosity index (right) of western Hudson Bay polar bears when the effect of sea ice drift is unaccounted for vs. when it is removed.

Table C1. Summary results of paired t-test comparing the mean daily speed and path tortuosity of polar bears western Hudson Bay polar bears when the effect of sea ice drift is unaccounted for vs. when it is removed. Significant results are bolded.

Metric	t-value	Degrees of freedom	p-value
Mean daily speed	7.69	109	<0.0001
Path tortuosity index	4.37	109	<0.0001

Appendix D. Summary values for the mean daily speed (km/h) of polar bears in western Hudson Bay, Manitoba, Canada. Values are shown by sex and age class and during each half of the ice season. Early Season and Late Season refer to the first and second half of the ice season, respectively. Range: minimum value – maximum value; SE = standard error; n=number of bears in each class.

Season	Class	Mean	Range	SE	n
Early Season	Subadults	1.30	0.91 - 1.50	0.19	7
	Adult Males	1.10	1.00 - 1.10	0.032	2
	Solitary Adult Females	1.80	1.70 - 1.90	0.2	2
	Females with winter cubs	1.20	0.70 - 1.70	0.21	24
	Females with yearlings	1.20	0.98 - 1.40	0.15	8
	Females with 2-year-olds	1.40	NA	NA	1
	All bears	1.30	0.70 - 1.90	0.073	44
Late Season	Subadults	1.00	0.54 - 1.20	0.19	12
	Adult Males	0.89	0.48 - 1.20	0.22	12
	Solitary Adult Females	1.10	0.83 - 1.30	0.18	9
	Females with spring cubs	0.79	0.55 - 1.00	0.14	8
	Females with yearlings	0.88	0.54 - 1.30	0.21	20
	Females with 2-year-olds	0.83	0.72 - 0.89	0.069	5
	All bears	0.92	0.48 - 1.30	0.056	66
Full Ice Season	Subadults	1.10	0.54 - 1.50	0.24	19
	Adult Males	0.92	0.48 - 1.20	0.21	14
	Solitary Adult Females	1.20	0.83 - 1.90	0.33	11
	Females with spring cubs	0.79	0.55 - 1.00	0.14	8
	Females with winter cubs	1.20	0.70 - 1.70	0.21	24
	Females with yearlings	0.96	0.54 - 1.40	0.24	28
	Females with 2-year-olds	0.92	0.72 - 1.40	0.23	6
	All bears	1.00	0.48 - 1.90	0.056	110

Appendix E. Summary values for the path tortuosity index of polar bears in western Hudson Bay, Manitoba, Canada. Values are shown by sex and age class and during each half of the ice season. Higher values are associated with lower path tortuosity. Early Season and Late Season refer to the first and second half of the ice season, respectively. Range: minimum value – maximum value; SE = standard error; n=number of bears in each class.

Season	Class	Mean	Range	SE	n
Early Season	Subadults	0.26	0.056 - 0.48	0.14	7
	Adult Males	0.29	0.25-0.32	0.045	2
	Solitary Adult Females	0.23	0.20-0.26	0.045	2
	Females with winter cubs	0.49	0.17-0.90	0.18	24
	Females with yearlings	0.39	0.16-0.49	0.1	8
	Females with 2-year-olds	0.73	NA	NA	1
	All bears	0.33	0.056-0.9	0.059	44
Late Season	Subadults	0.32	0.13-0.59	0.15	12
	Adult Males	0.26	0.042-0.87	0.23	12
	Solitary Adult Females	0.29	0.098-0.47	0.14	9
	Females with spring cubs	0.31	0.056-0.64	0.2	8
	Females with yearlings	0.33	0.085-0.76	0.2	20
	Females with 2-year-olds	0.51	0.23-0.88	0.32	5
	All bears	0.34	0.042-0.88	0.065	66
Full Ice Season	Subadults	0.3	0.056-0.59	0.14	19
	Adult Males	0.27	0.042-0.87	0.21	14
	Solitary Adult Females	0.28	0.098-0.47	0.13	11
	Females with spring cubs	0.31	0.056-0.64	0.2	8
	Females with winter cubs	0.49	0.17-0.9	0.18	24
	Females with yearlings	0.35	0.085-0.76	0.18	28
	Females with 2-year-olds	0.55	0.23-0.88	0.3	6
	All bears	0.36	0.042-0.90	0.056	110

Appendix F. Summary values for the home range size (km²) of polar bears in western Hudson Bay, Manitoba, Canada. Values are shown by sex and age class and during each half of the ice season. Early Season and Late Season refer to the first and second half of the ice season, respectively. Range: minimum value – maximum value; SE = standard error; n=number of bears in each class.

Season	Class	Mean	Range	SE	n
Early Season	Subadults	30000	2400 - 57000	17000	7
	Adult Males	19000	17000 - 20000	2200	2
	Solitary Adult Females	68000	50000 - 87000	26000	2
	Females with winter cubs	40000	8800 - 82000	16000	24
	Females with yearlings	33000	22000 - 55000	11000	8
	Females with 2-year-olds	71000	NA	NA	1
	All bears	38000	2400 - 87000	8700	44
Late Season	Subadults	13000	5500 - 27000	7400	12
	Adult Males	11000	1500 - 25000	6800	12
	Solitary Adult Females	16000	6300 - 31000	7700	9
	Females with spring cubs	16000	5400 - 37000	10000	8
	Females with yearlings	13000	4400 - 29000	6900	20
	Females with 2-year-olds	14000	10000 - 18000	2900	5
	All bears	14000	1500 - 37000	2300	66
Full Ice Season	Subadults	19000	2400 - 57000	14000	19
	Adult Males	12000	1500 - 25000	6900	14
	Solitary Adult Females	25000	6300 - 87000	24000	11
	Females with spring cubs	16000	5400 - 37000	10000	8
	Females with winter cubs	40000	8800 - 82000	16000	24
	Females with yearlings	19000	4400 - 55000	12000	28
	Females with 2-year-olds	24000	10000 - 71000	23000	6
	All bears	22000	1500 - 87000	6400	110

Appendix G. Summary values for migration dates of polar bears in western Hudson Bay, Manitoba, Canada. Values are shown by sex and age class. On-ice departure are expressed as the number of days after sea ice freeze up, while on-land arrival dates are expressed as number of days after sea ice breakup. Range: minimum value – maximum value; SE = standard error; n=number of bears in each class.

Migration metric	Class	Mean	Range	SE	n
On-ice departure date	Subadults	12.30	5-19	7.02	3
	Adult males	7.33	4-13	4.93	3
	Solitary adult females	5.75	1-13	4.10	8
	Females with winter cubs	6.84	1-16	4.33	31
	Females with yearlings	6.82	1-20	4.65	17
	All bears	6.98	1-20	4.57	62
On-land arrival date	Subadults	40.4	21 - 60	13.10	8
	Adult males	43.5	16 - 55	10.10	11
	Solitary adult females	43.4	26 - 51	9.94	5
	Females with spring cubs	44.8	18 - 72	13.60	20
	Females with yearlings	49.0	29 - 75	11.90	14
	All bears	37.7	14 - 55	14.40	68