Habitat use and movement ecology of polar bears (*Ursus maritimus*)

in western Hudson Bay

by

Alexandra Marie Claire Beatty

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ABSTRACT

Climate change is altering sea ice phenology, which forces polar bears (*Ursus maritimus*) to spend an increasing amount of time on land. Therefore, understanding movement ecology and terrestrial habitat selection of bears may become increasingly important for conservation planning. The Western Hudson Bay polar bear population spends ice-free summer months on land. While onshore, terrestrial feeding is minimal, and movements are limited to conserve energy. When the ice-free period ends, bears migrate onto newly forming sea ice. Our research objective was to assess terrestrial movement rate, tortuosity, directionality, habitat selection, and site fidelity of adult female polar bears on land during the ice-free period with locations from satellite-linked telemetry collars deployed on 106 adult female polar bears (2004-2017). The movements of females occupying two different regions were examined to assess the influence of biological and environmental correlates. Individual females had varied movement patterns: 35% moved inland (mean distance from coast = 36 km) before they returned to the coast during freeze-up, 51% of females remained near the coast (mean distance from coast = 11 km), and 14% did not fall into either category. Both interior and coastal females exhibited high path tortuosity possibly reflecting energy conservation, terrestrial feeding, and/or conspecific avoidance. Terrestrial movement rate (mean = 0.15 km/h, range: 0.0-6.25 km/h) was influenced by bear age, windspeed, time of day, days since ice breakup, and distance to coast. Movement rate increased with bear age, presence of daylight, and when bears were closer to the coast, but decreased with increased windspeed. By October, movement rate reached a minimum (mean = 0.08 km/h) and then increased during freeze-up (mean = 0.21 km/h) when bears migrated onto the sea ice. Habitat selection was investigated using telemetry locations from 122 females in 2004-2017 and land cover classes from a high-resolution terrestrial ecosystem map. A resource selection function with Akaike Information Criterion model selection was used to evaluate terrestrial habitat selection within Wapusk National Park, Manitoba, Canada. Females preferred freshwater ponds and riparian areas that provide water. At the population level, during the ice-free period (September to October), females avoided the coast. During freeze-up, females selected for the coast during migration to sea ice. Females exhibited regional site fidelity to western Hudson Bay during the ice-free period, but not site-specific fidelity.

PREFACE

This thesis is an original work by Alexandra M. C. Beatty. Data used in this research was acquired from telemetry collars deployed by Dr. A. E. Derocher at the University of Alberta, and Dr. N. J. Lunn at Environment and Climate Change Canada. Dr. A. E. Derocher and Dr. N. J. Lunn provided feedback on thesis content.

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

DEDICATION

To my recently departed uncle, grandfather, and grandmother, who are no longer here to see me graduate.

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CHAPTER 1 – General Introduction

Movement ecology is fundamental to the study of mobile species. Investigating individual movements to understand why and where animals move can provide insight into aspects of ecology of a species including: behaviour, foraging and resource availability, dispersal, and disease transmission (Nathan et al. 2008; Gurarie et al. 2016; Seidel et al. 2018). With advancements in telemetry technology, methods to study animal movement ecology have changed rapidly (Tomkiewicz et al. 2010; Kays et al. 2015). High resolution spatiotemporal telemetry data allows researchers to investigate animal movements on a scale not previously possible (Nathan et al. 2008; Gurarie et al. 2016; Seidel et al. 2018). Additionally, advancements allow telemetry data to be collected frequently and remotely, which is especially relevant for species that are difficult to monitor, such as polar bears (*Ursus maritimus*).

Polar bears are widespread across the Arctic in 19 populations (Hamilton and Derocher 2019). They are highly specialized apex predators that use sea ice to hunt ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*), their primary prey (Smith 1980; Stirling and Derocher 1993; Thiemann et al. 2008). The habitat of polar bears differs widely among populations. Some populations in the high Arctic remain and hunt on sea ice all year (Derocher et al. 2004), while the ice in other parts of the Arctic undergo large seasonal changes that result in migration onto land with associated fasts (Derocher and Stirling 1990; Messier et al. 1992; Born et al. 1997; Mauritzen et al. 2003a).

In western Hudson Bay, sea ice is seasonal, limiting the availability of primary prey to the on-ice period (Stirling et al. 1993; Derocher et al. 2004; Thiemann et al. 2008; Cherry et al. 2013). During the summer ice-free period, bears decrease activity to conserve energy (Latour

1981; Lunn and Stirling 1985; Derocher and Stirling 1990). Fat stores deposited while hunting in spring sustain polar bears throughout summer, augmented by scavenging, opportunistic hunting, or terrestrial foraging (Russell 1975; Derocher and Stirling 1990; Rode et al. 2015), although the energetic gains from terrestrial feeding are minimal (Rode et al. 2015). Although previous studies have investigated polar bear ecology on sea ice (Laidre et al. 2013; Pilfold et al. 2014; Cherry et al. 2016; Biddlecombe et al. 2020), few examined how bears behave in their terrestrial habitat during the ice-free period.

This thesis consists of two data chapters and a general discussion. Chapter Two, "Terrestrial movements of adult female polar bears in western Hudson Bay, Canada", describes how we explored terrestrial movement patterns with telemetry data from 2004-2017. A total of 106 females provided >25,000 locations that were analyzed. Movement metrics including speed, tortuosity, and directionality were assessed for females occupying interior or coastal areas within the terrestrial habitat in western Hudson Bay. Females closer to the Hudson Bay coast were expected to exhibit different movement patterns compared to females who move inland during the ice-free period. We investigated the relationship between biological, environmental, temporal, and spatial factors and movement rate. We anticipated that females would change their movement patterns in response to external conditions over the on-land period.

In Chapter Three, "Terrestrial habitat selection by adult female polar bears and site fidelity in western Hudson Bay, Canada", our research objective was to assess seasonal habitat selection and site fidelity of females on land during the ice-free period. A total of 122 females provided >50,000 telemetry locations used to assess terrestrial habitat selection during July to December, 2004-2017. We expected females to select different land cover classes and inland areas that would vary over the on-land period. Females were predicted to exhibit high site-fidelity when returning to their terrestrial habitat. This research summarizes how polar bears use their terrestrial environment during the ice-free period, thereby informing future management.

Chapter Four provides an overview of this thesis, as well as management implications and possible areas of future research.

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CHAPTER 2 - Terrestrial movements of adult female polar bears in western Hudson Bay, Canada

INTRODUCTION

Animal movement is a behavioural response to internal and external influences (Andrewartha and Birch 1954; Fahrig 2007; Gurarie et al. 2009). Movement may be affected by resource availability (Esslinger et al. 2014), sex (Pusey 1987), reproductive status (Blanchard and Knight 1991), environmental signals (Moore and Crimaldi 2004; Celesia et al. 2010), climate, and weather (Aublet et al. 2009; van Beest et al. 2012; Esslinger et al. 2014; Sassi et al. 2015). Movement is also influenced by benefits and costs (Johnson and Gaines 1990; Larsen and Boutin 1994). Resource intake can benefit from movement, but are offset by energetic costs. Animals may also face increased predation risk when moving (Van Vuren and Armitage 1994; Gustine et al. 2006; Bonte et al. 2012), which is further elevated during parental care (Pinshow et al. 1977; Bergerud and Page 1987; Côté 2000). Analyzing animal movement patterns can provide insights into how internal and external factors influence movement behaviour (Schick et al. 2008; Gurarie et al. 2009).

When temporal variation in resources exist, and food is only seasonally available, animals may move in response (Dingle and Drake 2007). Predator movements may change if their diet is seasonally variable (Bowen 1981; Lingle 2000) or if they follow prey movements (Parker 1973; Durant et al. 1988; Hofer and East 1993; Quinn et al. 2014). Alternatively, carnivores may switch prey if their primary prey is unavailable (Murdoch 1969). In northern latitudes, high variation in resources often forces species to migrate (Fancy et al. 1989; Avgar et al. 2014; Hauser et al. 2017) or to fast to conserve energy (Buck and Barnes 1999; Robbins et al. 2012). Arctic sea ice is an especially variable habitat, with high seasonal variation in resource abundance, that many marine mammals depend upon and have adapted to (Laidre et al. 2008).

Polar bears (*Ursus maritimus*) are adapted to live on sea ice where they hunt seals (Stirling and McEwan 1975; Smith 1980; Thiemann et al. 2008), mate (Ramsay and Stirling 1986), and travel (Larsen 1986; Mauritzen et al. 2001). On the sea ice, polar bear annual home range sizes are significantly larger than terrestrial mammals of similar size (Ferguson et al. 1999). Female polar bear movement rates vary by reproductive status, offspring mobility, and need to reduce negative conspecific interactions (Stirling et al. 1993; Parks et al. 2006; Freitas et al. 2012; McCall et al. 2015). While on sea ice, bears respond to prey availability and sea ice dynamics (Mauritzen et al. 2003b; Durner et al. 2017). Energy intake occurs primarily during spring seal pupping season (Stirling and Øritsland 1995; Pilfold et al. 2012) and energy stored in adipose tissue is available for use when seals are not accessible (Ramsay and Hobson 1991; Messier et al. 1992; Atkinson and Ramsay 1995). Polar bear movement patterns vary by season (Garner et al. 1990; Ferguson et al. 2000) and among populations as a response to differences in sea ice phenology (Messier et al. 1992; Born et al. 1997; Mauritzen et al. 2003a; Durner et al. 2017). In five of 19 populations, sea ice melts completely in summer. As a consequence, bears migrate onshore and fast for an extended period (Ferguson et al. 1997; Amstrup et al. 2006; Rode et al. 2015c; Sahanatien et al. 2015).

When Hudson Bay becomes ice-free, bears migrate to shore, and remain on land until sea ice forms again (Latour 1981; Derocher and Stirling 1990; Stirling et al. 1993; Towns et al. 2010). Fasting depletes polar bears' fat stores during the ice-free period (Arnould and Ramsay

1994; Derocher and Stirling 1995; Pilfold et al. 2016). To conserve energy, bears reduce movements until sea ice forms again in late autumn (Latour 1981; Derocher and Stirling 1990; Stirling and Parkinson 2006). Although some polar bears may forage while onshore (Russell 1975; Derocher et al. 1993; Gormezano and Rockwell 2013), terrestrial foods are low in energy in comparison to seals (Ramsay and Hobson 1991; Rode et al. 2015b; Pilfold et al. 2016).

During the ice-free period, bears segregate spatially. Males remain near the coast, while females with offspring or who are pregnant move inland (Stirling and Archibald 1977; Latour 1981; Derocher and Stirling 1990). Use of inland habitats reduces interactions with potentially infanticidal males (Derocher and Stirling 1990; Stirling et al. 1993; Stirling et al. 2004). Females move inland to their preferred denning habitat (Lunn et al. 2004; Richardson et al. 2005), which may also provide shelter to non-reproductive bears (Jonkel et al. 1972; Clark et al. 1997). Differing spatial patterns during movement inland may also be a result of females imprinting inland areas on their offspring as suitable denning habitat (Derocher and Stirling 1990; Scott and Stirling 2002; Parks et al. 2006).

Our objective was to use satellite telemetry to examine terrestrial movements (movement rate, tortuosity, and directionality) of Western Hudson Bay adult female polar bears in relation to biological, environmental, temporal, and spatial factors. We investigated spatial distribution of adult females to compare movements early and late in the ice-free period. We hypothesized females that move inland would exhibit more tortuous movement patterns than those which stayed closer to the coast because of movement through complex terrain and reduced conspecific encounters. We also examined (1) the relationship between bear age and reproductive status and movement rate, (2) whether movement rate was influenced by ambient temperature, precipitation, and windspeed, (3) if movement varied on a diurnal and annual scale, or if movement was affected by length of the ice-free period, and (4) how movement rate varied with distance from the Hudson Bay coast. We tested the hypothesis that change in polar bear movement rate was most significantly influenced by biological and environmental factors when compared to temporal and spatial variables. We predicted polar bear movement rate to decrease for females with two cubs and during periods of higher temperatures.

METHODS

Study area

The study area in western Hudson Bay was centered in Manitoba and included parts of Ontario, and Nunavut (Figure 2.1). The area is characterized as a transitional zone between the boreal forest and Arctic tundra (Ponomarenko et al. 2014). Fens, bogs, lakes, ponds, and rivers cover 41-50% of the inland areas (Ritchie 1960; Bello and Smith 1990). Inland areas are characterized by black spruce (*Picea mariana*), white spruce (*P. glauca*), larch (*Larix laricina*), willow (*Salix* spp.), and lichen tundra (Ritchie 1960). Coastal areas include intertidal flats, beach ridges, unvegetated areas that are frequently flooded with water and vegetated areas dominated by fen species (Ponomarenko et al. 2014).

Ice freeze-up begins in October to December and extends to its maximum in late winter (February to March) (Maxwell 1986; Prinsenberg 1988; Saucier et al. 2004; Gagnon and Gough 2005). Breakup begins in spring (May) with the summer and autumn ice-free (Maxwell 1986; Prinsenberg 1988; Saucier et al. 2004; Gagnon and Gough 2005). Mean temperatures in Churchill, Manitoba throughout the ice-free period range from -25°C to 17°C based on

Environment and Climate Change Canada's hourly weather records (www.climate.weather.gc.ca).

Capture and collar deployment

Adult female polar bears (≥5 years old) were captured and collared near Wapusk National Park, Manitoba during the ice-free period in 2004-2017 as part of ongoing, long-term research on the ecology of Western Hudson Bay polar bears (e.g., Ramsay and Stirling 1988; Derocher and Stirling 1995; Stirling et al. 1999; Regehr et al. 2007; Lunn et al. 2016). Satellite-linked global positioning system (GPS) collars (Telonics, Mesa, AZ) were programmed to provide one location every 4 h and were accurate to ca. 31 m (Tomkiewicz et al. 2010). Collars could not be deployed on males because their necks are wider than their heads. Location data collected within five days of collar deployment were excluded in order to allow immobilized bears to fully recover and for movement rates to be representative of those of fully recovered animals (Thiemann et al. 2013; Rode et al. 2015a). Bear age was estimated either by counting annuli in a vestigial premolar for adults or by tooth emergence patterns for dependent offspring (Calvert and Ramsay 1998). At capture, sex and reproductive status (female with cubs-of-the-year ca. 10 months old (COY), or yearlings ca. 22 months old (YRLG)) were recorded. Each female was assigned a unique bear identification number (bear ID). Animal capture and handling was conducted in accordance with the Canadian Council on Animal Care guidelines (www.ccac.ca) and approved by the University of Alberta BioSciences Animal Care and Use Committee.

Tortuosity movement metrics

Metrics that characterize adult female polar bear movement were calculated in R (R Core Team 2019, v 3.6.2) and included: speed, straightness index, turning angle, bearing, and distance to coast. Step-lengths between consecutive locations 4 h apart estimated speed (km/h). Daily straightness index (ST) was calculated as ST = D/L, where D = the Euclidian distance (km) between beginning and end point of a path, and L = the sum of the step-lengths within the 24 h moving window. Straightness index values close to 1 represent a straight path, whereas values <1 are more tortuous. Turning angle was calculated as the trajectory change (-180° to 180°) between consecutive telemetry locations. For analysis, turning angles were converted to absolute values (0° to 180°) (Ironside et al. 2017; Yee et al. 2017). Bearing was calculated as the orientation between sequential telemetry locations to true north (0° to 360° where 0°/360° = north). Distance to coast was calculated as the Euclidian distance (km) from a telemetry location to the closest point along the Hudson Bay coast.

Interior and coastal bears

To assess polar bear spatial ecology based on location, we used a K-means clustering analysis (Hartigan and Wong 1979) in R that divided telemetry locations into clusters based on distance to coast and ordinal date. Distance to coast and ordinal date were scaled, by subtracting the mean and dividing by the standard deviation, and the clustering algorithm assigned each telemetry location a cluster value. The K-means clustering analysis was run 5000 times to increase robustness (Hartigan and Wong 1979). We calculated an overall cluster value for each female by computing the cluster category mode for each telemetry location for individual females. The accuracy of the cluster analysis was visually inspected in QGIS (v. 3.10 Open Source Geospatial Foundation Project). Normality was tested using a Jarque Bera test in the 'tseries' R package (Jarque and Bera 1980). A Mann-Whitney *U* test was used because movement metrics could not be normalised using transformations. The Mann-Whitney *U* test compared speed, straightness index, and turning angle between clusters. A random sample of bearings from both clusters provided equal comparison sample sizes. Rayleigh's test was used to assess uniformity of bearing (Batschelet 1981) and Watson's two-sample test of homogeneity provided a comparison between clusters (Watson 1967).

For bears in the interior cluster, a second K-means clustering analysis was used to separate inland movement from migration movement towards the coast. We calculated switch date to determine when migration to the coast began. Switch date was the date movement behaviour changed from inland movements to directional movement towards the coast. Switch date was calculated as the mean date for the last inland location and the mean date for the first location in the coastal movement cluster using movement metrics and ordinal date (Figure 2.2). Telemetry locations before the switch date were considered inland movement and were considered coastal movement after the switch date. We visually confirmed females moved towards the coast after the switch date using QGIS.

We compared the movement metrics speed, straightness index, and turning angle between clusters using a Wilcoxon signed-rank test (Wilcoxon 1945). A rank test was used because a Jarque Bera test revealed the movement metrics were non-normally distributed and could not be normalized. Rayleigh's test was used to characterize uniformity of bearing for both inland movement and coastal movement. Locations were converted to categorical data where bearing was categorized into north, east, south, and west based on degrees (north = ≥315° and ≤45°, east = >45° and ≤135°, south = >135° and ≤225, and west = >225° and <315°). A two-sample test for equality of proportions without continuity correction was used to compare between inland and coastal movement for bearing. We used an alpha level of 0.05 and all results are median ± 1 standard deviation unless otherwise indicated.

Movement rate

Locations of collared bears that occurred on Hudson Bay were removed using QGIS to capture on-land locations only. Erroneous coordinates were excluded (<0.005% of locations), such as locations that were implausible based on geographic location (i.e., >400 km away from the study area) and coordinates that yielded speeds >6.25 km/h (25 km between relocation fixes) as a cut-off. Maximum movement rates for polar bears with four hour relocations were ~4 km/h (Andersen et al. 2008), however mean movement rate is considerably lower (~1 km/h) (Durner et al. 2017). Bears exhibit reduced terrestrial movement during the ice-free period (Latour 1981; Derocher and Stirling 1990) and rarely sustain high movement rates (Lunn et al. 2004; Parks et al. 2006; Pagano et al. 2018). Temperature and climate data were obtained from Environment and Climate Change Canada's hourly weather records from Churchill, Manitoba weather station (www.climate.weather.gc.ca). Presence or absence of daylight was determined by calculating local sunrise and sunset times employing the 'suncalc' package in R. We excluded telemetry locations from 2009 because fewer bears were collared resulting in substantially fewer locations in that year compared to other years. Data on sea ice breakup was provided by Environment and Climate Change Canada and derived from Special Sensor Microwave/Imager (SSM/I). The mean value from all pixels within the Western Hudson Bay population boundary were used to calculate sea ice concentration (Cherry et al. 2013). We calculated ice breakup date as the first day mean sea ice concentration was <50%. Telemetry locations were used to calculate distance to the Hudson Bay coast in R using the 'geosphere' package.

We fit a truncated regression Tobin model (Tobin 1958) using the 'censReg' package in R to assess the influence of biological, environmental, temporal, and spatial variables (Table 2.1) on movement rate. To avoid collinearity in the model, pair-wise correlations were examined among all variables with Pearson's coefficient $r \geq |0.6|$. We retained the variable with the lower Akaike Information Criterion (AIC) value. Quadratic terms for bear age, yearday, and days since ice breakup were tested in the model using AIC. AIC corrected for small sample sizes was used to identify a top model from a set of candidate models with an AIC_c weight (w_i) > 0.90 (Burnham and Anderson 1998; Henningsen 2010). First, variables were moved in and out of candidate models as biological, environmental, temporal, and spatial sets then individual variables were assessed using AIC_c and combined in candidate models. A random intercept of bear ID and time accounted for a lack of statistical independence since data included repeated observations of individuals across years (Gillies et al. 2006).

To compare movement rate throughout the day, we used a Kruskal-Wallis test, and pairwise comparisons using Wilcoxon rank sum and Bonferroni's correction. A Wilcoxon signed-rank test was used to compare movement rate from September 1 to October 15 and October 16 to December 31. These dates were used based on when movement rates reached a minimum and to compare groups with similar sample sizes. We included only two periods in the analysis because of insufficient location records for bear movement just after sea ice breakup.

RESULTS

Interior and coastal bears

The most parsimonious split yielded two clusters: interior bears and coastal bears. All females had some coastal values, a result of migration movement to and from the coast (Figure 2.2). Each female was assigned as either an interior bear (35%) or a coastal bear (51%) using the mode of cluster values for each location. To ensure consistency within clusters, 15 bears (14%) were excluded from analysis because their paths could not be classified as only interior or coastal. Speed (Mann-Whitney $U = 128{,}699{,}484$, $P < 0.0001$, $n_{interior} = 17{,}545$, $n_{coastal} = 12{,}989$), and straightness index values (Mann-Whitney $U = 111{,}750{,}000$, $P < 0.0001$, $n_{interior} = 16{,}397$, $n_{coastal} = 11{,}888$) were higher for interior bears than for coastal bears (Table 2.2). Coastal bears exhibited higher turning angle values (Mann-Whitney $U = 64{,}832{,}000$, $P < 0.001$, $n_{interior} = 13{,}031$, $n_{coastal} = 10{,}957$; Table 2.2). Bearing was non-uniform for both interior (Rayleigh $Z = 0.0907$, $P < 0.001$, r = 0.9, $n = 12{,}989$) and coastal bears (Rayleigh Z = 0.145, $P < 0.001$, r = 0.8, $n = 12{,}989$), with direction concentrated 340° to 0° or NNW to N (Figure 2.3). There was a significant difference in Watson's non-parametric two-sample test of homogeneity between interior and coastal bears ($U^2 = 4.77$, $P < 0.001$).

Interior bears: inland and coastal movement

The K-means clustering analysis divided interior bear telemetry locations into two clusters based on movement metrics: speed, straightness index, distance to coast, and ordinal date. Excluding turning angle and bearing resulted in the most parsimonious cluster split. The mean switch date from inland movement to coastal movement was October 27 ($n = 37$) with a range from October 5 to November 20 (Figure 2.4). Speed (Wilcoxon signed-rank Z = 1,598,752, n_{inland} = 5472, $n_{coastal}$ = 3,091, $P < 0.0001$) and straightness index values (Wilcoxon signed-rank Z = 1,420,800, n_{inland} = 2891, $n_{coastal}$ = 5,210, $P < 0.0001$), for coastal movement were greater than inland movement (Table 2.3). Inland turning angles were greater than coastal movement turning angles (Wilcoxon signed-rank Z = 1,187,100, n_{inland} = 2,512, $n_{coastal}$ = 4,648, $P < 0.0001$; Table 2.3). The analysis for bearing indicated non-uniform directionality for both inland (Rayleigh Z = 0.0769, $P < 0.001$, r = 0.9, n = 5,509) and coastal movement (Rayleigh Z = 0.1233, $P < 0.001$, r = 0.8 n = 3,054), with direction concentrated from 340° to 0° or NNW to N. The two-sample test for equality of proportions without continuity correction revealed north directional movement occurred more often for the coastal movement cluster (39%) when compared to inland movement (35%) (z = 9.7, $P < 0.001$).

Movement rate

Models investigating movement rate were based on 25,128 locations for 106 adult female polar bears in 2004-2017. We found multicollinearity between temperature, yearday, and days since ice breakup. AIC_c indicated days since ice breakup provided the best model fit. The top model contained bear age, windspeed, presence of daylight, days since ice breakup, and distance to coast as predictor variables (Tables 2.4, 2.5). The AIC_c weight for the top model was 0.85, however the top model was selected because it required fewer parameters (k = 10) than the competing global model (k =15). The only biological factor in the top model was bear age (Table 2.5). Movement rate was higher for younger and older bears and lower for middle-aged bears (Figure 2.5a). Mean female age was 15 years ± 0.03 (range from 5-26). 66 females travelled with one cub and 40 females had two cubs. More females (n = 71) had COY compared to YRLG (n = 35) cubs. An inverse relationship for windspeed and movement rate was included in the top model (Table 2.5, Figure 2.5b). Presence of daylight resulted in increased speed (Table 2.5). Speed increased at 1300 UTC (0.15 ± 2.11 km/h) and 1700 UTC (0.14 ± 2.26 km/h), decreased at 2100 UTC (0.05 ± 1.62 km/h), and were lowest at 0100 UTC (0.01 ± 1.43 km/h), 0500 UTC (0.01 ± 1.42 km/h), and 0900 UTC (0.01 ± 1.44 km/h) (Kruskal-Wallis test, H = 4,219.8, P < 0.0001, Figure 2.6). Pairwise comparison tests using Wilcoxon rank sum and Bonferroni's correction showed that movement rates at 1300 and 1700 were significantly higher than those at other times of the day. Speed and days since ice breakup were quadratically related (Figure 2.5c). The calculated mean speed for the entire ice-free period was 0.15 ± 0.43 km/h (range: 0.0-6.25 km/h). Speeds were significantly lower in September to October compared to November to December (Wilcoxon signed-rank Z = 110,050,000, P < 0.0001, r = 0.09). Movement reached a minimum on October 1 (0.08 ± 2.18 km/h, n = 15,847), but increased with increased days since ice breakup (0.21 ± 4.45 km/h, n = 14,978). Distance to coast was included in all top models (Table 2.4) and was negatively correlated with speed (Table 2.5, Figure 2.5d).

DISCUSSION

We found variation in terrestrial space-use patterns of adult female polar bears and that biological, environmental, temporal, and spatial variables influenced terrestrial movement rate. Although movement rate and tortuosity varied significantly between the first analysis of interior and coastal females and the second analysis comparing inland and coastal movements of interior females, these differences were numerically small and may not be biologically meaningful. Our analyses revealed most females remained along the coast and fewer moved inland although some females moved between both areas. Low movement rate and tortuous movement suggests animals are foraging (McIntyre and Wiens 1999; Liu et al. 2015), moving through complex terrain (Erlandsson et al. 1999; Hodges et al. 2014), and/or avoiding conspecifics or predators (Jachowski et al. 2013; Laidre et al. 2013; Hodges et al. 2014). Polar bears in western Hudson Bay forage on berries that occur primarily inland (Derocher et al. 1993; Cherry et al. 2011; Gormezano and Rockwell 2013). However, terrestrial foraging was not supported by habitat selection analyses that indicated bears were not selecting habitat types abundant with berries (Chapter 3). Inland Hudson Bay contains challenging terrain to travel through because of the abundance of rivers, creeks, ponds, and lakes (Ponomarenko et al. 2014). Interior bears may exhibit tortuous behaviour while foraging and moving through the complex inland environment, whereas, coastal females may move tortuously to avoid adult males that occupy coastal habitats. Intraspecific predation has been suggested as a reason for spatial segregation within polar bear populations (Derocher and Stirling 1990; Ferguson et al. 1997; Amstrup et al. 2001; Towns et al. 2010). The relative contribution of these factors affecting movements for interior and coastal females is unknown.

Declines in the Western Hudson Bay population size may have changed the terrestrial distribution patterns of females during the ice-free period. Previous research indicated females occupied areas inland and avoided the coast (Latour 1981; Derocher and Stirling 1990; Stirling et al. 1993; Clark and Stirling 1998), but distribution shifts within the population have been documented (Towns et al. 2010). Our findings suggest that while some females are still inhabiting inland areas, more females may occur along the coast than in the past. No temporal trend in movement rate was detected in our study period (2004-2017), possibly because an extended period of time is necessary to reveal trends. However, due to recent population declines (Lunn et al. 2016), there may be fewer males along the coast (Stirling and Parkinson 2006; Regehr et al. 2007), and we suggest that fewer interactions between bears allows more females to occupy coastal areas.

Females moved north more than any other direction, regardless of location, suggesting orientation along the coast. In western Hudson Bay, bears move southeast on sea ice towards shore during breakup, and move northwards on land during freeze-up (Derocher and Stirling 1990; Parks et al. 2006; Togunov et al. 2017, 2018). Previous research indicates during spring, (February to March), females emerging from dens orient northeast to return to the coast (Ramsay and Andriashek 1986; Yee et al. 2017). For females not denning, the north directional movement is towards the area were sea ice first forms in the Bay.

Age, windspeed, presence of daylight, days since ice breakup, and distance to the Hudson Bay coast influenced female movement rate during the ice-free period. Younger and older females exhibited increased movement compared to middle-aged females. Variation in movement with age, body condition, and reproductive status are well established in polar bears (Amstrup et al. 2001; Aars and Plumb 2010; Pilfold et al. 2017). We expected litter to influence movement rate, however, all bears included in the analysis had cubs, so it is possible we could not detect an effect of litter on movement rate. Body condition, litter size and litter mass are quadratically related to age (Derocher and Stirling 1994). Middle-aged bears may have better body condition and are less nutritionally stressed resulting in less movement.

Polar bears are a cold-adapted circumpolar species, however meteorological conditions can influence their movement on sea ice (Øritsland 1970; Sahanatien et al. 2015; Togunov et al. 2017, 2018). Bears decrease their movement on sea ice during periods of increased windspeeds (Jonkel et al. 1972; Rozhnov et al. 2015) or snowstorms (Schweinsburg 1979; Clark et al. 1997). Additionally, on sea ice, bears use cross-winds to search for prey (Togunov et al. 2017, 2018) and an increase in seal kills occurs in low windspeed conditions (Pilfold et al. 2015). We found female movement was negatively correlated with windspeed on land. While prey search is unlikely during the ice-free period, polar bears on land may reduce movement or find refuge during periods of high windspeeds and inclement weather similar to their sea ice behaviour.

Presence of daylight influenced female movement, with peak activity between 1300-1700. On sea ice, diurnal activity is correlated with prey (Stirling 1974), but bears also exhibit circadian rhythm patterns (Ware et al. 2020). Given the energy conservation state of our study animals, movement is reduced, but bears continue a diurnal, natural circadian rhythm during the ice-free period.

Ambient temperature was predicted to influence terrestrial movement based on Sahanatien et al. (2015) who found northern individuals, where the temperature was cooler, moved more than southern individuals. Days since ice breakup was highly correlated with temperature, but breakup date had a larger influence than ambient temperature on movement rate. This may be due to the Churchill temperature estimates not reflecting temperatures at telemetry locations. Further, the telemetry data may lack the resolution necessary to reveal movements in response to local environmental factors.

Sea ice phenology influenced female movements during the ice-free period. Earlier sea ice breakup and later freeze-up dates may alter movement exhibited by females on land. In our study, shortly after breakup, terrestrial movement declined to a minimum on October 1. This date was earlier than the reported lowest period of activity (November) by Derocher and Stirling (1990). Our findings may differ from Derocher and Stirling (1990) as a result of higher resolution locations in our study enabled by telemetry collars and/or a result of earlier sea ice breakup dates in our study period (Stern and Laidre 2016). Freeze-up movement was consistent with past research (Derocher and Stirling 1990; Parks et al. 2006), and we found after October, there was an increase in female movement rate.

When females moved towards the Bay, movement rate increased. Attributes of this directional movement to the coast can be defined as migration following Dingle and Drake (2007). Polar bears migrate towards the coast in preparation for returning to the sea ice and hunting. Our findings are corroborated by other on-land studies that found bears increased movement to migrate towards the coast in preparation for returning to the sea ice (Derocher and Stirling 1990; Parks et al. 2006; Cherry et al. 2013; Yee et al. 2017).

Sea ice cover in Hudson Bay has declined in recent decades (Parkinson 2014; Stern and Laidre 2016). Temporal trends in movement and distribution were not found, but ongoing changes in sea ice phenology may result in fluctuations in the seasonal timing of migratory movements. Given the complexity of biological and environmental factors involved in movement, detecting temporal trends may remain challenging. Continued monitoring could provide insight into this topic.

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TABLE 2.1 Variables used to examine movement patterns of adult female polar bears in the Western Hudson Bay population.

Variable	Definition	Range	Source
STEP_LENGTH	Response variable: distance travelled (km) by female bear during a 1 h period	0.00-6.2 km	Calculated using R
BEAR_ID	X number unique to each female	X03419 - X33693	Assigned at time of capture
BEAR_AGE	Age of adult females to the closest year	5-26 years	Tooth histology, extracted at time of capture
LITTER	Number of cubs with female	1 - 2	Assessed at time of capture
CUB_AGE	Age of cubs travelling with female	COY or YRLG	Assessed at time of capture
WIND	Windspeed (km/h)	0.0 - 85 km/h	Environment Canada Historical weather for Churchill, Manitoba Airport, 2004-2017
TEMP	Ambient ground temperature (°C)	-36.3 - 30.9 °C	Environment Canada Historical weather for

			Churchill, Manitoba Airport, 2004-2017
RAIN	Presence of rain	0 - 1	Environment Canada Historical weather for Churchill, Manitoba Airport, 2004-2017
SNOW	Presence of snow	0 - 1	Environment Canada Historical weather for Churchill, Manitoba Airport, 2004-2017
DAYLIGHT	Presence of sunlight	0 - 1	Calculated using the 'suncalc' package in R
YEARDAY	Ordinal date	169 - 365	
YEAR	Year of telemetry location	2004-2008, 2010-2017	
DAYS_BREAKUP	Number of days since sea ice breakup	137 - 183	Special Sensor Microwave Imager (SSM/I) Satellite data
DIST_COAST	Distance from western Hudson Bay coast (km)	0.0 - 393 km	Calculated using the 'geosphere' package in R

TABLE 2.2 Descriptive statistics and results for Mann-Whitney *U* test for interior (n = 37) compared to coastal (n = 54) adult female polar bears in western Hudson Bay from 2004-2008, 2010-2017. Movement metrics were calculated from female telemetry locations, captured in 4-h time intervals. SD = standard deviation of the mean.

Movement Metrics	Interior Bears Median (SD); Range	Coastal Bears Median (SD); Range	*P*-value	r
Speed (km/h)	0.01 (0.38); 0-6	0.00 (0.25); 0-6	< 0.0001*	0.15
Straightness index	0.84 (0.3); 0-1	0.72 (0.3); 0-1	< 0.0001*	0.2
Turning angle (°)	90 (58); 0-180	105 (58); 0-180	< 0.0001*	0.09

* significant *P*-values

TABLE 2.3 Descriptive statistics and results for Wilcoxon signed-rank test for inland and coastal movement patterns among interior bears (n = 37). Adult female polar bears in western Hudson Bay from 2004-2008, 2010-2017. Movement metrics were calculated from female telemetry locations, capture in 4-h time intervals. SD = standard deviation of the mean.

Movement Metrics	Inland Movement Median (SD); Range	Coastal Movement Median (SD); Range	*P*-value	r
Speed (km/h)	0.01 (0.21); 0-3	0.01 (0.46); 0-3.6	< 0.0001*	0.2
Straightness index	0.77 (0.3); 0-1	0.91 (0.3); 0-1	< 0.0001*	0.2
Turning angle (°)	96 (57); 0-180	87 (60); 0-180	< 0.0001*	0.05

* significant *P*-values

TABLE 2.4 Top five AIC_c models of factors influencing movement rate (speed) for adult female polar bears. Speed (km/h) was calculated from western Hudson Bay polar bear telemetry locations, in 4 h time intervals, from 2004-2017. BEAR_AGE = age of adult female, LITTER = litter size, CUB_AGE = age of cub, WIND = windspeed (km/h), RAIN = presence of rain, SNOW = presence of snow, DAYLIGHT = presence of daylight, YEAR = telemetry location year, DAYS_BREAKUP = days since ice breakup, DIST_COAST = distance from the coast (km), w_i = weight. Models are ranked based on Akaike Information Criterion for small sample sizes (ΔAIC_c) values.

Rank	Model	K	AIC_c	ΔAIC_c	w_i
1	BEAR_AGE + BEAR_AGE2 + DAYLIGHT + WIND + DAYS_BREAKUP + DAYS_BREAKUP2 + DIST_COAST	10	334467	0.0	0.85
2	BEAR_AGE + BEAR_AGE2 + LITTER + CUB_AGE + DAYLIGHT + WIND + RAIN + SNOW + YEAR + DAYS_BREAKUP + DAYS_BREAKUP2 + DIST_COAST	15	334470	3.4	0.15
3	WIND + RAIN + SNOW + DAYLIGHT + DAYS_BREAKUP + DAYS_BREAKUP2 + YEAR + DIST_COAST	11	334499	32.2	0.00
4	BEAR_AGE + BEAR_AGE2 + CUB+AGE + DAYLIGHT + DAYS_BREAKUP + DAYS_BREAKUP2 + DIST_COAST	10	334515	48.8	0.00

5	DAYLIGHT + YEAR + DAYS_BREAKUP + DAYS_BREAKUP2 + DIST_COAST	8	334548	81.2	0.00

TABLE 2.5 The estimate, standard error, t value, and statistical significance for coefficients included in the top model used to predict speed from telemetry locations for adult female polar bears in western Hudson Bay from 2004-2017. BEAR_AGE = age of adult female, WIND = windspeed (km/h), DAYLIGHT = presence of daylight, DAYS_BREAKUP = days since ice breakup, DIST_COAST = distance from the coast (km). For each covariate, values that are >1 indicate an increase in speed in relation to that predictor variable, and values <1 indicate a decrease in speed in relation to the variable.

Coefficients	Estimate	Standard Error	t value
INTERCEPT	30.42*	4.07	7.47
BEAR_AGE	0.31	0.49	0.63
BEAR_AGE2	0.92*	0.09	9.70
WIND	-1.66*	0.19	-8.55
DAYLIGHT	129.80*	4.07	31.86
DAYS_BREAKUP	3.82*	3.82	48.44
DAYS_BREAKUP2	0.08*	0.00	34.44
DIST_COAST	-92.72*	0.00	-47.08

*$P < 0.0001$

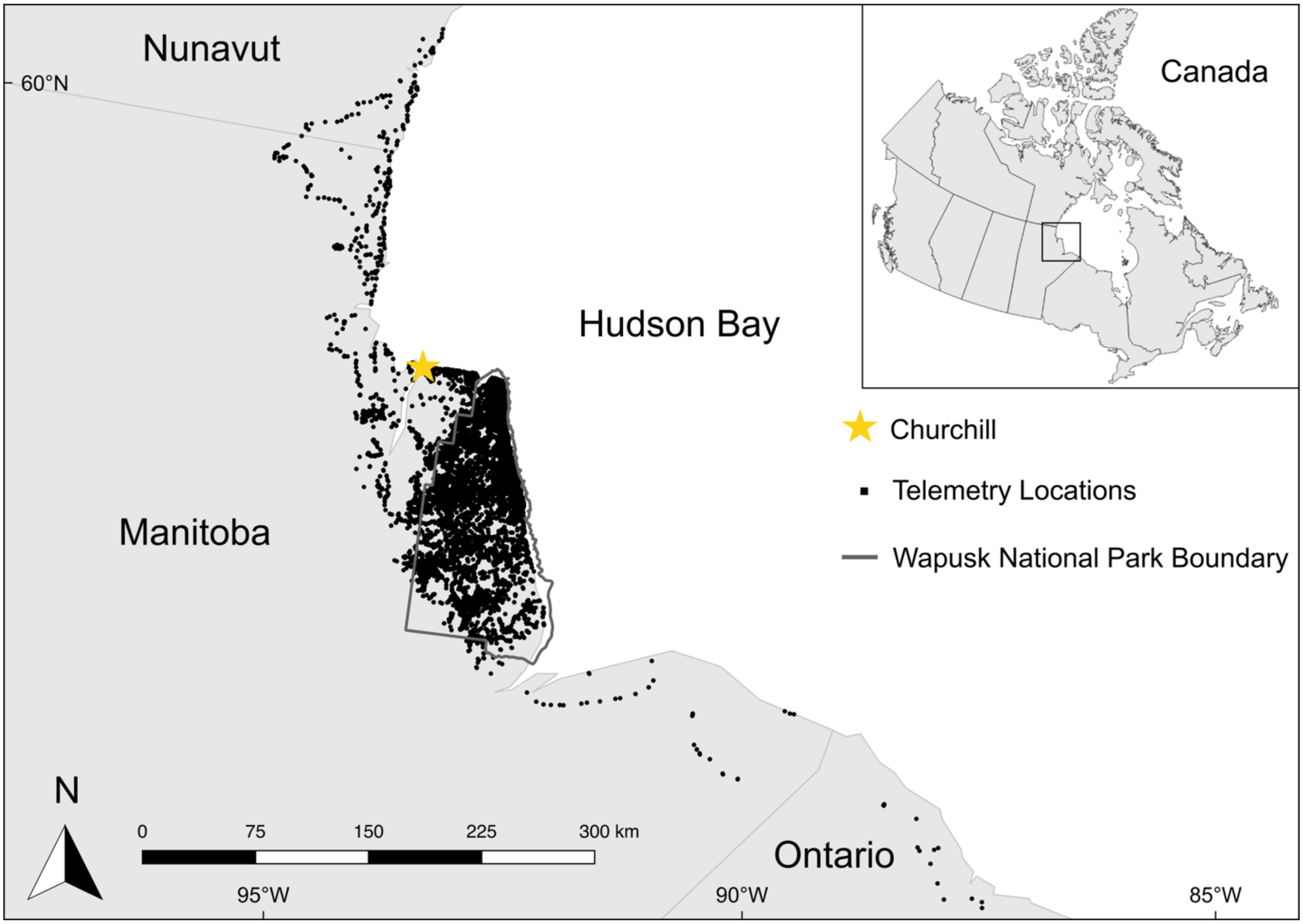

FIGURE 2.1 Western Hudson Bay study area with adult female polar bear terrestrial telemetry locations (n = 35,251), 2004-2017.

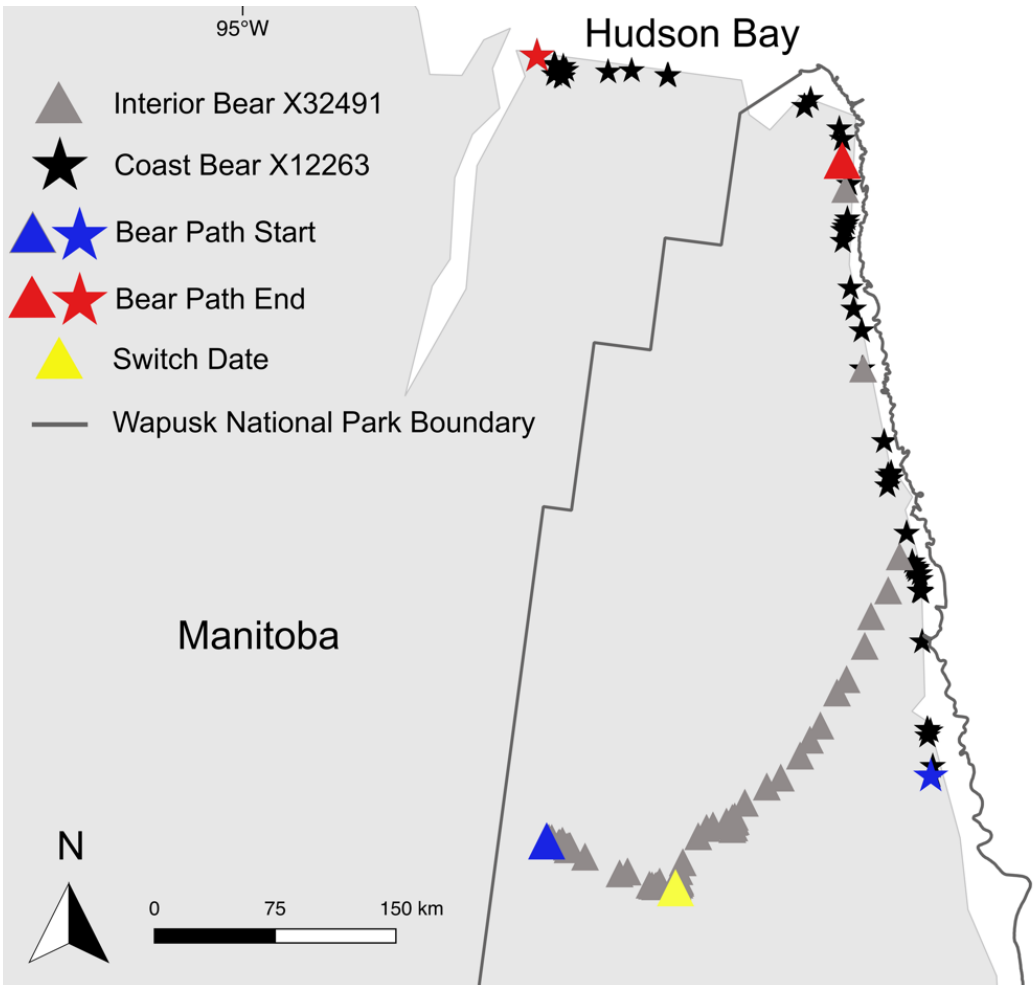

FIGURE 2.2 Examples of interior and coastal polar bear terrestrial movement patterns in western Hudson Bay. Bear X12263 indicates bear movement path along the coast from September 18 to November 12, 2007 (n = 191). Bear X32491 indicates bear movement path while inland during the ice-free period, from September 27 to November 23, 2010. Telemetry locations were divided into two clusters based on switch date. The switch date for Bear X32491 was November 3, 2010. All X32491 locations before the switch date indicate inland movement (cluster 1) telemetry locations (n = 176). All locations north of the switch date indicate coastal movement (cluster 2) telemetry locations (n = 93).

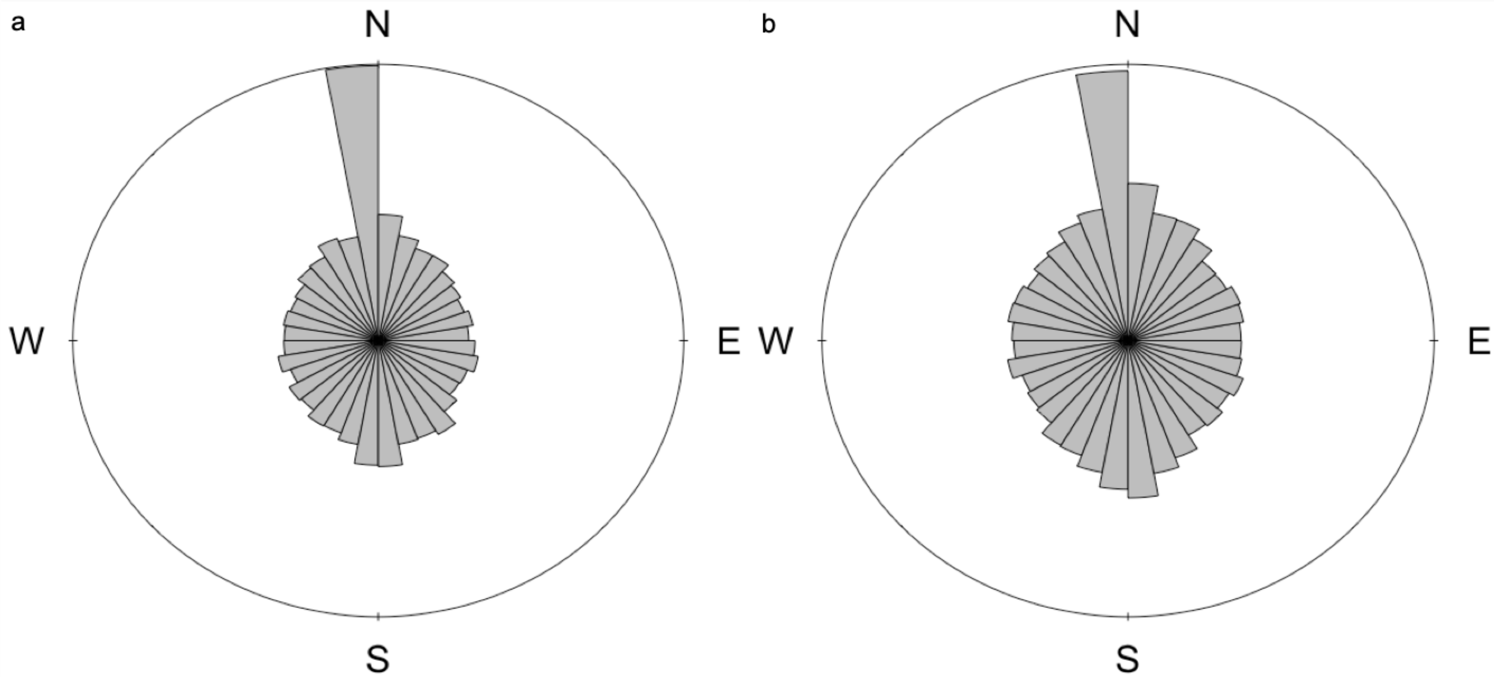

FIGURE 2.3 Rose diagrams (N = north, E = east, S = south, W = west) indicating bearing and magnitude of directional movement for a) interior and b) coastal bears in western Hudson Bay. Sample sizes for both interior (a) and coastal (b) bears had n = 12989 randomly selected from original data to allow for comparison. Both a) and b) demonstrate direction is concentrated from NNW to N.

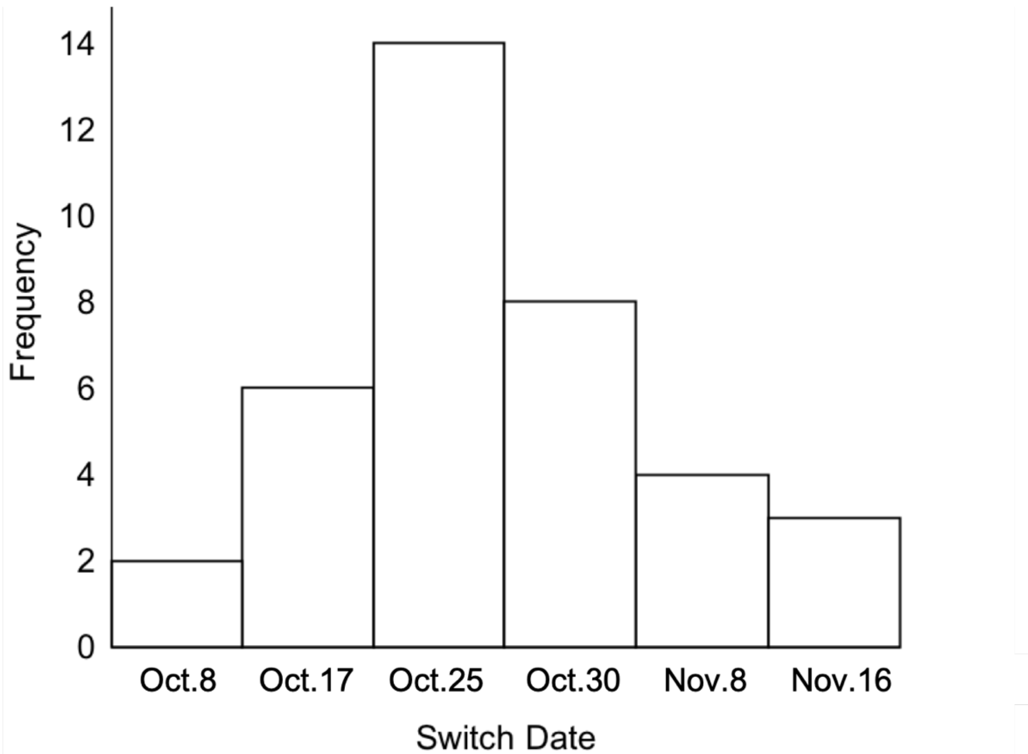

FIGURE 2.4 Histogram of switch dates when adult female polar bears in western Hudson Bay began directional movement towards the coast (n = 37). Mean switch date was October 27 (range: October 5 to November 20).

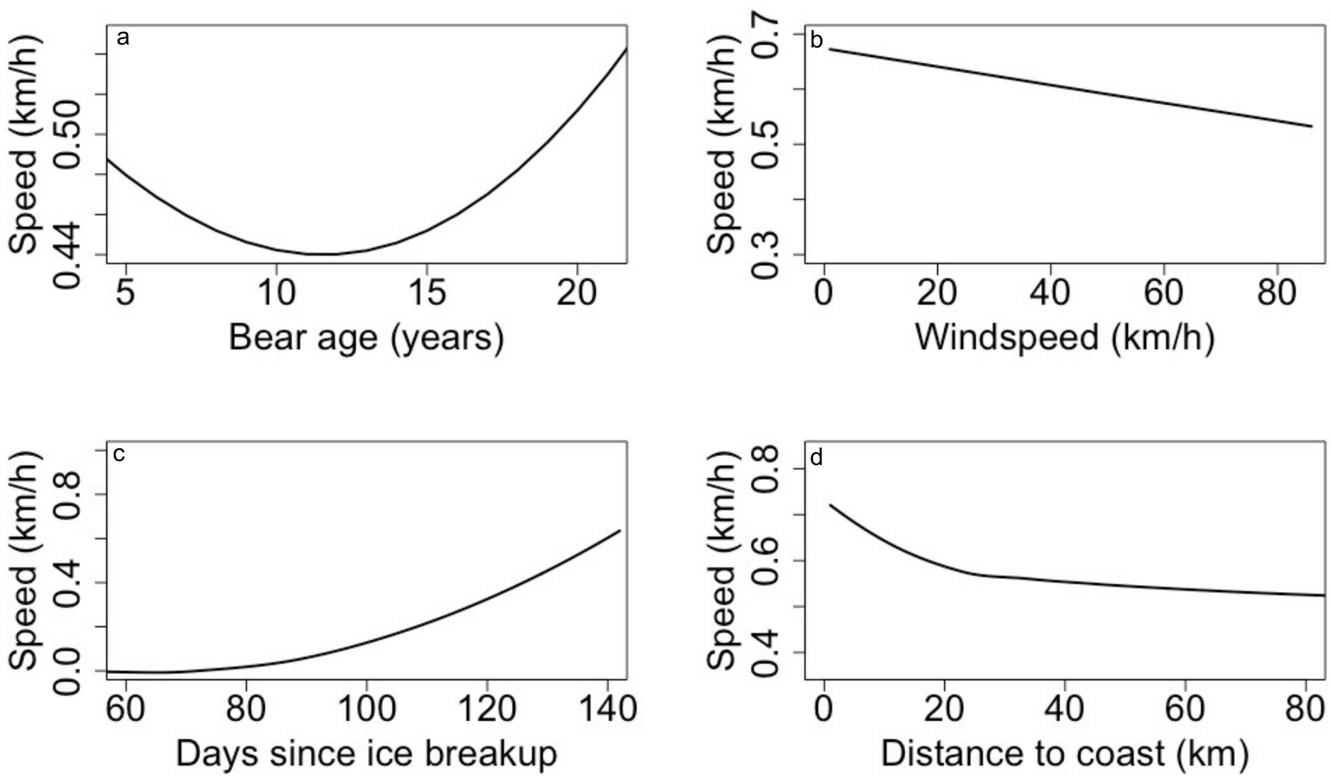

FIGURE 2.5 Model outputs for adult female polar bear terrestrial speed (km/h) as a function of predictor variables: a) bear age in years, b) windspeed (km/h), c) days since ice breakup, and d) distance to the western Hudson Bay coast (km). Speed was derived from polar bear telemetry locations at 4-hour intervals in western Hudson Bay, every four hours from 2004-2017.

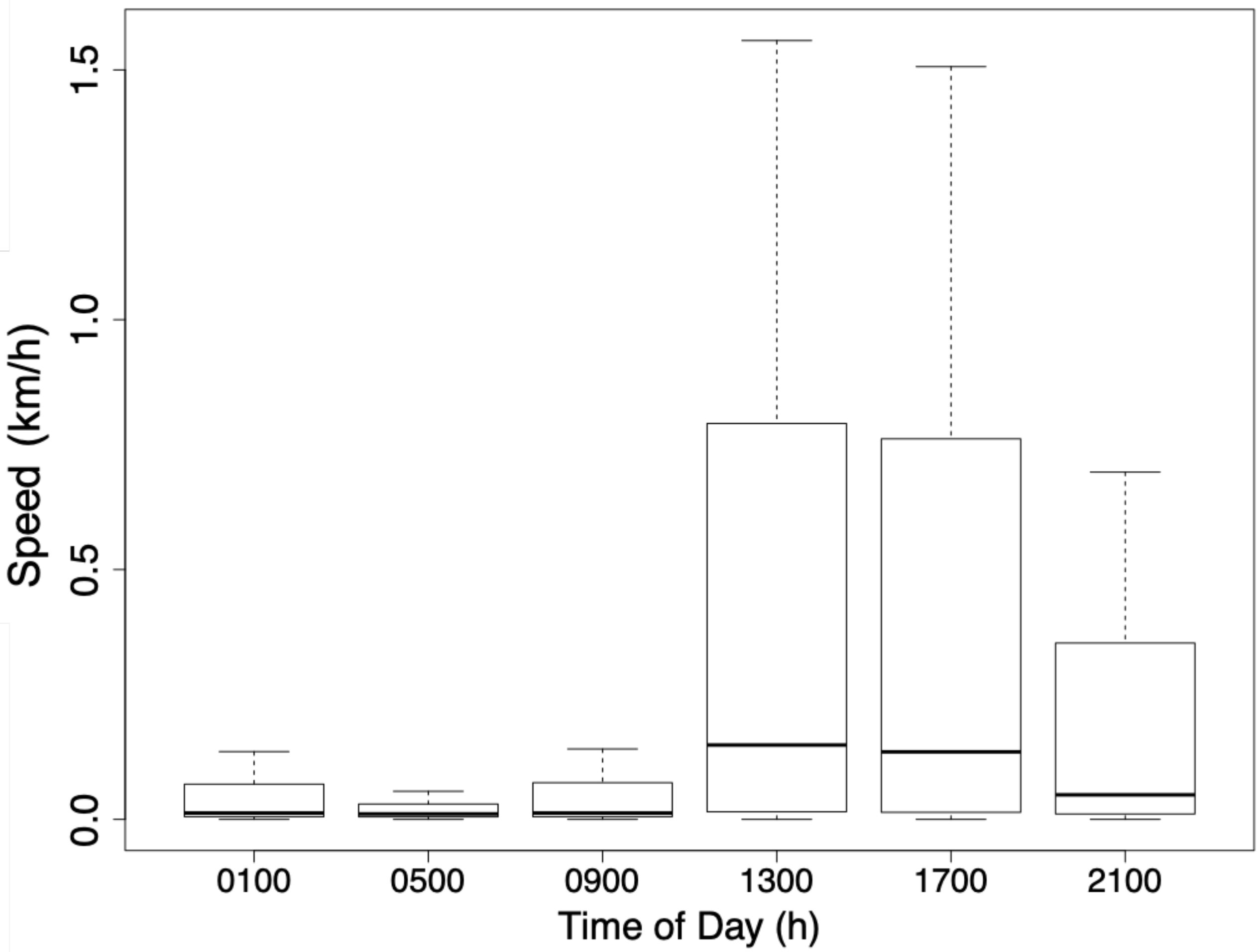

FIGURE 2.6 Speed (km/h) for adult female polar bears by time of day (UTC) (0100 n = 5,962, 0500 n = 5,700, 0900 n = 5,425, 1300 n = 5,484, 1700 n = 6,006, 2100 n = 5,595). Speed information was obtained from polar bear telemetry locations in western Hudson Bay every four hours from 2004-2017. Speeds reach a maximum of 6.25km/h, however to visualize speeds close to zero, outliers are not shown.

CHAPTER 3 - Terrestrial habitat selection by adult female polar bears and site fidelity in western Hudson Bay, Canada

INTRODUCTION

Animals select specific habitats to fulfill biological requirements and understanding how habitat selection affects those requirements provides insight into the behaviour of animals and may assist conservation strategies (Boyce and McDonald 1999; Rettie and Messier 2000; Guisan and Thuiller 2005; Wilmers et al. 2015). Habitat selection is influenced by many factors such as food availability (McLellan and Hovey 2001; McLoughlin et al. 2002), mate selection (Keeley et al. 2017), reproductive state (Grignolio et al. 2007; Spear et al. 2020), predator avoidance (DeMars and Boutin 2018; Courbin et al. 2019), and population density (Kie and Bowyer 1999). Other factors such as site fidelity, can also influence habitat selection (Matthews and Preisler 2010; Brough et al. 2017). Advances in telemetry and remote sensing have permitted greater insight into habitat selection and site fidelity. Analysis of habitat use, often with resource selection function models, can assess relative importance of habitats (Boyce and McDonald 1999; Koper and Manseau 2012). Identifying how a species uses its habitat is integral to foresee how a species could be affected in a changing environment. The importance of habitat selection examination increases in rapidly changing habitats such as the Arctic.

The Arctic is almost completely covered in snow and ice during winter; whereas, in the summer, sea ice declines significantly (Perovich and Polashenski 2012; Mudryk et al. 2018). Arctic sea ice habitat has decreased in recent years and the decline is predicted to continue (Parkinson 2014; Stern and Laidre 2016). Climate change and the resultant loss of sea ice is the foremost threat that challenges the existence of many Arctic marine mammals (Laidre et al. 2008; Kovacs et al. 2011) and the duration of ice-free summers in the Arctic is expected to increase (Durner et al. 2009; Overland and Wang 2013; Stern and Laidre 2016; Wang et al. 2018). The Arctic is dynamic and the seasonal cycle prompts animals that inhabit both sea ice and terrestrial habitats to adapt to fluctuating environments (Harington 2008).

Polar bears (*Ursus maritimus*) are a sea ice obligate species that rely on the ice as substrate to travel, hunt, and mate (Stirling et al. 1977; Schliebe et al. 2008; Lone et al. 2018) yet in some areas, including western Hudson Bay, an ice-free period forces bears ashore (Stirling and Archibald 1977; Ferguson et al. 1997; Towns et al. 2010; Sahanatien et al. 2015). During the ice-free period, males remain near the coast, while pregnant females and most mothers with offspring segregate and move inland (Stirling et al. 1977; Latour 1981; Derocher and Stirling 1990; Ramsay and Stirling 1990). By moving inland, females with offspring avoid potentially infanticidal adult males (Stirling et al. 1977; Latour 1981; Derocher and Stirling 1990; Ramsay and Stirling 1990). Pregnant females move inland to preferred denning habitat (Lunn et al. 2004; Richardson et al. 2005) and show fidelity to the same areas over time (Derocher and Stirling 1990; Ramsay and Stirling 1990; Scott and Stirling 2002). However, depending on environmental conditions and population distribution, some females with offspring remain near the coast (Chapter 2; Towns et al. 2010). While onshore, bears are largely in an energy conservation state and rely on fat reserves deposited during the spring hyperphagic period (Ramsay and Stirling 1988; Ramsay and Hobson 1991; Atkinson and Ramsay 1995). Terrestrial foraging by polar bears occurs (Derocher et al. 1993; Brook and Richardson 2002; Gormezano and Rockwell 2013), but it is unknown if bears select for areas on land abundant with food resources (e.g., berries).

Our research objectives were to use satellite-linked telemetry data and a high-resolution ecotype map of Wapusk National Park, Manitoba, Canada to (1) assess habitat selection and describe the relative probability of selection for females in terrestrial environments and (2) assess site fidelity of adult female polar bears in western Hudson Bay during the ice-free period. We hypothesized bears would show temporal changes in selection when on land during different periods, because of migration movement on and off sea ice. Based on findings by Clark and Stirling (1998), we predicted bears would select for areas near freshwater and avoid the coast during the ice-free period. During break-up and freeze-up, we predicted bears would show selection for the coast compared to other habitat types. We also expected bears to exhibit a high degree of fidelity to the same sites within Wapusk National Park.

METHODS

Study area

The study area is located along the coast of western Hudson Bay, Manitoba in Wapusk National Park (Figure 3.1). The Park covers approximately 11,475 km^2 and was established in part to protect polar bear maternal denning habitat (Lunn et al. 2002). The Park is characterized by abundant wetlands with fens, bogs, lakes, ponds, creeks, and rivers that cover 41-50% of the inland area (Ritchie 1960; Bello and Smith 1990). Inland forest areas include: black spruce (*Picea mariana*), white spruce (*P. glauca*), larch (*Larix laricina*), balsam poplar (*Populus balsamifera*), and willow (*Salix* spp.) (Ritchie 1960). The tundra habitat is composed of lichen and shrub species, including dryas heath (Ponomarenko et al. 2014). The coastal area of the Park includes both unvegetated beach ridges and shoreline and vegetated areas. Vegetation along the coast, where it exists, is fen with sedges (*Carex* spp.), willow, and coastal meadow shrubs (Ponomarenko et al. 2014).

Land cover classes were identified using a high resolution (5m x 5m: resampled as 10m x 10m) Terrestrial Ecotype Map (Ponomarenko et al. 2014), analyzed using QGIS (v. 3.10 Open Source Geospatial Foundation Project). The original ecotype map identified 24 land cover classes. We reclassified the map because of vegetation similarity (e.g., poor sedge fen and rich sedge fen were reclassified into one class) (Ponomarenko et al. 2014) (Table 3.1). If Pearson's correlation was $r \geq |0.6|$, indicating collinearity among habitat types, classes were pooled. The final six land cover classes were freshwater, riparian, coastal, forest, tundra, and wetland.

Capture and collar deployment

Adult female polar bears (≥5 years old) were captured in northeastern Manitoba in and near Wapusk National Park, during the ice-free period from August 30 to September 25 (Figure 3.1) as part of ongoing, long-term research on the ecology of Western Hudson Bay polar bears (e.g., Ramsay and Stirling 1988; Derocher and Stirling 1995; Stirling et al. 1999; Regehr et al. 2007; Lunn et al. 2016). Satellite-linked global positioning system (GPS) collars (Telonics, Mesa, AZ), accurate to ca. 31 m (Tomkiewicz et al. 2010), were deployed only on adult females as the necks of males are wider than their heads and will not retain a collar. Telemetry locations within five days of collar deployment were excluded to allow immobilized bears to return to normal movement (Thiemann et al. 2013; Rode et al. 2015a). Animal capture and handling complied with Canadian Council on Animal Care guidelines (www.ccac.ca) approved by the University of Alberta BioSciences Animal Care and Use Committee.

Resource selection function analysis

Telemetry locations were imported into QGIS and projected to coordinate system Ontario lambert, NAD 1983 CSRS EPSG 5321. A used versus available design was employed (Boyce and McDonald 1999; Manly et al. 2007), where used was defined as female telemetry locations, and available was defined as random points generated within a buffered polygon. A 1:1 ratio of available to random points was used with randomly generated locations constrained inside the buffer. We generated the buffer radius based on mean bear step-length. Randomly generated available locations and used locations were restricted to Wapusk National Park because habitat layer information was only available inside the Park. Third order habitat selection was considered (Johnson 1980) and a buffer surrounding each telemetry location, instead of home range, included only biologically relevant resource units (Ciarniello et al. 2007). To use all land cover classes for all females, a distance-based approach was employed. Distance to each respective feature was calculated for all land cover types rather than choosing a discrete choice of nearest telemetry location (Conner et al. 2003). Female habitat selection can vary with reproductive status (Stirling et al. 1993; Freitas et al. 2012), however, females were not monitored after capture, and the dataset only contains females with cubs, so reproductive status was excluded from analysis.

A generalized linear mixed model was performed to develop the habitat selection model (Manly et al. 2007) using individual bear identification (bear ID) as a random effect to account for repeated measures taken from the same individuals over time. The resource selection function compared the habitat selected by females to available habitat and returned the relative probability of use based on selection coefficients of the covariates (Manly et al. 2007). Akaike Information Criteria for small samples sizes (AIC_c) was used for model selection (Burnham and Anderson 1998; Henningsen 2010). Because a distance approach was employed, the negative selection coefficients for the variables included in the most parsimonious model indicate selection; whereas, positive selection coefficients indicate avoidance. Telemetry locations were subset into three periods: breakup (July to August), ice-free (September to October), and freeze-up (November to December). Periods were formed based on approximate seasonal changes and months were combined to increase sample size.

Site fidelity

Site fidelity was estimated for each female from June to October, 2004-2017. The months were constrained because telemetry locations did not extend past October of the second year. Terrestrial home range size was estimated in year one and the later year, then home range overlap and distance between centroids were measured. Home range size, interannual home range overlap, and distance between centroids were calculated using the 'adehabitatHR' package (Calenge 2006) in R (R Core Team 2019, v 3.6.2). Brownian bridge movement model home range (BBMM) was used because BBMM incorporates animal movement metrics in the utilization distribution (UD) estimation, resulting in an indication of space use (Horne et al. 2007; Kranstauber et al. 2012). Home range polygons were generated excluding 5% of the most extreme telemetry locations (White and Garrott 2012). A Jarque Bera test (Jarque and Bera

1980) revealed the difference between home range areas of each bear was non-normally distributed after transformation; thus a Wilcoxon signed-rank test for paired data compared differences in home range size between years for all females (Mann and Whitney 1947). Home range overlap was measured as utilization distribution overlap index (UDOI) (Fieberg and Kochanny 2005). UDOI values that equal zero indicate no overlap, values near one indicate a high degree of overlap, and values greater than one indicate overlap, but non-uniform distributions (Hurlbert 1978; Fieberg and Kochanny 2005). In addition, centroids were calculated for each BBMM polygon. For each female, distance between centroids was calculated as the Euclidian distance (km) from the centroid for the first year to the centroid for the later year (Gulsby et al. 2011; White and Garrott 2012; Sevigny et al. 2018). A combination of high UDOI values and low centroid distances indicate high overlap. A Pearson's correlation was used to examine temporal trends in fidelity. We used an alpha level of 0.05 and all results are median ± 1 standard deviation unless otherwise indicated.

RESULTS

Habitat selection

Location data was used from 122 females that provided 51,145 telemetry locations from August to December, 2004-2017. Sample size for the three periods varied (breakup n = 51 females, 5,284 locations, 50-800 locations per bear; ice-free n = 122 females, 33,299 locations; 50-800 locations per bear, freeze-up n = 111 females, 12,562 locations, 50-600 locations per bear). Mean female age was 15 years ± 1.4 (range from 5-26).

Females preferred freshwater ponds and riparian areas over other land cover classes in all three periods (Tables 3.2-3.7, Figures 3.2-3.4). Additionally, females avoided the coast during the ice-free period (Figure 3.3c). However, during breakup and freeze-up females did not avoid the coast. During breakup, the coast habitat was not included in the top model (Tables 3.2 and 3.3) and during freeze-up, females exhibited selection for the coast (Tables 3.6 and 3.7). The AIC_c weight for breakup was 0.7, however the top model was selected because there were fewer parameters. The most parsimonious ice-free model included selection for freshwater and riparian tall willow, and against coastal habitats (Tables 3.4 and 3.5, Figure 3.3). The next-closest model differed from the top model by >13 ΔAIC_c, indicating a decrease in model fit. A negative coefficient indicates the land cover class was strongly preferred (i.e., the distance to respective land cover class was small) (Tables 3.3, 3.5, 3.7).

Site fidelity

Site fidelity was assessed for 42 females from June to October, 2004-2017. Fidelity was assessed in consecutive years for 39 females and over three years for two females and seven years for one female (Table 3.8). Median terrestrial BBMM home range area for all years, calculated using 95% polygons, was 274 ± 924 km^2 (range: 3-5413 km^2). Home range size between years did not differ significantly (Wilcoxon signed-rank $Z = 405$, $P = 0.2$, Table 3.8). Home range UDOI was 0.39 ± 1.34 (range: 0-8.39) with 38 UDOI values between 0-0.63 and four values >1 (Figure 3.5). Mean distance between centroids was 117 ± 151 km (range: 12-592 km) and 14 females had centroid distances <25 km, 8 females >25 km and ≤50 km, 8 females >50 km and <100 km, and 12 females >100 km (Table 3.8). A weak but significant correlation was found between year and home range size (r = 0.14, $P = 0.01$), UDOI (r = 0.27), but not for year and distance between centroids (r = 0.14, $P = 0.35$).

DISCUSSION

Our study was the first to use telemetry data to examine terrestrial habitat selection by Western Hudson Bay adult female polar bears and was strengthened by a large sample of accurate locations. Past habitat studies did not use telemetry technology and relied on using capture location data (Clark and Stirling 1998).

Adult female polar bears selected for freshwater and riparian tall willow areas in all periods. Denning, refuge from environmental conditions, and proximity to a water source may affect selection exhibited by females during the ice-free period. Our findings support studies that suggest females select for areas near water (Clark and Stirling 1998) and areas of prime denning habitat (Scott and Stirling 2002; Richardson et al. 2005). Freshwater and riparian areas are critical to female polar bears, not only for denning (Richardson et al. 2005), but may also be refuge for females with offspring. Breezes provided by locations in proximity to lakes may reduce insect harassment (Jonkel et al. 1972; Derocher and Stirling 1990; Clark and Stirling 1998). Polar bears are vulnerable to hyperthermia (Øritsland 1970) and warmer temperatures during the ice-free period may increase the risk of hyperthermia and bears may select cooler areas. Further, warm conditions may increase water demand. While the physiological need for water during fasting is reduced (Derocher et al. 1990), access to freshwater sources may reduce dehydration, as seen in captive bears (Robbins et al. 2012).

A fundamental influence of habitat selection for any species is food availability, however, we did not find evidence for terrestrial selection motivated by food. During winter, polar bear habitat selection varies in response to sea ice hunting conditions (Stirling and Derocher 1993; Pilfold et al. 2012; Pilfold et al. 2015). Bears eat while on land (Russell 1975; Derocher et al. 1993; Gormezano and Rockwell 2013), but the energetic returns of limited terrestrial foraging are insufficient to sustain body condition (Ramsay and Stirling 1988; Ramsay and Hobson 1991; Rode et al. 2015b; Pilfold et al. 2016). When on land, females did not select for tundra, wetlands or forest, where several species of berry producing plants occur (Ponomarenko et al. 2014). Berries are found in other areas, and bears may still be consuming berries on land, but terrestrial foraging is not likely to be the primary determinant of habitat selection while onshore.

In addition to selection for freshwater and riparian areas, female habitat selection varied over time. From September to October, selection indicated females avoided the coast. Clark and Stirling (1998) found similar avoidance in adult females. Females inhabiting inland areas, may be doing so to ensure limited interaction with males. Several studies suggest females with offspring move further inland to avoid adult males and minimize infanticide (Latour 1981; Derocher and Stirling 1990; Stirling et al. 1993; Clark and Stirling 1998). Selection during freeze-up indicates females select for the coast, which was expected during migration. However, selection results for the coastal habitat class may not be accurate. Due to the methods creating a buffer around each telemetry location to create an available location, when calculating distance to coast, selection for the coast may be biased. It may be inaccurate to use distance from coast as a variable under selection using this framework for getting an estimate of available distances from coast. Further analysis using Wapusk National Park as the buffer to create available points would resolve this issue.

Females exhibited general fidelity by returning to the same region in subsequent years, but site-specific fidelity was low. Polar bears exhibit fidelity to sea ice areas (Stirling et al. 1977; Schweinsburg and Lee 1982; Garner et al. 1990; Mauritzen et al. 2001) with high fidelity to terrestrial areas in western Hudson Bay (Derocher and Stirling 1990; Ramsay and Stirling 1990). Environmental factors such as the timing and location of sea ice breakup in the Bay may influence terrestrial fidelity. In years when breakup occurs later, bears remain on sea ice longer (Stirling et al. 1999). Bears follow retreating ice to remain on sea ice for as long as possible (Pilfold et al. 2017; Togunov et al. 2017, 2018), and this may change their first on-land location after breakup. Decline in population size (Lunn et al. 2016) and expected changes in terrestrial distribution may affect fidelity if females in later years were able to inhabit higher quality areas that were previously unavailable due to competition (Chapter 2). Reproductive status may influence fidelity (Stirling et al. 1993; Freitas et al. 2012), and in our analysis, females in consecutive years had a different reproductive status in the later year, perhaps accounting for a lack of site-specific fidelity.

In our study, distance between centroids was greater than the distance between successive captures found by Ramsay and Stirling (1990) and Derocher and Stirling (1990). This divergence could indicate a change in terrestrial space use over time with bears exhibiting lower site fidelity now. Nevertheless, no temporal trend was revealed in our study. Further investigation into site fidelity is needed over an extended period of time.

In western Hudson Bay, females returned to the same general areas and exhibited habitat fidelity by selecting for specific terrestrial habitat types: freshwater and riparian areas. In recent years, the Western Hudson Bay population size has declined (Lunn et al. 2016) and it is predicted that future sea ice loss and terrestrial habitat alterations may increase (Stroeve et al. 2007; Overland and Wang 2013; Hu et al. 2015). Those predicted habitat changes may alter future polar bear population habitat selection and distribution.

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Table 3.1 Reclassified habitat variables included in the development of resource selection function models for habitat selection analysis of adult female polar bears in western Hudson Bay, 2004-2017. The original ecotypes that make up each reclass are listed (Ponomarenko et al. 2014). Land cover classes represent distance to the respective habitat feature.

Reclassified Land Cover Class	Original Ecotypes
WATER	Freshwater
WILLOW	Riparian Tall Willow
COAST	Coastal Fens, Coastal Low Willow, Coastal Tall Willow, Unvegetated
FOREST	Lichen Spruce Woodland, Spruce Larch Forests, Moist Forest-Burned, Moist Forest-Burned, Mesic Forest-Burned and Severely Burned
TUNDRA	Lichen Low Shrub, Lichen Dwarf Shrub, Dry Dryas Heath, Moist Rhododendron-Dryas Heath
WETLAND	Poor Sedge Fens, Rich Sedge Fens, Wet Sedge Fens, Sphagnum Bog or Fen, Low Shrub Fen, Low Shrub Fen, Larch Moss Fen, Goose Affected-Severe and Mild

TABLE 3.2 Model selection results from mixed-effects logistic regression testing for land cover classes influencing habitat selection by adult female polar bears in Wapusk National Park, Manitoba from July to August, 2004-2017. Models ranked based on Akaike Information Criterion for small sample sizes (ΔAIC_c) values and weight (w_i). All land cover categories represent distances to the nearest class.

Rank	Models	K	Log-likelihood	ΔAIC_c	w_i
1	WATER + WILLOW	5	-7213.6	0.0	0.7
2	WATER + WILLOW + COAST	4	-7213.4	1.7	0.3
3	WATER	3	-7254.5	80.0	0
4	WILLOW	3	-7251.1	73.0	0
5	FOREST	3	-7324.2	219.4	0
6	COAST	3	-7324.4	219.7	0
Null	null model: 1 + (1|xnumber)	2	-7325.2	219.3	0

TABLE 3.3 Selection coefficients included in the top model used to predict terrestrial habitat selection from telemetry locations for adult female polar bears in western Hudson Bay from July to August, 2004-2017.

Coefficients	Estimate	Standard Error	t value
INTERCEPT	0.02625*	0.03652	7.188
WATER	-0.0009715*	0.0001225	-7.927
WILLOW	-0.0004656*	0.00005898	-7.894

*$P < 0.0001$

TABLE 3.4 Model selection results from mixed-effects logistic regression testing for land cover classes influencing habitat selection by adult female polar bears in Wapusk National Park, Manitoba from September to October, 2004-2017. Models ranked based on Akaike Information Criterion for small sample sizes (ΔAIC_c) values and weight (w_i). All land cover categories represent distances to the nearest class.

Rank	Models	K	Log-likelihood	ΔAIC_c	w_i
1	WATER + WILLOW + COAST	5	-70674.4	0	1
2	WATER + WILLOW	4	-70682.3	13.8	0
3	WATER	3	-70691.6	30.4	0
4	WILLOW	3	-70884.1	415.4	0
5	FOREST	4	-70894.3	435.8	0
6	COAST	3	-70899.8	446.8	0
Null	null model: 1 + (1|xnumber)	2	-70902	449.3	0

TABLE 3.5 Selection coefficients included in the top model used to predict terrestrial habitat selection from telemetry locations for adult female polar bears in western Hudson Bay from September to October, 2004-2017.

Coefficients	Estimate	Standard Error	t value
INTERCEPT	0.06424542*	37.61	-84.117
WATER	-0.0006519255*	2.82	54.511
WILLOW	-0.00003075424*	0.40	21.805
COAST	0.00007118549*	13.78	-115.813

*$P < 0.0001$

TABLE 3.6 Model selection results from mixed-effects logistic regression testing for land cover classes influencing habitat selection by adult female polar bears in Wapusk National Park, Manitoba from November to December, 2004-2017. Models ranked based on Akaike Information Criterion for small sample sizes (ΔAIC_c) values and weight (w_i). All land cover categories represent distances to the nearest class.

Rank	Models	K	Log-likelihood	ΔAIC_c	w_i
1	WATER + WILLOW + COAST	5	-7213.6	0.0	0.9
2	WATER + WILLOW	4	-7213.4	4.1	0.1
3	WATER	3	-7254.5	33.6	0
4	WILLOW	3	-7251.1	76.4	0
5	FOREST	3	-7324.2	123.6	0
6	COAST	3	-7324.4	129.0	0
Null	null model: 1 + (1|xnumber)	2	-7325.2	128.9	0

TABLE 3.7 Selection coefficients included in the top model used to predict terrestrial habitat selection from telemetry locations for adult female polar bears in western Hudson Bay from November to December, 2004-2017.

Coefficients	Estimate	Standard Error	t value
INTERCEPT	0.11310000*	0.01757000	6.437
WATER	-0.00046430*	0.00005705	-8.139
WILLOW	-0.00007497*	0.00001299	-5.772
COAST	-0.00005286	0.00003012	-1.755

*$P < 0.0001$

TABLE 3.8 Home range size, overlap, and distance between home range centroids for adult female polar bears in western Hudson Bay from June to October, 2004-2017. Bear IDs denoted with * exhibited some spatial overlap despite low utilization distribution overlap index (UDOI) values. Years are consecutive except when denoted by [a,b,c].

Bear ID	Year1	Year 2	Year 1 home range size (km^2)	Year 2 home range size (km^2)	Home range overlap (UDOI)	Distance between centroids (km)
X11639*	2004	2005	587	63	0	17.1
X12478	2004	2006[a]	486	81	8.39	64.4
X12008	2004	2011[b]	274	47	0	32.1
X10670	2005	2005	267	478	0	31.9
X11569	2005	2006	19	3	0.02	24.1
X12753*	2005	2006	197	271	0	15.3
X11456*	2005	2007	432	137	0	50
X10875	2006	2006	728	1272	0	603.9
X11638	2006	2007	263	431	0	487.1
X12370*	2006	2007	111	246	0	15.4
X12553*	2006	2007	791	2233	0	137.5
X12746*	2006	2007	556	480	0	59.2
X03419*	2007	2008	52	73	0.28	24.7
X09472	2007	2008	613	889	0	89.6
X11477	2007	2008	1190	455	0.02	21.7
X12003*	2007	2008	50	173	0.1	29.4
X19319	2007	2008	21	257	1.49	16.6
X10228	2008	2009	76	46	0	72
X12502	2010	2011	190	28	0	93.3
X12689	2010	2011	273	190	0	109.2
X19602*	2010	2011	16	470	0.09	12.3

X32491*	2010	2011	168	328	0	15
X33382*	2010	2011	638	207	0	15
X11672*	2012	2013	237	1858	0	41.6
X19272*	2012	2013	351	1949	0	80
X19295	2012	2013	907	1233	0.02	488.9
X32463	2012	2013	171	600	0.47	232.6
X33510	2012	2013	494	773	0.63	33.8
X33519	2012	2013	22	1141	0	224.6
X11870	2013	2014	72	248	1.9	13.1
X19735*	2013	2014	99	246	0	22.1
X19827	2013	2014	415	203	0.11	59.3
X33110*	2013	2015[c]	2106	483	0.01	270.9
X12627	2014	2015	5129	746	0	239.4
X17339	2014	2015	489	1642	0.12	256.9
X19389	2014	2015	110	231	0	76.8
X19627	2014	2015	18	1251	0.52	42.7
X19826*	2014	2015	363	1232	0	12.3
X17466	2015	2016	421	175	0.56	28.3
X19939	2015	2016	296	166	1.49	24.6
X33410	2015	2016	5416	141	0.02	302.3
X33056	2016	2017	2892	228	0.01	427.8

a. X12478: two years between observations
b. X12008: seven years between observations
c. X33110: two years between observations

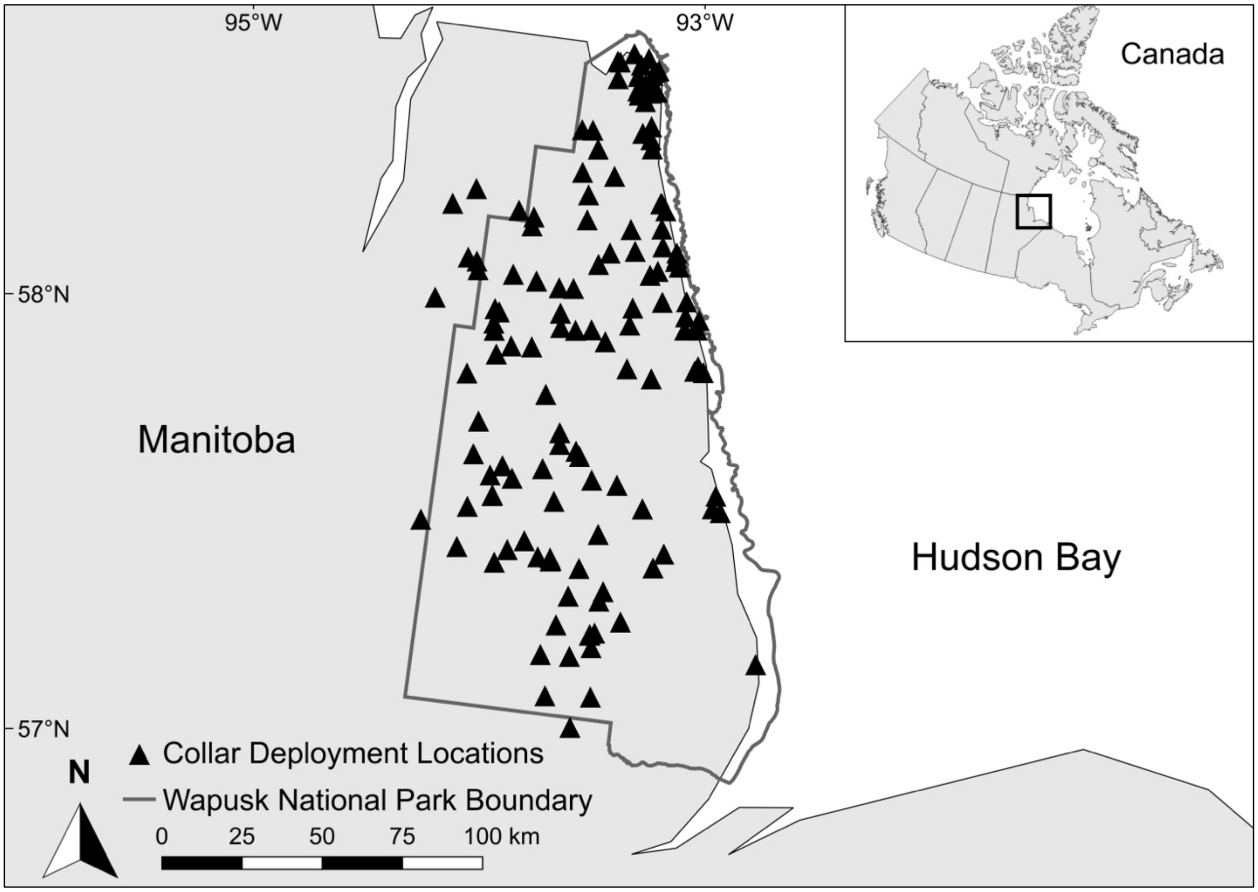

FIGURE 3.1 Study area map of Wapusk National Park within Manitoba, Canada. The black line indicates the Park boundary. Telemetry locations for adult female polar bears used in the habitat selection analysis were confined to within the Park boundary. Black triangles represent collar deployment locations from August 30 to September 25, 2004-2017.

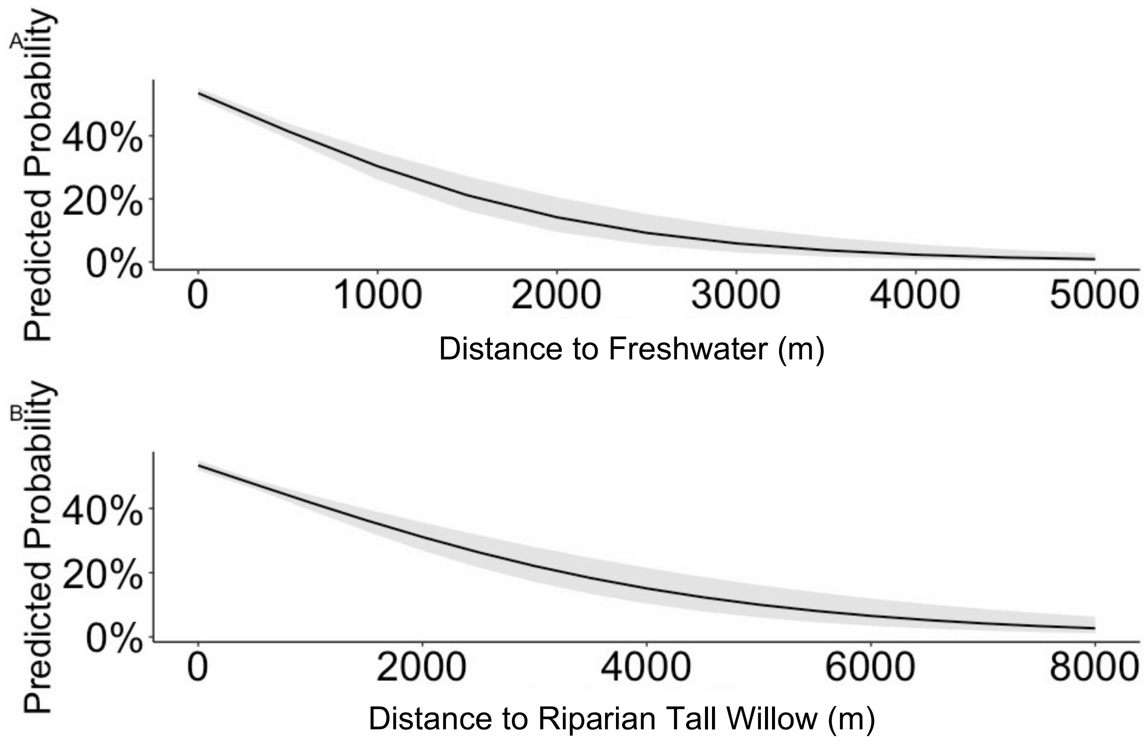

FIGURE 3.2 Relative predicted probability of adult female polar bear habitat selection related to distance in meters to habitat class, during the breakup period (July to August) in western Hudson Bay; (a) females are more likely to select for habitats closer to freshwater; (b) females are more likely to select for riparian tall willow areas.

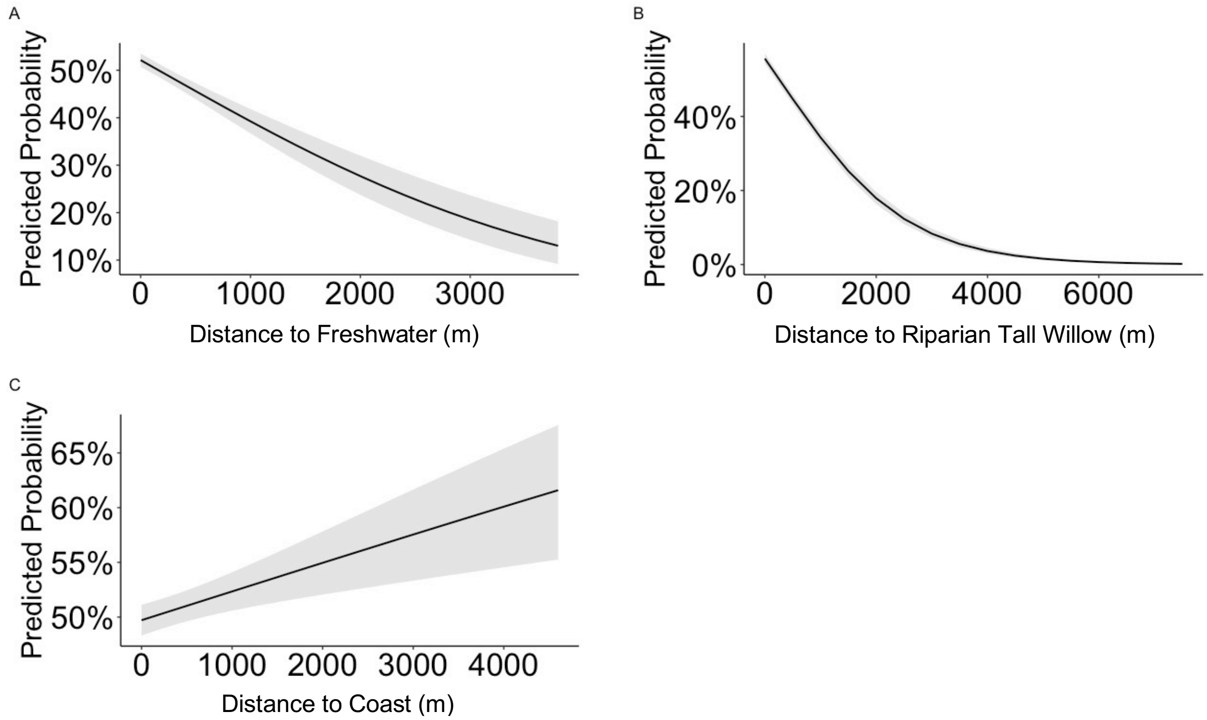

FIGURE 3.3 Relative predicted probability of adult female polar bear habitat selection related to distance in meters to habitat class, during the ice-free period (September to October) in western Hudson Bay; (a) females are more likely to select for habitats closer to freshwater; (b) females are more likely to select for riparian tall; (c) females are more likely to avoid areas close to the coast.

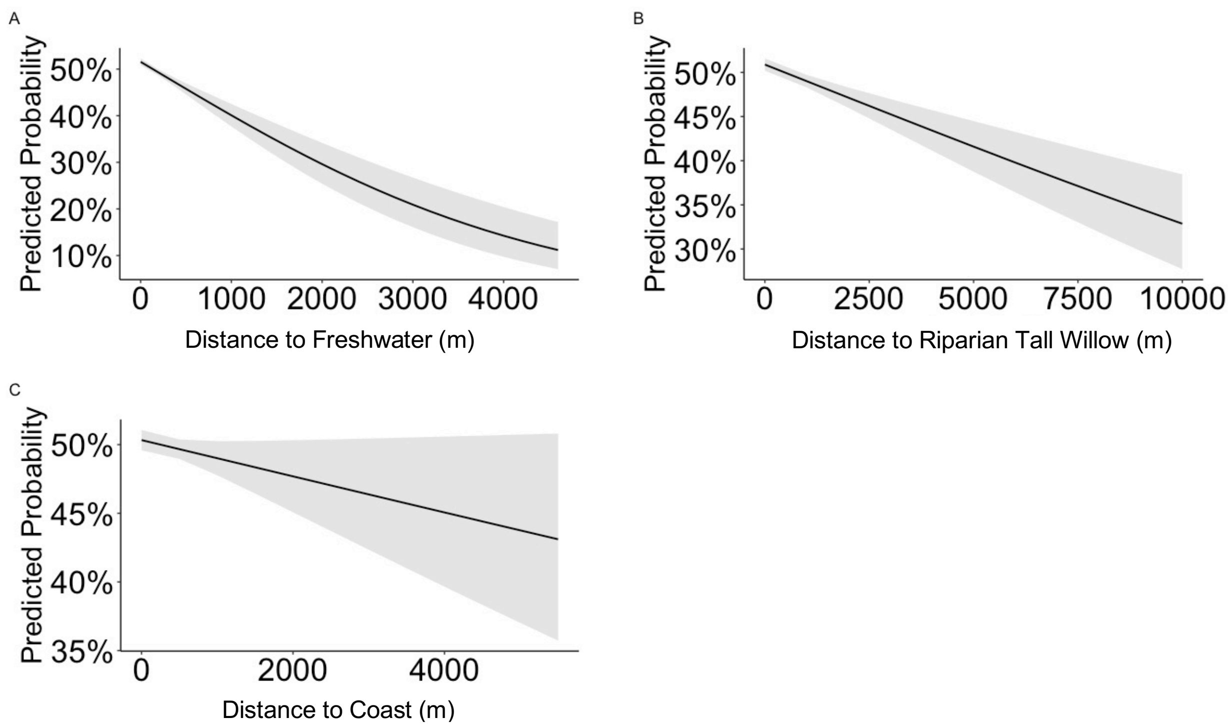

FIGURE 3.4 Relative predicted probability of adult female polar bear habitat selection related to distance in meters to habitat class, during the freeze-up period (November to December) in western Hudson Bay; (a) females are more likely to select for habitats closer to freshwater; (b) females are more likely to select for riparian tall; (c) females are more likely to select for areas near the coast.

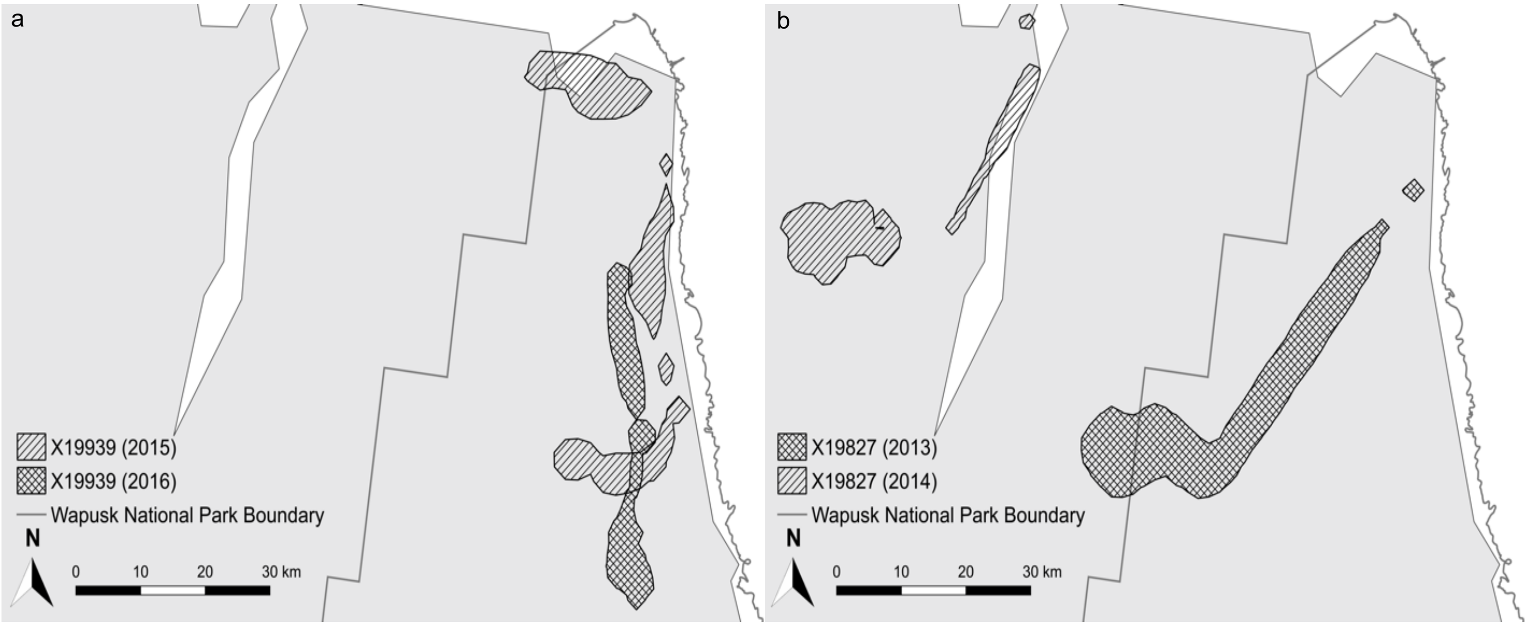

FIGURE 3.5 Home range 95% utilization distributions for adult female polar bears in western Hudson Bay, 2004-2017. a) Home range polygons for bear X19939 in 2015 and 2016 indicates 3.8% spatial overlap. b) Home range polygons for bear X19827 in 2013 and 2014 indicates no spatial overlap between years.

CHAPTER 4 – General Discussion

This thesis examined terrestrial polar bear movement ecology using telemetry technology over a 13-year period from 2004-2017. No temporal trends were found, however, 13 years may not be enough time to detect changes within the population. Continued telemetry monitoring of the Western Hudson Bay polar bear population and increased monitoring of other populations may provide new insights into the effects of climate change on polar bears. Climate change predictions expect an increase in sea ice loss in the future (Stroeve et al. 2007; Overland and Wang 2013). Western Hudson Bay is among areas expected to lose sea ice cover for the longest duration, thereby increasing the length of the ice-free period (Gough and Wolfe 2001; Gagnon and Gough 2005; Hochheim et al. 2010). The length of the ice-free period is a principal consideration when assessing future sea ice conditions and the consequences for polar bear populations. Ice-free period duration predictions suggest significant changes to the amount of time polar bears could spend on land (Stirling et al. 1999; Castro de la Guardia et al. 2013). After a threshold of time fasting (≥180 d), models predict Western Hudson Bay polar bears may be unable to recover from such a prolonged period and will suffer high mortality and population declines (Molnár et al. 2010; Castro de la Guardia et al. 2013; Molnár et al. 2014).

Climate change impacts on terrestrial habitats may also affect the Western Hudson Bay population. A decrease in permafrost in Wapusk National Park has been documented (Zhang et al. 2012). This loss is expected to increase (Stendel and Christensen 2002; Biskaborn et al. 2019). Decreased permafrost may lead to vegetation shifts over time (Pearson et al. 2013; van der Kolk et al. 2016). Increased tundra fires are also possible (Hu et al. 2015). Polar bears in Hudson Bay select for specific areas while on land (Chapter 3). These changes are predicted to negatively influence females denning within the park. For example, Richardson et al. (2007) revealed polar bears do not select for burned areas for denning. These predictions suggest an increasing need to monitor changing polar bear movement, behaviour, and body condition while on land during the ice-free period. Continued monitoring of terrestrial polar bear ecology involves increasing our knowledge of land use and movement by males and subadults, in addition to information at present collected about adult females. Future directions could include using ear tag or glue on radios to assess site fidelity and habitat selection of adult males and subadults. Additionally, the selection results in Chapter Three for the coastal habitat class may not be accurate. The methods used in the analysis when calculating distance to coast may have resulted in biased estimates. Further analysis using Wapusk National Park boundary as the extent to create random available points would resolve this issue.

The Western Hudson Bay polar bear population provides a challenge for terrestrial management because this population of polar bears extends beyond Manitoba, into Nunavut and Ontario. Within Manitoba, bears are not confined to Park boundaries. Unlike females, males are not tied to maternal denning habitat generally found within Wapusk National Park. Research outside of Wapusk National Park could support additional protected areas along the coast in Nunavut, beyond Polar Bear Provincial Park in Ontario and Wapusk National Park, Cape Tatnam Management Area, and Cape Churchill Wildlife Management Area in Manitoba (Lunn et al. 2002).

Advancements in technology may enhance research accessibility for all ages and sex classes of polar bears. The use of drones (Barnas et al. 2018) and camera traps (Laforge et al. 2017) may also provide supplementary information for long-term polar bear research, however, telemetry research should continue. While newer technologies gain popularity, their accuracy does not yet surpass that of telemetric methods, and the limitations of new technologies are greater (LaRue et al. 2015; Laforge et al. 2017; Barnas et al. 2018; Chabot et al. 2019). Changes in movement and behaviour are more accurately assessed by using telemetry (Cooke et al. 2004).

Accurate recording of terrestrial polar bear movement in western Hudson Bay may assist predictions of terrestrial patterns in populations further north. The Western Hudson Bay population has been studied for over 40 years. Fundamental polar bear knowledge has been gained from this population as a result of the continued long-term studies that have been used to inform additional polar bear research. Western Hudson Bay could provide a model to examine changes that may occur because of climate change. More polar bear populations are demonstrating similar seasonal patterns of terrestrial fasting (Stirling and Parkinson 2006; Durner et al. 2009). In the past, females in Alaska primarily denned offshore (Stirling and Andriashek 1992; Amstrup and Gardner 1994). In recent years, the reduction of sea ice along the Alaskan coast has increased the number of terrestrial dens used by females, compared to the number of sea ice dens, and this pattern of increased terrestrial use is expected to increase (Fischbach et al. 2007). The information gained from the Western Hudson Bay population may provide insights for other populations that are increasing their reliance on terrestrial habitats.

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