University of Alberta

Polar bear distribution and habitat selection in western Hudson Bay.

by

Alysa Grace McCall

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ABSTRACT

Sea ice in Hudson Bay is melting earlier and freezing later as the climate warms, resulting in declines in the condition, survival, and population size of polar bears (*Ursus maritimus*) in the Western Hudson Bay population. The objectives of this study are to analyze temporal variation in distribution and quantify patterns of seasonal habitat selection for polar bears on the sea ice in Hudson Bay to determine how they respond to changing sea ice conditions. Between 1990 and 2010, 137 satellite collars were deployed on 125 adult females yielding approximately 95 000 locations. Utilization distributions and a habitat selection model were developed. Distribution shifted seasonally and annually, and habitat selection was most affected by ice concentrations. Individual differences were most apparent during ice freeze-up and break-up. This research helps us understand how changes in sea ice alter polar bear habitat use and selection, important for predicting responses to future changes.

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TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER 2

CHAPTER 3

Figure 3.3. Examples of seasonal Resource Selection Functions for Western Hudson Bay polar bears represented by the same day averaged across four years (2006, 2007, 2008, and 2009) for each season. Each seasonal model was constrained to the 100% MCP of all bear locations in that season (including all years): a = freeze-up (December 7); b = early winter (February 1); c = late winter (May 5); d = break-up (June 27).

LIST OF TABLES

CHAPTER 2

CHAPTER 3

CHAPTER 1- INTRODUCTION

Polar bears (*Ursus maritimus*) have a circumpolar distribution with nineteen distinct populations totalling 20 000 to 25 000 bears (Schliebe et al. 2008). This animal has played an important role in human culture for thousands of years. In Cree, Dorset, Thule, and present-day Inuit cultures, it has provided sustenance, clothing, and economic opportunity (Henri et al. 2010). Europeans had interactions with polar bears in the Middle Ages during the exploration of Iceland and Greenland (Oleson 1950). As the European explorers moved into North America, polar bears remained a species of great interest and value. European-Canadians have interacted with Hudson Bay polar bears since the 1600s through exploration, fur trading, military activity, government management, sport hunting, research, and tourism (Peacock et al. 2010). Still today, images and stories of these massive white bears capture attention from people all around the world, even though relatively few will ever see them in the wild. While the polar bear is a popular symbol of the Arctic, its far northern location makes it difficult to study in its natural environment. One more accessible population, however, has provided much more insight than others. The best-studied and arguably most famous polar bears in the world are those of Western Hudson Bay (WH).

The WH population has the most complete long-term research on polar bear demography, body condition, population size, abundance, and reproductive success compared to any other population, contributing more to our understanding of the life history of polar bears than any other group (e.g., Ramsay and Stirling 1988; Derocher and Stirling 1992; Derocher et al. 1992; Derocher and Stirling 1995; Stirling et al. 1999; Regehr et al. 2007; Molnár et al. 2011). This population occurs near the southern limit of the species' range and can be considered a microcosm of the worldwide situation of the species (Peacock et al. 2010). Polar bears have a highly specialized diet that is maintained through the use of sea ice as the platform to hunt and travel. During the winter and spring months, the WH bears disperse on the ice cover of Hudson Bay to hunt primarily ringed (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) (Thiemann et al. 2008, 2011). The bears must have enough hunting success during winter and spring so that they can store sufficient adipose reserves to last them when energetically significant food sources are largely unavailable (Watts and Hansen 1987; Ramsay and Stirling 1988; Stirling et al. 2008). In the late summer and autumn months, Hudson Bay is completely ice-free and the WH population becomes confined to a restricted area of the western coast, spatially separated from their prey and reliant on fat reserves for approximately four months until the ice forms again (Stirling et al. 1977; Ramsay and Stirling 1988; Regehr et al. 2007). Because polar bears congregate on land in autumn in a relatively southern part of their range, both scientists and tourists are afforded the unique opportunity to study and view polar bears.

Tourists have been traveling to Churchill, Manitoba, since the 1980s (Dyck and Baydack 2004) to see the WH polar bears congregate in late autumn just before the ice freezes on Hudson Bay. Sea ice begins to re-form along the northwestern coast of Hudson Bay to Cape Churchill in late October (Markham 1986; Wang et al. 1994), and the bears assemble here to move onto the sea ice as soon as possible (Cherry et al. 2013). Several thousand people travel to this region to watch polar bears in their natural environment every year, including television and movie crews. As a result, these bears appear in pictures and films viewed all over the world. In common with tourism, easier access to the population and lower operating costs have drawn researchers to study this population since the 1960s.

The WH bears are much more concentrated (within about 250 km^2) when on land than other populations, so both survey flights and mark-recapture studies have the ability to collect more data per research dollar than in regions where the bears are dispersed. Also, Churchill is less expensive to get to than other areas of the high Arctic. Research on this population is longer than any other polar bear population, lasting over forty years, and has helped scientists answer many questions about polar bears. It is partly because of this long-term dataset that scientists realized how the changing climate has affected polar bears (reviewed by Stirling and Derocher 2012).

Because the polar bears of WH occur near the southern limit of the species' range, they were among the first to show population-level effects of climatic warming (Stirling and Derocher 1993). Sea ice in Hudson Bay has a distinct pattern of freeze-up and break-up where the annual sea ice usually begins forming in December, persisting until about June (Prinsenberg 1988), and being completely gone by mid- to late summer (Gough and Wolfe 2001). Over the last 50 years, however, spring temperatures in this region have increased by 2-3°C (Skinner et al. 1998; Gagnon and Gough 2005a) resulting in the ice breaking up approximately three weeks earlier than it did 30 years ago (Stirling and Parkinson 2006) and a significant trend in western Hudson Bay of more than 0.8 days per year (Stirling and Derocher 1993). In fact, by 2003, ice break-up was about 26 ± 7 days earlier than in 1971 (Gagnon and Gough 2005b). Hochheim and Barber (2010) reported that the Hudson Bay area has undergone a climate regime shift recently (in the mid-1990s), resulting in a significant reduction in sea ice during the freeze-up period. In 1993, Stirling and Derocher predicted that the first negative impacts of longer ice-free periods on polar bears would become apparent at the southern limits of their distribution, namely James and Hudson bays. Indeed, the WH population is now forced off of the sea ice earlier, thereby shortening the spring foraging period and reducing the ability of polar bears to accumulate enough fat reserves to survive while stranded onshore (Stirling and Derocher 1993; Stirling et al. 1999; Regehr et al. 2007), with negative consequences for the population.

When the ice breaks up early, the time for polar bears to feed before coming ashore is shortened and the fasting period is lengthened. Progressively earlier dates of sea ice break-up were related to WH polar bear body condition. Earlier break-up dates have been tied to a decline in the mean body condition index of polar bears on shore during the ice-free period (Stirling et al. 1999; Regehr et al. 2007) and a decline in the survival of juvenile, subadult, and senescent-adults (Regehr et al. 2007). Furthermore, a decrease in WH population size, from 1200 in 1984 (Lunn et al. 1997a) to 935 animals in 2004, was related to the earlier break-up of sea ice (Regehr et al. 2007; Peacock et al. 2010). Molnár et al. (2010) estimated that 3–6% of adult males in western Hudson Bay would die of starvation before the end of a 120 day summer fasting period, but 28–48% would die if climate warming increases the fasting period to 180 days. Furthermore, from 1965 through 1993, the body length of WH females declined significantly but this trend was not evident in males (Atkinson et al. 1996). Adult females reach adult body size faster than males and consequently having fewer opportunities to make up for years with lower food availability. Therefore, they may be the first group to demonstrate effects of a long-term decline in nutrition on growth rates and body size (Atkinson et al. 1996).

If, over time, females kill fewer seals and therefore reduced energy intake, the condition, growth and survival of their cubs would be affected. Multiple instances of declining body mass, a proxy for body condition, and resulting negative effects on reproduction and cub survival in WH females have been statistically linked to the earlier break-up of sea ice. For example, the earlier break-up of sea ice was linked to a decline in the mean weights of suspected pregnant females before maternity denning (Stirling and Parkinson 2006). Also, the mass of WH pregnant females declined between 1966 and 1992, as did the production of litters (0.48–0.34 litters/female/yr) (Derocher and Stirling 1995), and the survival of cubs from spring to autumn has declined (from 73.0% in 1980–1984 to 48.8% in 1987–1992) (Derocher and Stirling 1996). The earlier that break-up occurs, the poorer the mean body condition of the bears when they come ashore to fast through the ice-free season; delayed freeze-up further intensifies the problem. However, it is not only the timing of the transition periods of break-up and freeze-up that are important for the healthy body conditions of polar bears, but also the condition of the ice throughout the on-ice period which may affect movements and foraging success.

It has been hypothesized that increasing amounts of open water between the residual pack ice in the polar basin and terrestrial denning areas might make it more difficult for pregnant females to access traditional denning areas (Derocher et al. 2004) and at least one denning area has already been lost in Svalbard (Derocher et al. 2011). As the climate warms and the sea ice becomes progressively less compacted, the floes drift further apart and are more easily moved by wind and currents. Therefore, polar bear movement rates are likely to increase with climate warming as sea ice becomes more mobile, forcing polar bears to move more actively if they want to maintain position (Mauritzen et al. 2003). For example, an analysis of polar bear sea ice habitat in the Foxe Basin area north of Hudson Bay suggested that habitat fragmentation may have negative effects on polar bears and that increased energy costs for moving between and within habitat patches while foraging could reduce energy stores necessary to endure a longer ice-free period caused by earlier melting (Sahanatien and Derocher 2012). Smaller patches of suitable habitat may entail more and longer swimming events as suitable habitat becomes more interspersed with open water, and increased swimming may have a negative impact on cub survival due to increased risk of hypothermia (Blix and Lentfer 1979; Monnett and Gleason 2006; Durner et al. 2011). Polar bears will continue to be affected by the large-scale changes in the annual patterns of break-up and freeze-up, and it is possible that present boundaries between populations may change as a result (Derocher et al. 2004). Therefore, it is important to understand when and where polar bears in particular populations are moving when out on the sea ice and what types of habitat are important to them. Though questions like these used to be challenging to answer, new insight into the WH population is being gained through the use of technologies that allow scientists to understand polar bear movements and distribution across space and through time. These advancements may allow insights into resource use, foraging strategies, and population dynamics (e.g., Jones 1977; Johnson et al. 2002; Fortin et al. 2003).

In recent years, the use of satellite and global positioning system (GPS) technology has increased, making it easier to examine the movements of large, wide-ranging animals, particularly in areas that are mostly inaccessible to humans (e.g., Jouventin and Weimerskirch 1990; Fritz et al. 2003). The polar bear, a non-territorial carnivore, travels thousands of kilometers over sea ice to hunt prey, but it is only relatively recently that scientists have been able to exploit GPS technology to better understand the structure and dynamics of polar bear distribution. Satellite tracking studies in the Beaufort Sea, the eastern high Arctic, Greenland, and the Barents Sea have revealed a significant degree of variation in movement patterns both within and between populations (Born et al. 1997; Messier et al. 2001; Mauritzen et al. 2003; Durner et al. 2004). Considering the different movement patterns among polar bears and the expectation that climate change will affect ice conditions (Gough and Wolfe 2001; Maslowski et al. 2001) and thus seal distribution (IUCN 2013; Chambellant et al. 2012b) differently in different regions of the Arctic, it is likely that individual polar bear population responses to climate change will vary.

Seal distribution, and therefore the distribution of polar bears, is influenced by shore leads, polynyas, and patterns of freeze-up and break-up of sea ice (Stirling and Øritsland 1995;

Stirling 2002). While there is this basic understanding of polar bear distribution, it may be hard to predict their distribution as sea ice habitat is dynamic and different demographic groups may use habitat in different ways. For example, females with cubs may select habitat differently from males by avoiding areas that have dynamic ice (to reduce cub mortality) and avoiding adult males that put the cubs at risk for predation (Stirling et al. 1993; Ferguson et al. 1997). The presence and age of cubs can also affect the home range size and location of the family group, as cubs of different ages have different energy requirements, consequently affecting the female's distribution and movements (Amstrup et al. 2000; Mauritzen et al. 2001). Therefore, to predict and understand change in a polar bear population, it is important to understand habitat selection.

Polar bear habitat selection differs between seasons, among populations and regions (Arthur et al. 1996; Ferguson et al. 2000; Mauritzen et al. 2003; Durner et al. 2009), and in response to the relative abundance of habitats (Mauritzen et al. 2003). Habitat selection by polar bears may be influenced by habitat characteristics such as ice age, concentration, and floe size, as well as snow depth, distance to shore, bathymetry (which influences productivity (Ryther and Yentsch 1957), including the breeding of ringed seals (Smith and Stirling 1975)), and proximity to open water (polar bears often hunt seals near open leads (Stirling et al. 1993)). Polar bears in the Canadian Archipelago and Baffin Bay regions follow seasonal changes in ice, and their selection for habitat was best explained by specific types of ice thought to represent areas where the most seal pupping occurred in spring (Ferguson et al. 2000). Polar bears may also adjust their habitat use or selection if habitat conditions change over time, known as a functional response. A functional response, where selection for a specific habitat attribute changes as a function of the attribute's abundance on the landscape (Mysterud and Ims 1998; Hebblewhite and Merrill 2008; Houle et al. 2010), can serve as a behavioural indicator of changes in the habitat quality for a species (Mysterud and Ims 1998; Hebblewhite and Merrill 2008; Herfindal et al. 2009; Gillies and St. Clair 2010). Thus, understanding how changes in sea ice affect habitat selection in polar bears over space and time may be important for the management.

The objective of Chapter 2 is to examine the distributions of WH female polar bear home ranges over time to determine if home range size and location change between seasons, across years, or between decades. I compare annual home range sizes between the 1990s and 2000s, as well as seasonal home range sizes from 2004 to 2010. I consider the reproductive classes of the bears and test whether this plays a role in home range size or location. Additionally, I examine the centroids of each home range to determine how far they are from the coast and if this distance is changing across years, as well as comparing centroid shift in different seasons to explore seasonal differences in distribution. When examining home range size and location, I consider the reproductive class of each bear, the effects of large-scale climate patterns, and the timing of ice break-up and freeze-up to assess if any of these factors may play a role. Furthermore, I examine the present WH boundary to assess its utility for population management throughout a given year. I hypothesize that WH distribution will change between seasons and across years in response to shifting ice conditions, with both the timing of ice events and reproductive class being important factors.

In Chapter 3, I examine habitat selection of WH polar bears by building a discrete-choice model with random effects to consider individual differences within the population. Eleven habitat covariates are used to find which parts of the sea ice environment might be most important to Hudson Bay polar bears. I hypothesized that WH bears will exhibit a functional response whereby their habitat selection will vary as a function of what is available on the seascape. Ice conditions will vary in importance based on the time of year. I believe that individual bears will make different choices and that this will be most clear during freeze-up and break-up, the two most dynamic seasons where bears have to make more choices than during the more stable, completely ice-covered seasons. Finally, because WH bears exhibit site fidelity, I hypothesize that the distance to their denning area will be an important factor in habitat selection, especially during late winter and break-up, as the bears get closer to coming back on land.

Currently, polar bears are designated as Threatened in the United States (FWS 2008), as a species of Special Concern in Canada (COSEWIC 2008), and listed as Vulnerable internationally (Schliebe et al. 2008). The status of polar bears is based on observed and projected declines in sea ice and the resulting negative impact on polar bear body condition, survival, reproduction, abundance, and distribution. The predicted impact of climate change on ice conditions varies among regions, but it is believed that declines in seasonal ice will affect each polar bear population (Derocher et al. 2004; Stirling and Parkinson 2006). However, the populations may be affected differently with respect to reproduction and survival, depending on the regional distribution, abundance, and characteristics of sea ice (Stirling et al. 2008; Durner et al. 2009; Amstrup et al. 2010). The earlier melting and later reformation of sea ice will challenge the survival and reproduction abilities of polar bears, making it increasingly difficult for them to thrive (Stirling and Parkinson 2006; Molnár et al. 2010). Even for the weakest future scenario of greenhouse gas forcing, the ice-free season in Hudson Bay is predicted to be longer, due to both an earlier ice breakup and later freeze-up (Gagnon and Gough 2005b). If sea ice conditions further deteriorate in Hudson Bay, it is unlikely that there are sufficient resources to support viable populations of polar bears forced to live on land (Rode et al. 2010). It is possible that polar bears will disappear from the southern portions of their range within 30–40 years if the warming continues and sea ice is eliminated (Stirling and Derocher 2012; Castro de la Guardia et al.

2013). A better understanding of the WH situation may help us understand the effects that climate change will have on other, more northern, polar bear populations in the near future.

My study is the first to examine the on-ice movements of WH bears using GPS satellite collar data, allowing a further understanding of the complex relationship between sea ice extent and the population dynamics of polar bears. This habitat assessment of WH polar bears will help identify critical polar bear habitat and provide a better understanding of how climate change and associated changes in ice condition affect polar bear distribution and movement patterns. It is expected that sea ice will continue to decline in Hudson Bay (Castro de la Guardia et al. 2013); recognition of essential habitat, for polar bears as well as other sea ice-dependent animals, will help ensure that native species can persist in this region in the coming decades.

CHAPTER 2- HOME RANGE DISTRIBUTION OF POLAR BEARS IN WESTERN HUDSON BAY.

Introduction

The distribution of animals and the geographic range of species are largely influenced by climate and the spatial patterning of habitat resources (Andrewartha and Birch 1954; Brown 1984; Parmesan and Yohe 2003; Thomas et al. 2004). Animals may use habitat resources in a manner that identifies an underlying mechanism or mechanisms such as foraging (MacArthur and Pianka 1966), inter- and intraspecific competition (MacArthur and Levins 1964; Charnov 1976; Elkin and Reid 2010), and mating (Orians 1969; Emlen and Oring 1977). In the past, climate shifts have led to the modification or loss of habitats and the creation of new ones; these shifts are often followed by adaptive radiations and extinctions, population expansions and contractions, and changes in individual dispersal and breeding behavior (Hewitt 1989, 1986, 2000; Weider and Hobaek 2000). Recent climate warming coupled with climate models that project a warming trend (Vinnikov et al. 1999; Comiso 2003; IPCC 2013 Walsh 2008) point to habitats being affected worldwide. Similar to past climate shifts, the ranges of many species are expected to shift northward or to higher elevations as animals seek suitable conditions and appropriate habitat, though the time scale over which these shifts will happen will depend on the region and species (Thomas and Lennon 1999; Root et al. 2003; Parmesan 2006; Grebmeier 2012).

Polar marine environments will be particularly impacted by climate change and recent warming has already been associated with environmental changes in these habitats. Increased temperatures were linked to changes in sea ice cover, sea level, water temperature, and ocean currents (Parkinson and Cavalieri 2002; Comiso and Parkinson 2004; Walsh 2008). Sea ice is especially sensitive to climate change, showing reductions in area, thickness, and timing of ice cover with warming (Maslanik et al. 1996; Parkinson 2000; Serreze et al. 2007; Markus et al. 2009); these reductions are expected to continue (Holland et al. 2006; Stroeve et al. 2007; Joly et al. 2010; Castro de la Guardia et al. 2013). Distribution shifts for sea ice-dependent animals are difficult to predict because warming temperatures and altered atmospheric circulation can cause considerable changes in the extent, duration, and character of annual sea ice that vary geographically (Vinnikov et al. 1999; Lindsay and Zhang 2005; Stroeve et al. 2005). Decreases in sea ice affect productivity and the entire food web in polar and subpolar waters (Arrigo et al. 2004; Smetacek and Nicol 2005; Chambellant et al. 2013). Climate change is amplified at higher latitudes (Hassol 2004; Bekryaev et al. 2010) and thus impacts on Arctic species have become increasingly apparent in recent decades (O'Corry-Crowe et al. 1997; Palsbøll et al. 1997; Andersen et al. 1998; Mellows et al. 2012). Arctic marine mammals are considered particularly at risk to climate change because many of these species rely on sea ice (Stirling and Derocher 1993; Tynan and DeMaster 1997; Laidre et al. 2008). Changes in sea ice have already affected Arctic marine mammals through loss of habitat (Laidre et al. 2008), declining health and condition (Burek et al. 2008), altered prey availability and foraging behaviour (Bluhm and Gradinger 2008), and increased human activities (Hovelsrud et al. 2008). Southern areas, such as Hudson Bay, Canada, have seen particularly significant changes in sea ice over the past several decades (Gagnon and Gough 2005; Hochheim et al. 2011).

Sea ice in Hudson Bay has a distinct pattern of freeze-up and break-up where the annual sea ice forms typically in November and persists until about June (Prinsenberg 1988). Freeze-up begins along the coast north of Rankin Inlet in late October and moves southward, forming a rim of ice several kilometres wide. A recurrent lead rings the Bay near the shore and at fast ice edges when the wind blows offshore (Stewart and Barber 2010). These leads most commonly occur along the west shore of Hudson Bay from Churchill to Coral Harbour, as well as in northern Hudson Strait (Markham 1986). There are recurring polynyas throughout the Bay region including northwest and southeast Foxe Basin, islands along the southeast coast, and in James Bay (Martini and Protz 1981; Stirling and Cleator 1981; Gilchrist and Robertson 2000). The ice begins to break-up in May and is completely gone by mid- to late summer, with the last of the major ice floes occurring off the coast of Manitoba and Ontario (Gough and Wolfe 2001). Spring temperatures in this region have increased by 2-3°C over the last 50 years (Skinner et al. 1998; Gagnon and Gough 2005; Castro de la Guardia et al. 2013) and, as a result, the sea ice now breaks up approximately three weeks earlier than it did 30 years ago (Stirling and Parkinson 2006). These sea ice changes are affecting many species (Higdon and Ferguson 2009; Bailleul et al. 2012; Gaston et al. 2012).

Mounting evidence suggests rising global temperatures may alter the timing and magnitude of seasonal environmental changes and disturb annual movement patterns of many Arctic mammals (Tynan and DeMaster 1997; Freitas et al. 2008; Moore and Huntington 2008), including polar bears (*Ursus maritimus*) (see review by Stirling and Derocher 2012). Changing ice patterns affect the Western Hudson Bay (WH) polar bear population because they depend on sea ice for foraging, travelling, and some aspects of reproduction (Stirling and Derocher 1993; Amstrup 2003; Derocher et al. 2004). Polar bears rely on ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) as their primary prey (Thiemann et al. 2008, 2011). Distribution of seals, and therefore distribution of polar bears, is influenced by many factors including shore leads, polynyas, bathymetry, ice thickness and size, and patterns of freeze-up and break-up of sea ice (Stirling and Øritsland 1995; Stirling 2002). Sea ice patterns in turn can be linked to wind, currents, and temperatures (Bourke et al. 1987; Wadhams 2012) as well as large-scale weather patterns. Climate indices such as the Arctic Oscillation (AO) and the North Atlantic Oscillation (NAO) were linked to sea ice dynamics on regional scales (Serreze et al. 2000; Gong et al. 2007; Turner et al. 2007). Higher than normal sea-level pressure (negative index) over the Arctic results in colder conditions in northern areas, while lower sea-level pressure (positive index) over the Arctic results in a warming pattern and a northward influx of warmer Atlantic water. These large-scale atmospheric patterns can affect Arctic species due to their effects on climate and ability to alter habitat conditions (Aanes et al. 2002; Forchhammer and Post 2004; Derocher 2005; Chambellant et al. 2013).

The early break-up and/or late freeze-up of sea ice in Hudson Bay increases the on land fasting period for polar bears (Stirling et al. 1993; Derocher et al. 2004; Stirling and Parkinson 2006; Laidre et al. 2008). Earlier ice break-up was linked to declines in body condition, reproduction, survival, abundance, and increased human-bear conflict (Stirling et al. 1999; Stirling and Parkinson 2006; Regehr et al. 2007; Towns et al. 2009). These changes are thought to result from nutritional stress caused by reduced energy intake in combination with prolonged fasting. Before coming ashore, polar bears in Hudson Bay experience a hyperphagic period, which overlaps with the ringed seal pupping and breeding season (Ramsay and Stirling 1988; Stirling and Derocher 1993). Polar bears have high hunting success during the pupping season due to the availability of vulnerable and naïve pups (Stirling and Archibald 1977; Pilfold et al. 2012). This period of food abundance is critical for the reproductive success of females emerging from maternity dens with cubs in February/March (Derocher and Stirling 1994; Derocher et al. 2004; Molnár et al. 2011). Earlier spring break-up shortens the opportunity for polar bears to feed immediately before the ice-free fasting period and years with delayed freeze-up have detrimental effects on WH polar bears by postponing migration back to the sea ice (Stirling and

Derocher 1993; Derocher et al. 2004; Cherry et al. 2013). The date of freeze-up has been getting progressively later in many regions of Hudson Bay (Gagnon and Gough 2005; Hochheim and Barber 2010) resulting in increased concerns about future declines in reproduction and survival rates (Molnár et al. 2010, 2011).

Changes to the timing of the sea ice cycle could affect the distribution patterns of polar bears. Polar bears in WH show fidelity during summer to maternity denning areas near the Manitoba coast between the Churchill and Nelson rivers (Derocher and Stirling 1990; Stirling et al. 2004). Patterns of ice break-up, however, influence the movement of polar bears as they are returning to shore (Cherry et al. 2013). Because the last remaining ice during break-up is present adjacent to Manitoba and Ontario (Wang et al. 1994; Gough and Allakhverdova 1999; Saucier et al. 2004), if break-up takes place early, WH bears must either extend their hunting time by remaining on ice as it drifts towards the Ontario coast or leave the ice before it melts adjacent to Manitoba, resulting in a longer onshore fasting period. There is a balance between the length of time that bears can remain on the ice (hunting seals to accumulate fat) before it is no longer energetically cost-effective, and the amount of energy the bears would have to expend walking back along the coast if they were passively carried away from the study area on the drifting pack ice (Stirling et al. 1999; Cherry et al. 2013). Difference in break-up and freeze-up among years could affect the distribution of polar bear home ranges but this remains unexplored.

WH polar bears share Hudson Bay with two other populations: the Foxe Basin (FB) population and the Southern Hudson Bay (SH) population. The FB population uses northern Hudson Bay, while the SH population uses the south-eastern part of the Bay, including James Bay (Peacock et al. 2010). The established SH population boundaries generally reflect the spatial distribution of female polar bears in this population (Obbard and Middel 2012). The distribution of WH bears is less well understood, but overlap with the other two populations is evident (Peacock et al. 2010). Polar bears are not territorial, but have home ranges that vary in size depending on seal distribution, year or time of year, sea ice conditions, reproductive status, and individual behaviour (Ferguson et al. 1998; Mauritzen et al. 2001). The presence and age of cubs can affect a mother's home range size and location. In most populations, female polar bears keep their offspring for about 2.5 years before weaning, and thus mate every 3 years (DeMaster and Stirling 1981; Amstrup and DeMaster 1988; Ramsay and Stirling 1988). Cubs of different ages have different energy requirements, thus the reproductive status of the female (i.e., whether she is alone or accompanied by cubs, and the number and age of those cubs) may affect their family's distribution and movements (Amstrup et al. 2000; Mauritzen et al. 2001). Consequently, both changes in sea ice timing and maternal energy demands could affect female polar bear movement and distribution.

The WH population is the most studied polar bear population in the world, and one of the most southerly, providing an opportunity to examine the temporal dynamics of distribution in relation to a changing climate. Despite intensive research on the WH polar bears, there has been little investigation of their distribution during the on-ice period. In this study, I examine the distribution of adult female polar bears in the WH population using satellite telemetry to determine temporal dynamics in their home range areas and distributions. I compare annual minimum convex polygons (MCPs) of female polar bears in the 1990s to the 2000s, and examine annual and seasonal utilization distributions (UDs) in the 2000s. I hypothesize that there will be annual and seasonal changes in home range size, distance to land, and directional shifts over time related to changes in sea ice caused by shifting climate patterns in the region.

Materials and Methods

Study Area and Population

The shallow inland sea of Hudson Bay has a mean depth of 125 m and encompasses approximately 10^6 km^2 (Jones and Anderson 1994). Hudson Bay currents follow a large-scale counterclockwise gyre that moves south from Foxe Basin and exits through the Hudson Strait (Prinsenberg 1988). Ice starts forming mid- to late autumn in the northwest, and is pushed south by the gyre along the west coast towards Manitoba and Ontario. From late December until late April, ice cover reaches >9/10 with the maximum extent in April. From May to mid-August, break-up occurs due to warming temperatures; as the southernmost ice begins to melt, ice from the northwest is pushed south along the west coast (Maxwell 1986; Saucier et al. 2004). The Ontario coast usually has the last of the ice (Gough et al. 2004). The boundary of the WH polar bear population is bordered by 63°10'N and 88°30'W and includes coastal regions of Nunavut, Manitoba, and northwestern Ontario (Stirling et al. 1977, 1999) (Figure 2.1).

In summer and autumn, Hudson Bay is ice-free and the WH population is confined to a restricted area of the western coast (Stirling et al. 1977, 1999); the bears are spatially separated from their prey and must rely on fat stores until ice forms again. Female polar bears in this area come off of the ice about 21-28 days after the ice reaches 5/10 or less in Hudson Bay and an earlier break-up is correlated with the bears being in poorer condition (Cherry et al. 2013). Pregnant females must remain on land in maternal dens, give birth, and nurse until their cubs are large enough to venture onto the sea ice in early spring; this results in the females undergoing an extended fast lasting up to eight months (Ramsay and Stirling 1986; Watts and Hansen 1987). In winter and spring, the WH population disperses over the Bay to hunts seals.

Polar bear captures

Polar bears were captured and collared during two periods, 1990-98 and 2004-10, along the western coast of Hudson Bay between 57°00’N–58°50'N and 92°25'W–94°15'W, almost exclusively within Wapusk National Park, Manitoba (Figure 2.1). Bears were located from a helicopter and immobilized via remote injection of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®, Laboratories Virbac, Carros, France; Stirling et al. 1989). The location, sex, and reproductive status of the bears were recorded. All captures occurred on land either in August-September during the ice-free period. Adult females were collared with Doppler shift (DS) Argos® satellite-linked collars in 1990-98, and Telonics Gen III and IV global positioning system (GPS) Argos® satellite-linked collars in 2004-10. Collars were programmed to acquire 6 GPS locations per day (i.e., every 4 h) and one good location for each fix time was used when available. On-land locations were included for MCP calculations but were removed for all other analyses; locations with obvious errors (i.e., sudden far-reaching movements that were biologically impossible) were excluded from analyses.

Collars were deployed on solitary females and females with cubs-of-the-year (COYs) or with 1-year-old cubs (yearlings). Collared bears were classified according to reproductive status at the time of collaring. For all bears, status was updated for recaptured bears and as of each January 1, cub ages advanced one year. For example, if females were collared with COYs in September, those cubs were reclassified as yearlings at the start of the next Late Winter season (in order to not have the same bear with two reproductive statuses in Early Winter). If it was not possible to know the cub status of a female, she was classified as ‘‘unknown reproductive status’’ 1 year after capture. Males were not tracked because their necks are wider than their heads and collars could not be secured. Animal handling procedures were approved by the

University of Alberta BioSciences Animal Policy and Welfare Committee and the Animal Care Committee of the Canadian Wildlife Service (Prairie and Northern Region).

Statistical analyses

Bear locations were plotted as latitude north and longitude west (North American Datum 1983) and converted to universal transverse mercator coordinates for zone 15 in ArcGIS version 10.0 (Environmental Systems Research Institute Inc., Redlands, CA).

The area used to examine sea ice patterns was defined by a minimum convex polygon (MCP) for all on-ice bear locations (~56 000) (Figure 2.1). For seasonal analyses, I divided the year into four biologically relevant seasons based on both bear behaviour and ice conditions: freeze-up, early winter, late winter, and break-up. The four seasons were defined using mean ice concentrations within the MCP. Freeze-up was defined as 1/10 ice cover, winter at 9/10 cover, break-up 4/10 cover, and summer at 1/20 cover. I used ArcGIS to extract daily ice concentrations that were approximated from daily Special Sensor Microwave/Imager (SSM/I) passive microwave data (25x25 km resolution) from the National Snow and Ice Data Center (Boulder, Colorado). Dates when each ice concentration was realized were converted to ordinal number (e.g., January 1 = 1) and averaged over the study to compare polar bear locations used during the same periods each year. The same seasons were compared over time.

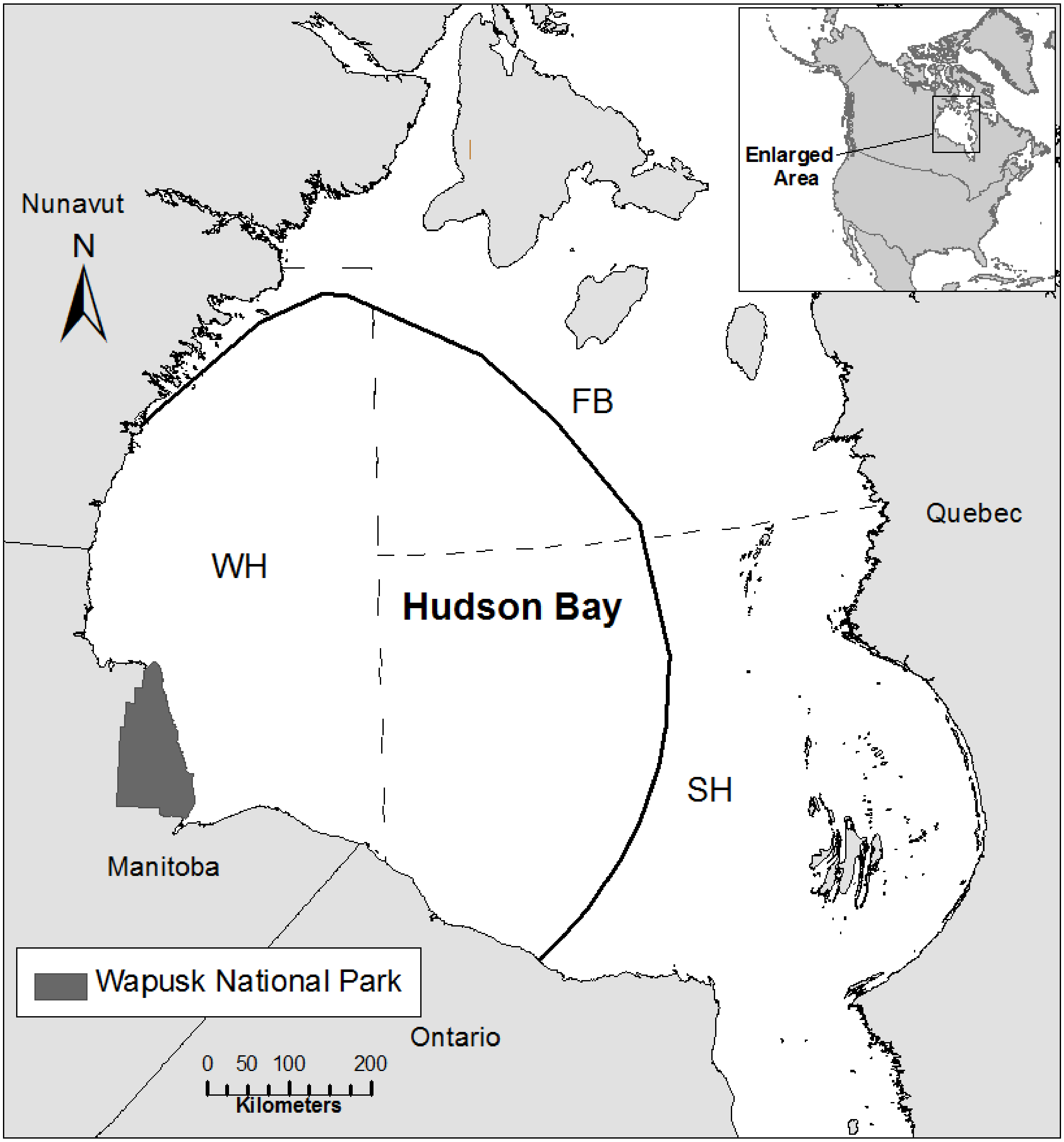

Figure 2.1. The 95% minimum convex polygon (black line and coastline of western Hudson Bay) of all on-ice GPS locations of western Hudson Bay polar bears from 2004-2010. Mean sea ice concentrations within this area were used to divide the on-ice period of polar bears into four seasons. Most polar bear captures occurred in Wapusk National Park (shaded area). The dashed line indicates the boundaries for the Western Hudson Bay (WH), Foxe Basin (FB), and Southern Hudson Bay (SH) populations as recognized by the IUCN/SSC Polar Bear Specialist Group (PBSG 2010).

I calculated both minimum convex polygon (MCP) (Hayne 1949) and the utilization distributions (UD) for annual home range sizes. Annual MCPs were created with ArcGIS for both 1990s DS data and 2000s GPS data using both on land and on ice locations. MCPs facilitate comparisons with other polar bear populations. I also calculated the number of locations inside and outside of the WH population boundary (PBSG 2010) by year and season. Argos® provided quality indices for the accuracy of each DS location and only locations with accuracy <1000 were used for MCPs. Accuracy of GPS collars is < 30 m. To compare the DS data to the GPS data, I subsampled the number of locations in the GPS data by randomly sampling a maximum of one location per week per bear and calculating mean MCP sizes with the subsample. The mean number of locations per year for the older satellite collars was 420 ± 96 (± 1 SE) and, after rarefying, the mean number of locations per year for GPS collars was 377 ± 55. Annual MCPs used locations from September 1 to August 31.

Smoothing factors and UDs were estimated using the KS package (Duong 2011) and adehabitat packages (Calenge 2006) developed for the R statistical computing software (R Development Core Team, Vienna, Austria). The areas of 95% UDs were calculated with ArcGIS. UDs define the home range boundary (x–y plane) and intensity of use (z-axis) throughout the home range (Millspaugh et al. 2004). Individual seasonal UDs were calculated when there were ≥ 20 locations in a season following Parks et al. (2006). I estimated seasonal 95% UDs for each GPS-collared bear using on ice data from 2004–2010 using fixed kernel analysis (Worton 1989) with the least-squares cross-validation method to determine the smoothing factor. Gitzen et al. (2006) found that the least-squares cross validation method produced an accurate estimate of a known UD when describing animal locations with a general distribution and a large sample size, like those seen for polar bears. Each UD represented a relative probability of use (sum to 1) and was directly comparable across bears.

All linear statistics were performed with SPSS® version 21.0 for Windows (SPSS Inc., Chicago, IL). For all analyses, I tested the null hypothesis that measured variables were independent of reproductive class, season, or decade using one-way ANOVAs or t-tests when data conformed to statistical assumptions of normality and equal variance. ANOVAs were followed by either Bonferroni test or nonparametric Tukey's test (Zar 1999) to determine significant differences. Non-normal data were transformed using used a $\log_{10}$ transformation but if heteroskedasticity remained, I used the Kruskal–Wallis *H* or Mann–Whitney *U* nonparametric test (Sokal and Rohlf 2001). Pearson's product-moment correlation (coefficient reported as *r*) was used for correlation. I correlated all variables with year to identify temporal relationships. When temporal trends were found, I tested whether they were correlated with ice events within that season (e.g., date of break-up). I correlated individual home range sizes and centroid distances with year and season to determine if some bears had consistently larger home ranges or longer distances from land than others. Additionally, I looked at correlations between successive seasons to determine if, for example, a large freeze-up range would be related to a large early winter range. I also examined relationships between home range size (annual MCP, annual UD, and seasonal UD) with the AO Index. Daily AO values from 2004-11 from the National Oceanic and Atmospheric Administration (www.noaa.gov), were averaged annually from September 1 to August 31 and seasonally for each of the four seasons for each year. This index represents the state of atmospheric circulation over the Arctic (Thompson and Wallace 1998). For all analyses, values are means ± 1 SE. Results were considered significant at $P \leq 0.05$.

To determine the seasonal distribution of animals, the distance between UD centroids and the nearest land on the west coast of Hudson Bay (from western James Bay to Chesterfield Inlet) was measured using the Feature to Point tool in ArcGIS. Home range centroids are a method that can be used to calculate distances and direction of shift for individuals in a population (Howery et al. 1996; Pellerin et al. 2008; Walter et al. 2009). I also constructed seasonal population home range UDs for each year by pooling all animals. To measure distribution changes, I used centroid shift and circular statistics calculated with ArcGIS. Vectors were calculated between centroids in concurrent years within the same season for 2004-10. The trend for a set of line features was measured by calculating the mean angle of the lines, known as the directional mean, which measures both the mean direction and orientation of the lines (Zar 1999). For each season, I calculated and mapped the mean direction and directional variance of centroid shift, distance of centroid shift, and geographic center of centroid shift.

The number of bears collared and transmission intervals varied, thus sample sizes differ for each analysis. Because the seasonal progression of freeze-up to break-up spans different years, I labeled all concurrent seasons with the year in which freeze-up occurred, referred to as Collar Year in figures, so that a collar that started being tracked during freeze-up of 2005 had all seasons of that year labeled under Collar Year 2005, even though parts of early winter, all of late winter, and all of break-up took place in 2006.

Results

DS collars were deployed on 46 females in 1990-98, and GPS collars on 79 females in 2004-10 (11 bears were collared twice, and 1 bear was collared three times). For DS collars, 3781 locations were analyzed totaling 63 bear years (17 bears had usable data for more than 1 year). For GPS collars, 53 079 locations were analyzed, totaling 81 bear years and 236 bear seasons (15 bears had usable data for more than 1 year; 16 collars failed to provide usable data). The number of GPS locations analyzed varied by season: 6418 for freeze-up, 21 665 for early winter, 23 942 for late winter, and 1054 for break-up.

Seasons

The start dates of the classified ice concentrations varied by year. The four on-ice seasons examined were: freeze-up (November 27 - December 18, 22 d), early winter (December 19 - March 14, 86 d), late winter (March 15 - July 1, 109 d), and break-up (July 2 - 14, 13 d). Winter was split at March 15, which approximates when mothers with newborn cubs should be on the sea ice, seals are starting to pup, and the mating season is starting.

Home Range Areas

The mean MCP size from 1991-98 ($\bar{x}$ = 264 356 ± 30 551 km^2, n = 81) was significantly different ($t_{(14)}$ =-2.13, P = 0.05) from the MCP size in 2004-10 ($\bar{x}$ = 357 750 ± 30 277 km^2, n = 88). The smallest annual MCP was recorded in 1998-99 while the largest was in 2010-11 (Figure 2.2). MCP data were normally distributed and not correlated with year (r = 0.41, P = 0.12) or mean annual AO values (r = 0.23, P = 0.39).

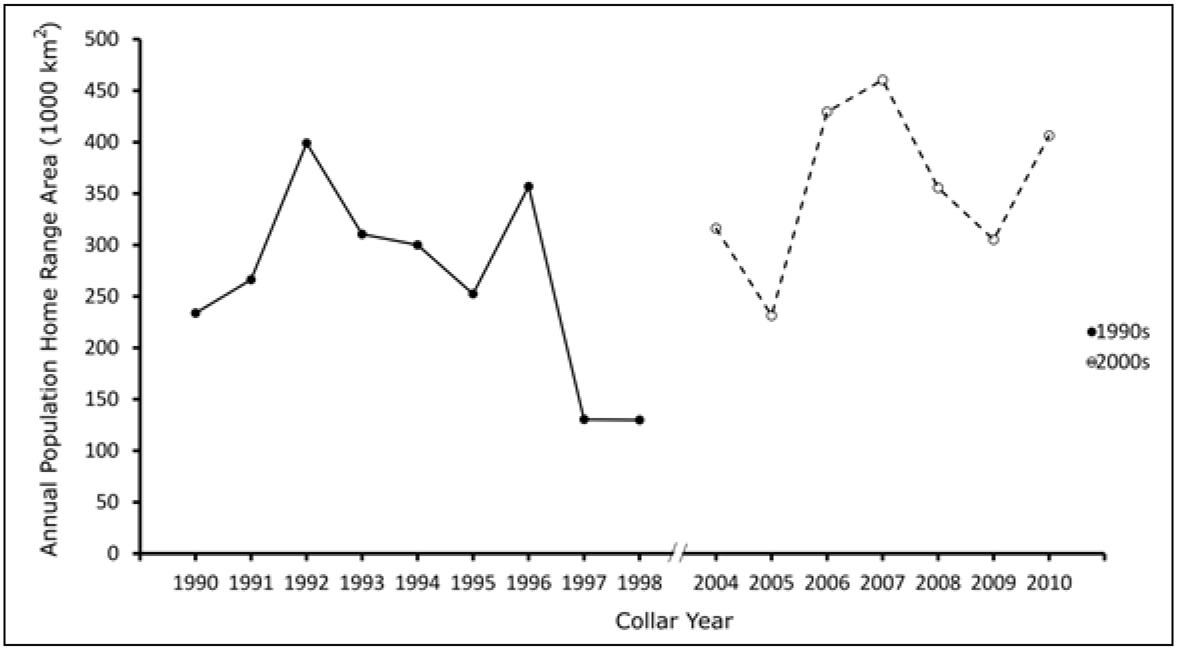

Figure 2.2. Annual minimum convex polygon area (1000 km^2) for collared western Hudson Bay female polar bears. Data include both on land and on ice locations; years run from September 1 to August 31. Data from the 1990s are from satellite collars and 2000 data are from GPS collars. GPS collar data was rarefied to 1 location per week per bear to be comparable to the satellite collar data.

The mean 95% UD home range size for all GPS collar data from 2004-10 was 135 953 ± 21 993 km^2. The smallest 95% UD was in 2007-08, while the largest was in 2010-11 (Table 2.1)

Table 2.1. Pooled annual 95% UD home range size (km^2) for all collared female polar bears in western Hudson Bay. Only on-ice values are included. Years run from November to July.

Collar year	Annual 95% UD area (km^2)	n
2004	171 889	9
2005	163 185	10
2006	74 745	11
2007	57 676	21
2008	98 847	15
2009	175 350	10
2010	209 976	11

Pooled annual 95% UDs in 2004-10 revealed substantial variation in use of Hudson Bay (Figure 2.3). There were areas in just west of the middle of Hudson Bay that included all annual

UDs while areas in the northern and eastern parts had more limited use. Data were normal and area was slightly negatively correlated with the mean annual AO (r = -0.68, P = 0.09).

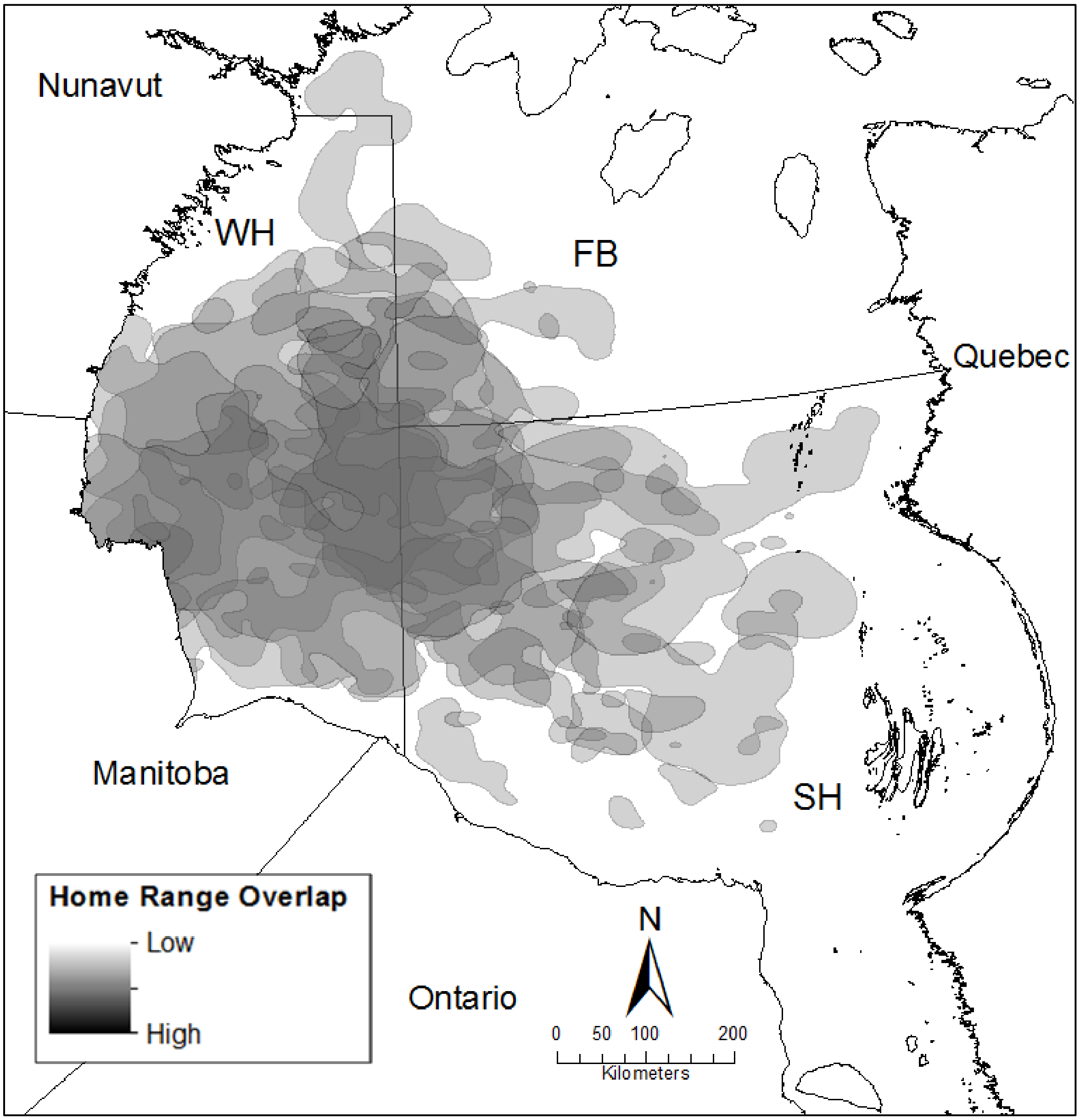

Figure 2.3. All annual 95% utilization distributions (UD) for 2004-10 for western Hudson Bay polar bears. Darker grey areas show more overlap of UDs while lighter grey areas show less overlap. The solid lines indicate the boundaries for the Western Hudson Bay (WH), Foxe Basin (FB), and Southern Hudson Bay (SH) populations as recognized by the IUCN/SSC Polar Bear Specialist Group (PBSG 2010).

The number of locations that fell within the WH population boundary varied by season and year (Table 2.2). Freeze-up had the highest mean number of locations inside the boundary, while early winter had the lowest mean number.

Table 2.2. The percent of locations of WH female polar bears that fell within the designated WH population boundary by year and season, 2004-11.

Collar year	Freeze-up (%)	Early winter (%)	Late winter (%)	Break-up (%)	$\bar{x}$ ± SE
2004	54	36	55	NA	48 ± 6
2005	87	63	100	100	88 ± 9
2006	84	13	55	38	48 ± 15
2007	37	35	81	65	55 ± 11
2008	61	28	45	60	49 ± 8
2009	100	52	67	100	80 ± 12
2010	88	26	49	48	53 ± 13
$\bar{x}$ ± SE	73 ± 9	36 ± 6	65 ± 7	68 ± 11	

Seasonal home range sizes for individuals were also found to be quite variable. Overall, the largest seasonal home range was during freeze-up, and the smallest home range was during early winter (Table 2.3); both were recorded from females with yearlings.

Table 2.3. Pooled seasonal 95% utilization distribution home range sizes (km^2) of satellite-collared female polar bears from the western Hudson Bay population, 2004-11.

Season	Mean ± SE (km^2)	*n*	Minimum (km^2)	Maximum (km^2)
Freeze-up	29 170 ± 4079	59	818	172 962
Early winter	29 027 ± 2454	73	21	106 345
Late winter	30 733 ± 2535	69	77	67 936
Break-up	1404 ± 294	34	34	7410

For all seasons together, home range size was somewhat negatively correlated with year (r = -0.12, P = 0.06). Successive seasons' home range sizes were not correlated with each other (freeze-up and early winter: r = -0.13, P = 0.34; early winter and late winter: r = 0.06, P = 0.62; late winter and break-up: r = -0.15, P = 0.41). However, home range sizes significantly varied with season (ANOVA, $F_{(3,231)} = 15.12$, $P < 0.01$) (Table 2.4; Figure 2.4) for all reproductive classes. The Bonferroni test for multiple comparisons showed that break-up season (1404 ± 294 km^2) had smaller home ranges than freeze-up (29 170 ± 4079 km^2), early winter (29 027 ± 2454 km^2), and late winter (30 733 ± 2535 km^2). Home range size also varied with reproductive class (ANOVA, $F_{(2,232)} = 3.28$, $P = 0.04$) but the Bonferroni test for multiple comparisons showed no significant differences between groups.

Table 2.4. Seasonal 95% utilization distribution home range sizes (km^2) of satellite-collared female polar bears from the western Hudson Bay population, 2004-2011, divided by reproductive status.

	Freeze-up		Early Winter		Late Winter		Break-up	
Reproductive class	Mean ± SE (km^2)	*n*	Mean ± SE (km^2)	*n*	Mean ± SE (km^2)	*n*	Mean ± SE (km^2)	*n*
Female with COYS	32 846 ± 6152	35	29 202 ± 3130	43	NA		NA	
Solitary female	13 783 ± 7310	3	24 896 ± 18 773	5	30 546 ± 3763	29	512 ± 184	11
Female with yearlings	25 242 ± 6152	21	29 551 ± 3371	25	30 868 ± 3459	40	1830 ± 399	23
Overall	29 170 ± 4079	59	29 027 ± 2454	73	30 733 ± 2535	69	1404 ± 294	34

Note: COYS are cubs-of-the-year.

There were no significant differences in home range size among reproductive classes during freeze-up (Kruskal-Wallis, $H = 1.79$, $P = 0.41$), so classes were pooled. Freeze-up home ranges decreased by 77% from 45 621 km^2 to 10 458 km^2 from 2004 to 2010 ($r = -0.34$, $P = 0.01$), and the correlation between size and freeze-up date ($r = -0.44$, $P < 0.01$) was significant.

There were no significant differences in home range size among reproductive classes during early winter (Kruskal-Wallis, $H = 2.35$, $P = 0.31$), so classes were pooled. Early winter mean home range was negatively correlated with year ($r = -0.24$, $P = 0.05$), but was not to the freeze-up date ($r = 0.19$, $P = 0.12$).

During late winter and break-up, I could not assume that mothers had COYs, so I compared solitary females to females with yearlings. There were no significant differences in home range sizes across reproductive classes in late winter (Mann-Whitney *U* test, $U = 566$, P =0.86), so classes were pooled. There was no relationship between home range size and year in late winter (r = 0.07, P = 0.59). Late winter home range area was negatively correlated to freeze-up date (r = -0.24, P = 0.05) but not to break-up date (r = 0.09, P = 0.46).

During break-up, solitary females had smaller home ranges than females with yearlings (Mann-Whitney *U* test, *U* = 56.5, *P* = 0.01). For both mothers with yearlings (r =0.17, P = 0.43) and mothers with COYs (r = -0.26, P = 0.43), mean home range size was not related to year (no telemetry data during break-up was available for 2004). Overall, home range area during this season was not significantly correlated to break-up date (r = 0.14, P = 0.41) even when controlled by reproductive class (r = -0.20. P = 0.91).

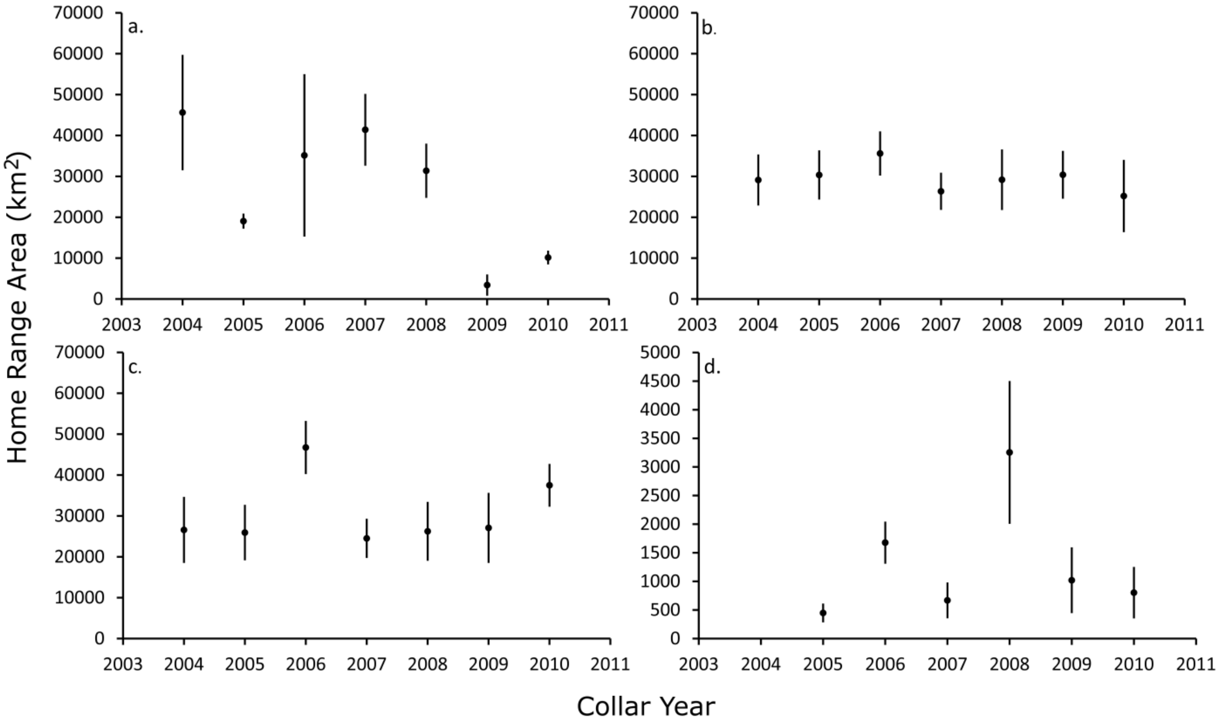

Figure 2.4. Mean seasonal home range size (km^2) ± 1 SE for western Hudson Bay female polar bears for 2004-10: a = freeze-up, b = early winter, c = late winter, d = break-up.

Seasonal home range size was positively correlated to the mean seasonal AO value (r = 0.22, P < 0.01).

Home Range Centroids

The centroid farthest from land was recorded during early winter for a female with yearlings, and several centroids were on shore during freeze-up and break-up for all females (Table 2.5). Values of 0 km for early winter were removed as they were likely due to maternity denning; values of 0 in freeze-up and break-up were included because ice conditions could result in use of land.

Table 2.5. The seasonal population 95% utilization distribution centroid distance from land (km) for satellite-collared female polar bears from the western Hudson Bay population, 2004-11.

Season	Mean ± SE (km)	*n*	Minimum (km)	Maximum (km)
Freeze-up	103 ± 11	59	0	288
Early Winter	199 ± 8	73	16	323
Late Winter	140 ± 9	69	11	300
Break-up	70 ± 10	34	0	199

Centroid distribution was non-normal and $\log_{10}$ transformed. Centroid distance to land was not related to individual (ANOVA, $F_{(62,172)} = 0.74$, $P = 0.92$). Distance to land was negatively correlated with freeze-up date ($r = -0.31$, $P < 0.01$), and also differed significantly with break-up date ($r = 0.30$, $P < 0.01$), even when controlled by year ($r = 0.31$, $P < 0.01$) and season ($r = 0.45$, $P < 0.01$). Centroid distances were positively correlated with seasonal AO mean ($r = 0.15$, $P = 0.03$).

Concurrent season home range sizes were not related to each other (freeze-up and early winter: $r = -0.5$, $P = 0.29$; early winter and late winter: $r = -0.03$, $P = 0.80$; late winter and break-up: $r = 0.13$, $P = 0.50$). Distance to land varied by season (ANOVA, $F_{(3,231)} = 18.71$, $P < 0.01$) (Table 2.6; Figure 2.5); the Bonferroni test indicated that both early winter ($\bar{x}$ =199 ± 8 km) and late winter (140 ± 9 km) differed significantly from all other seasons, but freeze-up (103 ± 11 km) and break-up ($\bar{x}$ = 70 ± 10 km) did not differ from each other. For all seasons grouped, distance to land varied by reproductive classes of polar bear (ANOVA, $F_{(2,232)} = 4.48$, P = 0.01). Solitary females had smaller centroid distances to land than females with COYs (Bonferroni test).

During freeze-up, there were no significant difference in centroid distance between reproductive classes (Kruskal-Wallis, $H = 2.56$, $P = 0.28$) (Table 2.6). Classes were pooled for further analyses. Mean centroid distance to land was 111 ± 30 km in 2004 compared to 56 ± 24 km in 2010, and centroid distance to land in this season was negatively correlated with year (r = -0.28, P = 0.04).

Table 2.6. Seasonal 95% utilization distance from land distances from land (km) for satellite-collared female polar bears from the western Hudson Bay population, 2004-11, divided by reproductive status.

	Freeze-up		Early Winter		Late Winter		Break-up	
Reproductive class	Mean ± SE (km)	*n*	Mean ± SE (km)	*n*	Mean ± SE (km)	*n*	Mean ± SE (km)	*n*
Female with COYS	106 ± 13	35	185 ± 13	43	NA		NA	
Solitary/unknown female	24 ± 12	3	79 ± 49	5	131 ± 15	29	77± 20	11
Female with yearlings	109 ± 20	21	191 ± 16	25	147 ± 11	40	67 ± 11	23
Overall	103 ± 10	59	180 ± 10	73	140 ± 9	69	70 ± 10	34

Note: COYS are cubs-of-the-year.

In early winter, there were no significant differences in centroid distances among reproductive classes (Kruskal-Wallis, $H = 4.62$, $P = 0.10$), so classes were pooled. In 2004, mean distance to land was 164 ± 32 km compared to 160 ± 32 km in 2010; distance to land was not associated with year (r = -0.04, P = 0.76).

In late winter, I could not assume that mothers had COYs, so I compared unknown/single females to females with yearlings and found no significant differences between reproductive classes (Mann-Whitney *U* test, $U = 501$, $P = 0.34$). Distance to land was not correlated with year (r = 0.02, P = 0.86).

During break-up, centroid distances were comparable for solitary females (77 ± 20 km, n=11) and females with yearlings (67 ± 11 km, n=23) (Mann-Whitney *U* test, $U = 118$, $P = 0.77$). I could not assume COYs during this season, so only the two groups were compared. Mean centroid distance to land was 24 km ± 12 in 2004 compared to 159 ± 23 km in 2010 and was positively correlated with year (r = 0.41, P = 0.03), but was not with break-up date (r = -0.05, P = 0.81).

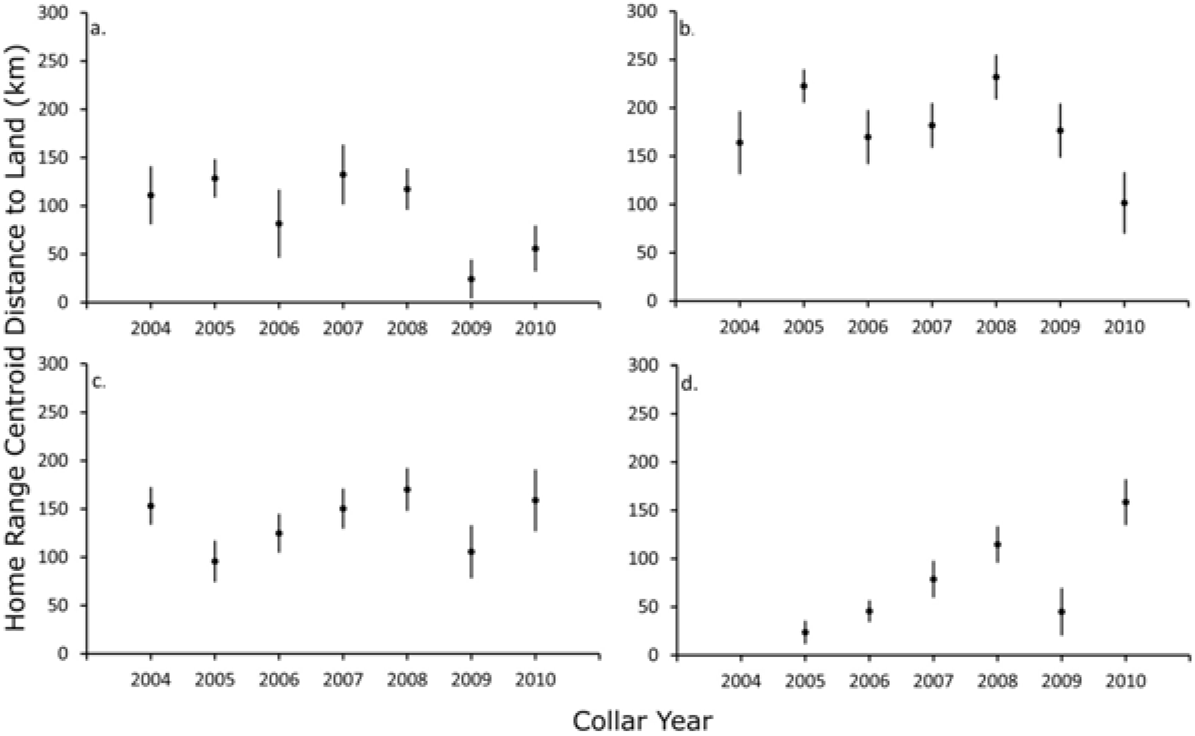

Figure 2.5. Mean seasonal home range centroid distance to land (km) ± 1 SE for WH female polar bears from 2004-10: a = freeze-up, b = early winter, c = late winter, d = break-up.

Home range centroids shifted location each year with various magnitudes and directions in different seasons. The two transition seasons have also had opposite shifts, with freeze-up centroids having shifted toward the west coast of Hudson Bay and break-up centroid having shifted away from the coast (Figure 2.6: Table 2.7). Early winter centroids have shifted north-westerly while late winter seasonal centroids shave shifted south-easterly.

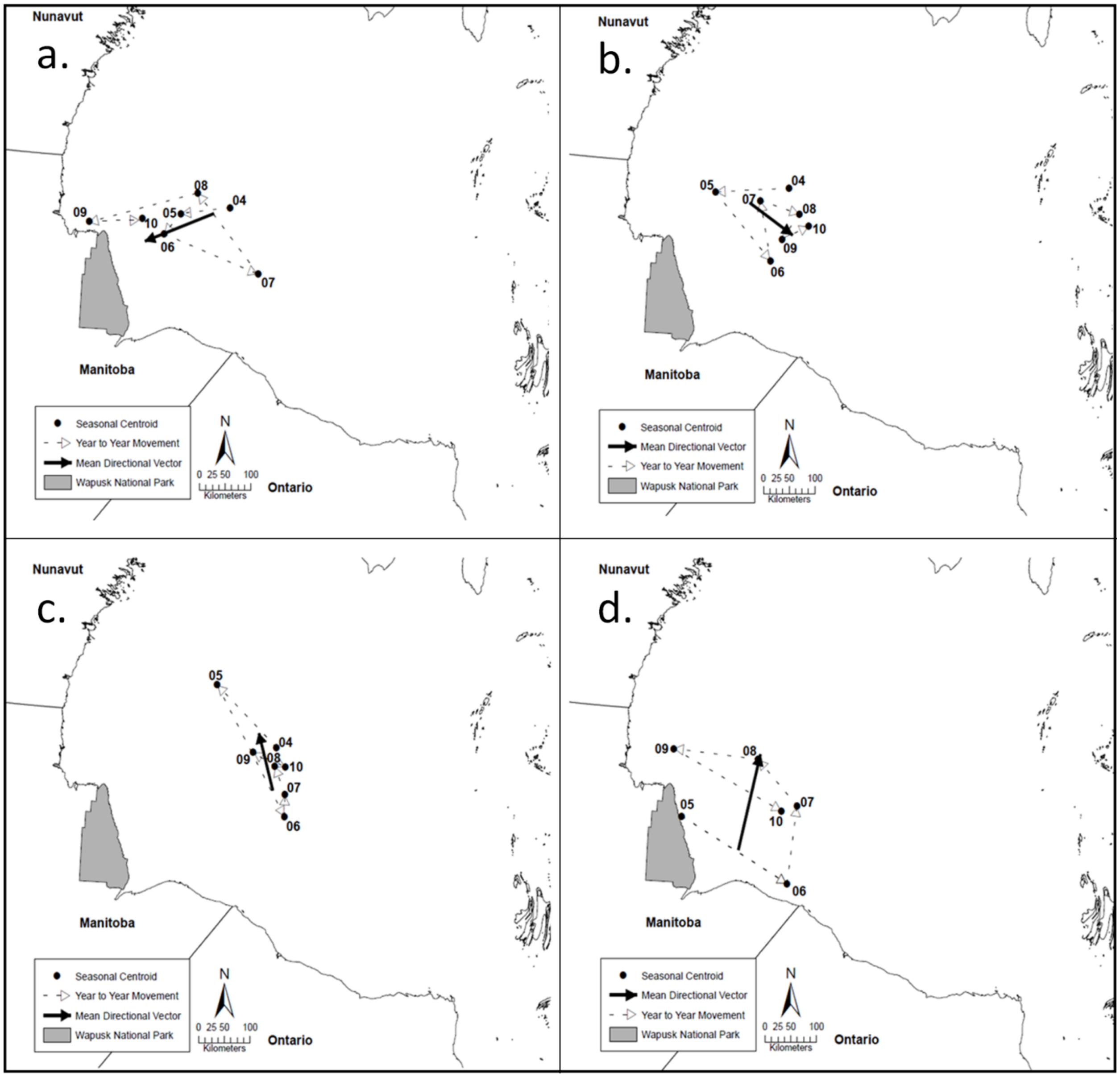

Figure 2.6. The seasonal home range centroid shifts (dotted lines) for WH polar bears by year with the mean linear directional vector (solid lines): a = freeze-up, b = early winter, c = late winter, d = break-up.

All seasons had a relatively high level of circular variance (Table 2.7): a circular variance of 0 would indicate all vectors have the exact same (or similar) variance, whereas a circular variance of 1 suggests that the input vectors cover the entire compass.

Table 2.7. The linear directional mean of seasonal centroid vectors from 2004 to 2010.

Season	Direction (°)	Circular variance	Mean length of shift (km) ± SE
Freeze-up	249	0.8	144 ± 28
Early winter	345	0.7	108 ± 38
Late winter	125	0.9	103 ± 19
Break-up	144	0.8	180 ± 25

Late winter had the highest circular variance while early winter had the lowest; break-up had the largest mean distance between seasonal centroids while late winter had the smallest mean length of centroid shift.

Discussion

Satellite collars have been used to determine multiple polar bear population home range sizes in different environments. Polar bear home range size is influenced by the availability and predictability of prey (Ferguson et al. 1999; Mauritzen et al. 2003). Home range sizes are larger where when they encompass considerable amounts of multiyear ice or land, such as the Beaufort Sea or Arctic Archipelago (Stirling and Øritsland 19995; Ferguson et al. 1999) and smaller where there is annual ice and shallow water, such as in Hudson Bay. This is due to the polar bear's main prey, ringed seals and bearded seals, preferring shallower water (Kingsley et al. 1985; Gjertz et al. 2000) and being less abundant in multiyear ice (Kingsley et al. 1985; Frost et al. 2005). The largest ranges were reported in the Beaufort Sea (166 694 km^2; Amstrup et al. 2000) and the Canadian Archipelago (125 500 km^2; Ferguson et al. 1999), expansive regions with multiyear sea ice, and were highly variable, with some as large as 600 000 km^2. The combination of annual ice, higher solar input than northern areas, and shallow depths means that Hudson Bay productivity is high (Maxwell 1986; Roff and Legendre 1986) compared to other areas at higher latitudes. Hudson Bay is considered productive with a mean productivity (mainly estimated in southeastern Hudson Bay) of 35 g of C/m^2, the highest levels (175 g of C/m^2

annually) being found around the small islands located in eastern Hudson Bay (Roff and Legendre 1986). Arctic shelves, in comparison, have an average annual productivity of 40 - 90 g C/m^2 (Hill and Cota 2005), with the Arctic Basin at <7 g C/m^2 (Lee and Whitledge 2005). Seals have access to the entire Bay and are found at higher densities than in other areas of the Arctic (Lunn et al. 1997). Furthermore, hunting and mating occur exclusively on the ice, thus this on-ice period is critical to polar bear survival and reproductive success (Stirling and Derocher 1993; Atkinson and Ramsay 1995; Derocher et al. 2004). This study examined annual and seasonal patterns of polar bear distribution on the sea ice of Hudson Bay in the 1990s and 2000s. I found that the seasonal home range size of WH polar bears varied between seasons and across years, relating to the timing of ice freeze-up and break-up, AO, and reproductive class. Changes in on-ice movements, both annually and seasonally, are expected to be due to the changing climate and resulting shift in ice conditions during the period of this study. In particular, there was a difference in annual home range size between the 1990s and 2000s.

The annual home range of WH polar bears reported by Parks et al. (2006) using MCPs constructed with DS satellite data from the 1990s found that WH polar bear movement patterns were not dependent on reproductive status but changed with season. They also showed a decreased area covered from 1991 to 1998 that was correlated with earlier break-up in Hudson Bay. Parks et al. (2006) suggested the decline in polar bear condition was due to decreased prey, not energy expenditure. The annual home range size decrease reported by Parks et al. did not continue into the 2000s. In contrast, my MCPs indicate that the 1990s and 2000s had significantly different annual population home range sizes, with the 2000s being larger. While the area covered by the population may have increased, individuals differ in how they use Hudson Bay. This was illustrated by comparing MCPs and UDs in the 2000s. For example, the

MCP for 2007 was relatively large, but the corresponding annual 95% UD was considerably smaller. This indicates that in that given year, most bears used a relatively small part of Hudson Bay but some individuals used a different region and covered a much larger area. It is unclear why this difference exists and multiyear tracking of individuals will be necessary to determine the importance of repeated use of areas and if they correspond to particular ice conditions.

Minimum ice cover in Hudson Bay has decreased by 11% per decade from 1968–2008 (Tivy et al. 2011), a trend tied to an advance in break-up date and ice clearance (Gagnon and Gough 2005; Hochheim et al. 2010). Variations in sea ice concentration and extent throughout both the Arctic and sub-Arctic were ascribed to both anthropogenic greenhouse gas emissions and low-frequency oscillations in atmospheric circulation (Johannessen et al. 2004; Holland et al. 2006). Hudson Bay may have undergone a climate regime shift in the mid-1990s, resulting in a significant reduction in sea ice during freeze-up (Hochheim and Barber 2010). They proposed that these climate shifts were related to atmospheric indices including the East Pacific/North Pacific, NAO, and AO indices, which were highly correlated with each other. Furthermore, Chambellant et al. (2012) proposed that a decadal-scale biological cycle accounted for fluctuations in climatic variables, including the sea ice regime, in Hudson Bay. My results may reflect this, demonstrating a link between AO and polar bear home range size, as well as AO and home range centroid distance to land. Such shifts in large-scale climate patterns can have direct impacts on sea ice dependent species. For example, changes in marine bird diets were related to NAO and ensuing changes in ice break-up dates in Hudson Bay during the mid-1990s (Gaston et al. 2012). Further, Ferguson et al. (2005) reported differences in density and demographic parameters of Hudson Bay ringed seals between the 1990s and 2000s. In the 1990s, environmental conditions were unfavorable for ringed seals, but conditions improved in the

2000s and ringed seals responded with a higher proportion of pups and juveniles; there were three times as many ringed seal pups in the 2000s than in the early 1990s (Ferguson et al. 2005; Chambellant et al. 2012). While we see both a healthier seal population and larger polar bear home range sizes in the 2000s, there is also a higher proportion of polar bears with poor body condition compared to the early 1990s, likely related to the decreased hunting time for polar bears (Stirling et al. 1993; Stirling et al. 1999; Derocher et al. 2004; Stirling and Parkinson 2006; Regehr et al. 2007) but the larger home ranges also raise concerns about increased energy expenditure.

Freeze-up has been progressively more delayed in the last decade (Gough et al. 2004; Gagnon and Gough 2005; Hochheim and Barber 2010) and as a result, polar bears now get onto the ice later than several decades ago (Stirling and Parkinson 2006; Cherry et al. 2013). This later freeze-up date has consequences: by this time of the year, polar bears have already gone without food for up to five months and an additional period of fasting could have negative consequences (Stirling et al. 1999; Regehr et al. 2007; Molnár et al. 2010). Though the freeze-up season was shorter than both winter seasons in my study, large movements occur when polar bears first get on the ice to hunt (Stirling et al. 1977; Derocher and Stirling 1990). Some bears travel as far as possible as the ice is forming, following the expanding ice edge to hunt seals. In my study, the largest individual seasonal home range was observed during freeze-up. Such far-ranging movements that occur during freeze-up may explain why the date of ice freeze-up was related to home range size for this season. A later freeze-up means that bears have less time for travelling before the early winter season, resulting in smaller seasonal home range sizes. This time restriction also affects how far polar bears can get from land during this season. As a result, during freeze-up from 2004 to 2010, the center of activity for WH bears moved closer to the coast of Wapusk National Park. Less centroid shift was recorded during the winter seasons, and in both cases the overall direction of shift was not directly away or toward land. Circular variance was high across all seasons likely due to the bears responding to prey and ice conditions. Early winter centroids were the farthest from land recorded, but overall home range size during this season was fairly consistent over time and similar to the late winter range sizes. Late winter, which experienced the smallest mean centroid shift by distance, encompassed most of April to June, when both ringed seals and bearded seals haul out onto the ice to moult or pup. Naïve and vulnerable seal pups, which are 50% fat by wet mass, become plentiful (Stirling and McEwan 1975; Kingsley and Stirling 1991; Stirling and Øritsland 1995) and bears need to obtain enough fat stores to sustain themselves throughout the ice-free period. If the ice-free period begins earlier, polar bears have less time to accumulate fat, thus the timing of Hudson Bay's to being ice-free is critical for the bears.

By 2010, WH polar bears were farther from land during the break-up season than they were in 2004. Furthermore, directional vectors indicate that break-up centroids have shifted northeast in Hudson Bay from 2004 to 2010, moving away from Wapusk National Park where these bears were spent the ice-free period. Yet, Cherry et al. (2013) showed that this same population was arriving on land earlier during break-up than in previous years. This may mean that polar bears are staying out on the ice to hunt as long as they can, but travel quickly back to land once the ice reaches a certain point of break-up. Earlier break-up in Hudson Bay negatively affects the body condition, reproduction, and population numbers of polar bears due to increased time fasting (Stirling et al. 1993; Derocher et al. 2004; Stirling and Parkinson 2006; Regehr et al. 2007). Furthermore, a decrease in this population from 1194 to 935 animals (22%) (1984-2004) was related to the earlier break-up of sea ice (Regehr et al. 2007). WH females may be staying on the ice longer, even if their ice habitat is less suitable, to build up fat stores, but such patterns may vary by individual. For example, the large variances in home range size and centroid distances during freeze-up and break-up compared to early and late winter, suggest that individuals make different movement choices, especially when their habitat is changing quickly. The choices of whether to stay to hunt or to move to land may be partially based on a female's reproductive status and energetic demands.

There is selection for females that take care of their offspring and have them survive to adulthood, thus females may adjust their movement choices based on the presence and abilities of cubs. One concern for mothers is cannibalism. Male polar bears can kill and cannibalize polar bear mothers and their cubs (Taylor et al. 1985; Amstrup et al. 2006), thus females with cubs may adjust their spatial distribution to occupy habitats that reduce contact with adult males to reduce risk of infanticide (Derocher and Stirling 1990; Stirling et al. 1993). Even without aggressive males, females have higher energy demands when accompanied by dependent offspring, and therefore may adopt different space-use strategies (Amstrup et al. 2000; Mauritzen et al. 2001). For example, females with young cubs are less mobile and their small size results in greater vulnerability to hypothermia (Blix et al. 1979). Polar bear reproductive status also influenced home range size and distribution during break up and solitary females had smaller ranges and stayed closer to land than females with COYs. Similarly, solitary females in the Barents Sea were closer to and used land more than females with cubs (Mauritzen et al. 2003). Furthermore, solitary females had the smallest mean annual home ranges in WH population in the 1990s (though not significantly different from other reproductive classes) and their annual mean displacements were significantly lower than the other classes (Parks et al. 2006). Female mammals with young have a daily energy expenditure of approximately four times their basal metabolic rate due to lactation and food-sharing (Ricklefs et al. 1996). Thus, female polar bears with COYs need to eat more than other females in late winter and break-up. Emergence from maternity dens may coincide with seal pupping and moulting to maximize the energetic returns (Ramsay and Andriashek 1986; Amstrup and Gardner 1994). However, female polar bears with offspring had significantly lower body mass, less total body fat, and less fat per unit lean body mass than solitary females (Atkinson and Ramsay 1995), indicating that it is difficult for females with cubs to store as much fat as other bears. Changes in the ecosystem that affect the timing of sea ice and therefore the amount of hunting time can affect the distribution of females with cubs, arguably the most important demographic in a population.

Considering the recent climatic changes in Hudson Bay and the resulting shifts in WH polar bear distribution, it is important to consider if the established geographic population boundary is still appropriate. Obbard and Middel (2012) concluded that the established population boundary for the Southern Hudson Bay polar bear population (SH) reflects the current spatial distribution, an important finding for management. The WH and SH populations overlap in the middle of Hudson Bay, but the extent of overlap is unknown. While the genetic consequences are not fully understood, it is likely that gene flow between the three populations is substantial given that the mating occurs during spring. From 2004-10, the WH population boundary encompassed less than half of the total locations across seasons, particularly during early winter. Early winter was also had the farthest centroid distances from land, indicating that polar bears traveled far into the Bay as the ice stabilized. Given the substantial number of locations outside of the recognized population boundary, the WH population boundaries should be revisited for management purposes and needs to be reconsidered for ecological investigations.

Managers of this population need to consider long-term climate patterns and their effect on both polar bears and seals. Derocher (2005) suggested that some aspects of polar bear health might be linked to the AO in Svalbard, and there is evidence that large-scale climate conditions affect ice conditions in Hudson Bay. Continuing changes in sea ice will likely have negative consequences for ringed seals as they depend on sea ice for reproduction (Smith and Stirling 1975; Stirling 2002; Ferguson et al. 2005; Laidre et al. 2008) although the relationships are complicated and outcomes are challenging to predict (Tynan and DeMaster 1997; Kovacs et al. 2010). The life-history events of upper trophic level organisms can be affected by changes at lower trophic levels (Moline et al. 2008) and as such, these consequences on seals can have far-ranging impacts on polar bears. In such a dynamic ecosystem, longer data series on multiple species are important and continued monitoring is critical.

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CHAPTER 3- SEASONAL HABITAT SELECTION BY POLAR BEARS IN WESTERN HUDSON BAY.

Introduction

Observations and models show that global climate change is occurring at an increasing rate and warming temperatures are predicted to be amplified in Arctic and subarctic habitats (Manabe et al. 1992; Comiso 2003). Parts of the Arctic are experiencing increased temperatures and changes in atmospheric circulation, which have affected the area, timing, and character of sea ice (Vinnikov et al. 1999; Lindsay and Zhang 2005; Serreze et al. 2007; Markus et al. 2009), an important habitat for many species. Sea ice provides critical habitat for marine mammals (Smith and Stirling 1975; Wiig et al. 1999; Laidre et al. 2008) and birds (Gaston et al. 2005) and as such, its alteration and loss will affect many species (Wilcove et al. 1998; Groom and Vynne 2006; Foden et al. 2013). These changes in temperature and the resulting changes in sea ice characteristics are expected to continue (Holland et al. 2006; Stroeve et al. 2007), affecting biodiversity through habitat loss (Hansell et al. 1998; Schipper et al. 2008; Carscallen et al. 2012).

Climate change has been identified as a major modifier of habitat and cause of habitat loss in many species (Moline et al. 2008; Schipper et a. 2008; Stirling and Derocher 2012). To understand how climate change may affect a species, it is necessary to understand patterns of habitat selection (Durner et al. 2009; Morris and Dupuch 2012). Habitat selection occurs when an animal chooses which habitat components to use (Johnson 1980) by making instinctive or learned behaviour decisions about the use of habitat at different scales (Hutto 1985), resulting in the disproportional use of some resources over others (Hall et al. 1997). Insight into how animals meet survival requirements is possible if it is assumed that species preferentially select high quality resources over those of lower quality (Manly et al. 2002). Conventional methods of measuring habitat selection assume that habitat use is directly proportional to habitat availability (Johnson 1980; Hall et al. 1997). However, such methods may be inappropriate if a change in relative habitat availability results in a change in relative habitat use, thus affecting habitat selection (Arthur et al. 1996; Mysterud and Ims 1998; Mauritzen et al. 2003). Habitat use and selection can vary both temporally and spatially (Rosenzweig 1991) making variance in resource abundance and availability across space and time important to consider when examining habitat use (Southwood 1977), especially in dynamic habitats such as Arctic sea ice.

Changes in sea ice have affected Arctic marine mammals through habitat loss (Tynan and DeMaster 1997; Laidre et al. 2008), declines in overall health (Burek et al. 2008), altered prey availability and foraging behaviours (Bluhm and Gradinger 2008), and increased human activities (Hovelsrud et al. 2008). In particular, the highly specialized polar bear (*Ursus maritimus*) is at risk from climate change (Stirling and Derocher 1993; Stirling et al. 1999; Derocher et al. 2004; Stirling and Derocher 2012). Polar bears are designated as Threatened in the United States (FWS 2008), a species of Special Concern in Canada (COSEWIC 2008), and Vulnerable internationally (IUCN 2013). The status of polar bears is based on observed and projected declines in sea ice and the resulting negative effects on polar bear body condition, survival, reproduction, abundance, and distribution (review by Stirling and Derocher 2013). There are 19 polar bear populations in the circumpolar Arctic (PBSG 2010) and declines in seasonal ice will affect reproduction and survival in each population differently depending on the regional changes in distribution, abundance, and characteristics of sea ice (Derocher et al. 2004; Stirling and Parkinson 2006; Stirling et al. 2008; Durner et al. 2009; Amstrup et al. 2010). Understanding how polar bears select their habitat over space and time will be important for management. The Western Hudson Bay (WH) polar bear population lacks habitat selection information yet is showing rapid change related to sea ice loss (Stirling and Derocher 1993, Stirling et al. 1999; Stirling and Parkinson 2006; Regehr et al. 2007; Molnár et al. 2010).

In winter and spring, the WH population disperses over the frozen Hudson Bay to prey predominantly on ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) (Thiemann et al. 2008, 2011). Distribution and abundance of seals, and therefore the distribution of polar bears on sea ice, is influenced by shore leads, polynyas, and patterns of freeze-up and break-up of sea ice (Stirling and Øritsland 1995; Stirling 2002). In summer and autumn, Hudson Bay is ice-free and the WH population uses a restricted area of the western coast (Stirling et al. 1977). Female polar bears show fidelity to their summering areas (Derocher and Stirling 1990) and come off of the ice about 21-28 days after ice cover drops to 50% (Stirling et al. 1999). The bears are spatially separated from their prey and rely on fat reserves for 4-5 months until they return to the ice in autumn or up to eight months for pregnant females that overwinter on land in maternity dens (Watts and Hansen 1987; Ramsay and Stirling 1988). WH polar bears must store sufficient adipose reserves while on the sea ice to last them through the ice-free period when energetically significant food sources are largely unavailable (Ramsay and Stirling 1988; Stirling et al. 2008; Rode et al. 2010).

Early break-up and/or late freeze-up in Hudson Bay increases the amount of time polar bears spend on land fasting, having detrimental effects to their physical condition (Stirling et al. 1993; Stirling et al. 1999; Stirling and Parkinson 2006). Spring air temperatures in this region have increased by 2-3°C over the past 50 years, (Skinner et al. 1998; Gagnon and Gough 2005) and, as a result, the sea ice now breaks up approximately three weeks earlier than it did 30 years ago (Stirling and Parkinson 2006; Castro de la Guardia et al. 2013). Consequently, the WH population is forced off of the sea ice earlier, thereby shortening the spring foraging period and reducing the ability of polar bears to accumulate enough fat reserves to survive while onshore (Stirling and Derocher 1993; Stirling et al. 1999; Regehr et al. 2007). Before coming ashore, polar bears in Hudson Bay experience a hyperphagic period, which overlaps with the ringed seal pupping season and breeding season (Ramsay and Stirling 1988; Stirling and Derocher 1993). During the seal pupping season, polar bears have high hunting success due to the availability of naïve seal pups (Hammill and Smith 1991; Pilfold et al. 2012). Earlier spring break-up shortens the hunting opportunities for polar bears immediately before the shore-bound fasting period. Sea ice in Hudson Bay, Canada, has been experiencing significant changes over the past several decades and these changes are predicted to continue (Hochheim et al. 2011; Castro de la Guardia et al. 2013), and concurrent changes in polar bear habitat use (Parks et al. 2006; Chapter 2).

Polar bear habitat selection differs between seasons, among populations and regions (Arthur et al. 1996; Ferguson et al. 2000; Mauritzen et al. 2003; Durner et al. 2009), and in response to the relative abundance of habitats (Mauritzen et al. 2003). Habitat characteristics that may influence habitat use by polar bears include ice concentration and distance to shore (Durner et al. 2009), bathymetry (Ryther and Yentsch 1957; Smith and Stirling 1975), proximity to open water (Stirling et al. 1993), and dates of ice freeze-up and break-up (Chapter 2). While prey availability is likely the main factor affecting polar bear distribution for much of the year, we lack detailed information on the abundance and location of seals in Hudson Bay. As such, the habitat metrics that I consider when modelling polar bear habitat selection, are a proxy for prey data. Bathymetry influences both biological productivity (Ryther and Yentsch 1957) and the breeding habitat of ringed seals (Smith and Stirling 1975). Proximity to water is important because polar bears often hunt near open leads (Stirling et al. 1993). For example, Canadian Archipelago and Baffin Bay polar bears follow seasonal changes in ice, and their habitat selection was best explained by specific types of ice representing areas with high occurences of seal pupping (Ferguson et al. 2000). However, if habitat conditions change over time, as seen in sea ice, animals may demonstrate a functional response where their selection for a specific habitat attribute changes as a function of the attribute's abundance on the landscape (Mysterud and Ims 1998; Hebblewhite and Merrill 2008; Houle et al. 2010). Functional responses in habitat selection can serve as indicators of changes in habitat quality (Mysterud and Ims 1998; Hebblewhite and Merrill 2008; Herfindal et al. 2009; Gillies and St. Clair 2010), particularly for endangered or threatened species (Mauritzen et al. 2003; Moreau et al. 2012) because declining populations may have lower levels of intraspecific competition (McLoughlin et al. 2010). As such, habitat selection models can provide insight into the distribution of high quality patches for low density populations.

Currently, the WH population of polar bears has more extensive, long-term demographic data than any other population. While the WH polar bears are well studied on land (e.g., Ramsay and Stirling 1988; Stirling et al. 1999; Regehr et al. 2007; Molnár et al. 2010), there has been little examination of their habitat selection on the sea ice. Hudson Bay has exclusively annual sea ice and is relatively shallow (Jones and Anderson 1994) with high productivity (Roff and Legendre 1986) compared to other polar bear habitats, so habitat selection may differ from other populations. A habitat selection model can help to predict important areas and aspects of Hudson Bay sea ice in relation to WH polar bear population dynamics.

Resource selection functions (RSF) can evaluate habitat selection and predict the relative probability of habitat use (Manly et al. 2002). To construct RSFs I used information gained from global positioning system (GPS) collars in association with geographic information system (GIS). Using logistic regression, I characterized used units as 1 and available units as 0 and estimate an RSF that is proportional to the probability of use (Manly et al. 2002). This design results in a relative probability because the intercept, or $ß_0$ coefficient, is incorrectly scaled due to the true population-sampling fraction being unknown (Boyce and McDonald 1999).

Here I examined the seasonal habitat selection of WH polar bears from 2004 to 2010. I predict that polar bears will show a functional response between seasons, preferring different habitat variables at different times of the year depending on ice conditions and hunting opportunities. The application of random effects to my habitat selection models enables examination of variation among individuals and whether selection changes with availability (Gillies et al. 2006; Gillies and St. Clair 2009). I expect differences within the population with respect to habitat selection but predict that, in general, areas of high seal abundance will be important, as will the distance to the denning area (which is also refuge habitat during the ice-free period) throughout the freeze-up and break-up periods.

Materials and Methods

Study Area and Population

Hudson Bay is a shallow inland sea with a mean depth of 125 m with a broad coastal shelf < 80 m deep, sloping slowly to a smooth sea floor (Josenhans and Zevenhuizen 1990; Stewart and Lockhart 2005). It encompasses about 10^6 km^2 (Jones and Anderson 1994) and is considered productive relative to higher latitude areas (Roff and Legendre 1986; Hill and Cota 2005; Lee and Whitledge 2005).

Hudson Bay currents follow a large-scale counterclockwise gyre that moves south from Foxe Basin and exits through the Hudson Strait (Prinsenberg 1988). Ice starts forming in mid-October in the northwest part of the Bay, then is pushed south by the gyre along the west coast towards the coasts of Manitoba and Ontario. From late December until late April, ice cover is

>90% throughout the Bay with the maximum extent occurring in April. From May to mid-August break-up occurs due to warming temperatures; as the southernmost ice begins to melt, ice from the northwest is pushed south by currents along the west coast (Maxwell 1986; Saucier et al. 2004). The Ontario coast usually has the last of the ice, and the entirety of Hudson Bay is ice-free by September (Gough et al. 2004).

Data Collection

Polar bears were captured and collared in autumn from 2004-2010 between 57°00'N–58°50'N and 92°25'W–94°15'W, almost exclusively within Wapusk National Park, Manitoba (Figure 3.1). Bears were located from a Bell 206B JetRanger helicopter and immobilized via remote injection of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®, Laboratories Virbac, Carros, France; Stirling et al. 1989). I recorded the location, sex, and reproductive status of the bears. Animal handling procedures were approved by the University of Alberta BioSciences Animal Policy and Welfare Committee and the Animal Care Committee of the Canadian Wildlife Service (Prairie and Northern Region).

Adult female polar bears were collared with GPS satellite-linked collars (Telonics, Mesa, Arizona). Accuracy of these collars is < 30 m. Collars acquired GPS locations every 4 h but only one location per day was used per collar. Sample sizes differ for each analysis because the number of bears collared each year varied and some collars failed prematurely. If a collar worked year-round, it was tracked from freeze-up to break-up of the following year. If a collar worked intermittently, I used locations when they were applicable to a given study period. Locations with obvious errors were removed from the dataset (i.e., biologically impossible movements). Males were not tracked because they have necks wider than their heads and were unable to wear collars. Bear locations were converted to universal transverse mercator (UTM) coordinates for zone 15 in ArcGIS version 10.0 (Environmental Systems Research Institute, Inc. 2005) using the North American Datum 1983 coordinate system.

I divided the year into four biologically relevant seasons based on both bear behaviour and ice conditions: freeze-up, early winter, late winter, and break-up. The four seasons were defined using mean ice concentrations within the MCP. Freeze-up was defined as 1/10 ice cover, winter at 9/10 cover, break-up 5/10 cover, and summer at 1/20 cover. Sea ice data were obtained from the National Snow and Ice Data Center (Boulder, Colorado). I was only concerned with on-ice locations and movements, thus terrestrial locations were removed for all analyses. Sea ice patterns were examined in the minimum convex polygon (MCP) for all polar bear locations (~56 000) (Figure 3.1) using a GIS to extract daily ice concentrations with 25 km resolution that were approximated from daily Special Sensor Microwave/Imager (SSM/I) passive microwave data.

Figure 3.1. The 95% minimum convex polygon (black line and coastline of western Hudson Bay) of all on-ice GPS locations of western Hudson Bay polar bears from 2004-2011. Mean sea ice concentrations within this area (excluding land) were calculated and used to divide the on-ice period of polar bears into four seasons. Polar bear captures were largely in Wapusk National Park (shaded area) or nearby.

The ordinal number (e.g., January 1 = 1) of each time the Hudson Bay ice concentration reached one of the date cut-offs was averaged over the study and recorded with mean ± SE. I wanted to compare polar bear habitat selection during the same periods every year and then examine differences across seasons.

Habitat Attributes

The mean daily step length (i.e., distance between consecutive locations 24 h apart) of all polar bears in each season (all years pooled) was calculated with ArcGIS 10.0. All habitat variables were calculated for each available location.

To build the RSF models, I built an initial suite of covariates (predictor variables) from the observed sea ice record. Covariates were examined for nonlinearity using quadratic and natural log transformations. The daily estimates of total sea ice concentration for each pixel was termed ice_conc. A quadratic transformation of sea ice concentration (ice_con2) was used for modelling because it provided lower univariate log-likelihood scores across seasons and other polar bear habitat studies reported similar nonlinear associations (Durner et al. 2004, 2006, 2009). Habitat covariates included depth (a bathymetry layer of Hudson Bay based on the International Bathymetric Chart of the Arctic Ocean) (Jakobsson et al. 2012), shifted to positive values for ease of interpretation), dist_den (distance to the coast of Wapusk National Park where bears were collared and most females denned), and dist_coast (distance to the west coast of Hudson Bay from NW James Bay to Chesterfield Inlet). I further defined covariates based on distances to boundaries that separated ice concentration thresholds including: ≥15% ice (dist_15), ≥30% ice (dist_30), ≥50% ice (dist_50), ≥75% ice (dist_75), ≥85% ice (dist_85), 100% ice (dist_100). While open ocean is rarely used by polar bears, especially in the Arctic basin (Arthur et al. 1996; Mauritzen et al. 2003; Durner et al. 2006), open water in Hudson Bay is important seal habitat and, in turn, important polar bear habitat. Therefore, I included distance to open water (dist_0), calculated when there was no ice cover within the 25 km resolution of the ice data. Thus, each pixel, in both the data used to build the RSFs and in the data used to extrapolate the RSFs, included eleven main effects (ice_conc, dist_15, dist_30, dist_50, dist_60, dist_75, dist_85, dist_100, dist_coast, dist_den and depth) and one second-order effect (ice_conc2).

Habitat covariates and distances to sea ice contours were calculated using ArcGIS (Nielsen 2010). Before modelling, covariates were examined for collinearity using tolerances scores following Menard (2002), which resulted in the removal of dist_15 and dist_30 from the *a priori* set of models.

Resource Selection Model

Discrete choice models are commonly applied in polar bear studies (Arthur et al. 1996; Durner et al. 2009), as they allow resource availability to be defined separately for each individual. As sea ice conditions change on a daily basis, a discrete choice design allows used points to be matched temporally to available points within a defined buffer. For this study, used points were taken once per 24-hr period, and buffers were circles with a radius equal to the median daily step length of all study individuals for each season. Each choice set was defined as a used point matched to five available points within the buffer.

Habitat selection by adult female polar bears can vary with reproductive status and life history stage (Stirling et al. 1993; Freitas et al. 2012). The reproductive status of females in my study could not be consistently monitored after collar deployment. To account for individual variation in habitat selection between adult females of varying reproductive status, a random-effect conditional logistic regression was employed following Duschesne et al. (2010). The inclusion of random effects is useful to account for unbalanced sample design and individual or group behaviour in RSF models (Gillies et al. 2006; Hebblewhite and Merrill 2008). The utility (U_{njt}) that a polar bear *n* determines at location *j* and time *t* was specified as:

$$U_{njt} = \boldsymbol{\beta}_n^{'}\boldsymbol{x}_{njt} + \varepsilon_{njt}$$

where $\boldsymbol{x}_{njt}$ was the vector of observed habitat covariates, $\boldsymbol{\beta}_n^{'}$ was the vector of animal-level random coefficients normally distributed with a zero mean, and ε_{njt} was the extreme value error term (Train 2009; Duchesne et al. 2010). Due to the conditional design, there is no intercept term, and random effects are included as coefficients only. I assumed that selection for all habitat covariates was subject to variation between individuals. I tested whether the inclusion of random coefficients improved model fit by comparing global fixed-effect and random-effect models using Akaike's Information Criterion with a correction for finite sample sizes (AIC_c). Minimization of log-likelihood values was determined using the mxlmsl package (Train 2006) in MATLAB 2013a (MathWorks Inc., Natick, Massachusetts).

To examine the functional response of adult females to variation in sea ice conditions between seasons, I used a constrained modelling approach to determine a constant set of parameters to compare across seasons. I ran the same set of *a priori* models for each season, and evaluated them using AIC_c. Covariates were then ranked by importance using the sum Akaike weights (w_i) averaged across seasons (Burnham and Anderson 2002). As there is no set cut-off value for Akaike weight to denote significance (Burnham and Anderson 2002: 78-79), determining covariate inclusion in the final model was subjective.

The mean coefficients of habitat covariates were determined with a random-effect conditional logistic regression. Each coefficient was given a normalized distribution with estimated mean and standard deviation (Train 2009). The mean coefficient is the selection parameter, with positive values indicating increased preference and negative values indicating decreased preference, and its standard error indicates the significance of the standard deviation. The standard deviation indicates how much the selection parameter varies in the population, and this standard deviation's own standard error is a measure of the significance of that variation (Train 2009). Any overlap of this standard error with 0 suggests non-significant variation. These values were used to help determine if there were seasonal and/or individual differences in selection for WH polar bears.

The overall top model was used to create habitat maps for habitat covariates using one randomly chosen day out of each season, averaged across four different years (2006, 2007, 2008, and 2009), at a grain of 25 km. Each map was limited to the 100% MCP of all used locations for that season and year. Pixels were generated in ArcGIS using 10% quantiles which show linearly distributed data.

Results

Collars provided 8487 used locations included in analyses from 62 individual polar bears, totaling 74 bear years (i.e., 12 bears were followed for two years). The number of used locations included varied by season: 919 for freeze-up, 3551 for early winter, 3610 for late winter, and 407 for break-up. Median daily step lengths (the buffer radius in which available points were placed) by season were: freeze-up at 27.6 km; early winter at 19.4 km; late winter at 18.5 km; break-up at 27.7 km.

Seasons

The dates of the *a priori* ice concentrations used to distinguish seasons varied by year. Freeze-up started from November 21 in 2004 to December 5 2009 with a mean of November 27 ± 2 days. Winter started from December 8 in 2004 to December 21 in 2007, with a mean of December 19 ± 3 days. Break-up varied from June 16 in 2006 to July 7 in 2009 with a mean of June 23 ± 4 days. Winter, originally December 19 to June 23, was deemed too long to give the desired resolution. Therefore, winter was split roughly in half at March 15 because by this date, mothers with newborn cubs are on the sea ice, seals are starting to pup, and the mating season is starting. The four seasons examined were: freeze-up (November 27- December 18, 22 d), early winter (December 19- March 14, 86 d), late winter (March 15- June 22, 100 d), and break-up (June 23- July 14, 22 d).

Seasonal Resource Selection Functions

Twenty-one models were estimated for each season. Inclusion of random coefficients improved model fit so the random-effect model was used instead of the fixed-effect model (Table 3.1). The improvement in model fit was the lowest in late winter, suggesting little variation between individuals during this season as compared to freeze-up and break-up. The freeze-up season indicated the most selection variation among individuals.

Table 3.1. Comparison of AIC_c values for global RSF models of female Western Hudson Bay polar bears (2004-2010), constructed with fixed and random coefficients across seasons.

Season	Fixed-effect AIC_c	Random-effect AIC_c	ΔAIC_c
Freeze-up	2,016.5	1,880.6	135.9
Early winter	11,037.5	10,986.9	50.6
Late winter	11,737.9	11,720.0	17.9
Break-up	1,354.6	1,264.3	90.3

Eleven covariates including ice concentration, the quadratic of ice concentration, bathymetry, distance to the denning area, distance to the west coast of Hudson Bay, dist_0, dist_50, dist_60, dist_75, dist_85, and dist_100% ice were consistently retained in top-ranked models for all seasons (Table 3.2). Models containing the top eleven covariates were consistently ranked high out of all competing models. Distance to the denning area was the strongest driving covariate for each season (Table 3.2).

Table 3.2. Akaike weights (w_i), corrected for finite sample size, for covariates in resource selection function models for each season for female polar bears of western Hudson Bay (2004-2010). Covariates are ranked by their mean AIC_c weight.

Covariates	Freeze-up	Early winter	Late winter	Break-up	Mean AIC_c w_i	Rank
dist_den	1.000	1.000	1.000	1.000	1.000	1
ice_conc + ice_conc2	1.000	0.919	0.999	1.000	0.979	2
dist_75	0.980	0.958	1.000	0.878	0.954	3
dist_coast	1.000	1.000	0.685	1.000	0.921	4
dist_50	1.000	0.512	1.000	0.998	0.877	5
dist_0	1.000	0.387	1.000	1.000	0.847	6
depth	0.998	0.956	0.437	0.984	0.844	7
dist_60	1.000	0.369	1.000	0.818	0.797	8
dist_85	1.000	0.807	0.986	0.363	0.789	9
dist_100	0.024	0.871	0.750	0.960	0.651	10

The overall top model for all seasons included all covariates (Table 3.3). Despite overall similarity among the four seasonal RSF model structures, differences in the magnitude of the parameter estimates indicated seasonal differences in polar bear habitat selection (Table 3.3; Figure 3.2). Polar bears in all seasons preferred deeper depths but it was least important in late winter. Distance to the coast was positively selected for during freeze-up, but negatively selected for in the other three seasons indicating polar bears were far from the coast as the ice starting forming in autumn, but selected to be closer to the coast in the seasons where the ice was more stable in winter and during break-up. Only 6 of 44 standard deviations were not significant (Table 3.3) indicating that, overall, individual selection for habitat covariates varied. The non-significant variations include dist_50 in early and late winter, dist_60 and dist_75 in early winter, and ice_conc2 in late winter and break-up.

Table 3.3. The mean coefficients of habitat covariates with their standard error, standard deviation, and the standard error of the standard deviation. Mean coefficients were determined with a random-effect conditional logistic regression with normally distributed coefficients, for adult female polar bears of western Hudson Bay (2004-2010). Bolded values indicate non-significant variation within the population.

		Season			
Habitat Covariate		Freeze-up	Early winter	Late winter	Break-up
ice_conc	Mean coefficient (SE)	0.1675 (0.0565)	0.1031 (0.1360)	-0.0552 (0.0228)	-0.0483 (0.0233)
	Std Dev of coefficient (SE)	0.0236 (0.0149)	0.0592 (0.0332)	0.0061 (0.0110)	-0.0448 (0.0188)
ice_conc2	Mean coefficient (SE)	-0.0009 (0.0004)	-0.0005 (0.0008)	0.0002 (0.0002)	-0.0002 (0.0003)
	Std Dev of coefficient (SE)	-0.0002 (0.0002)	-0.0002 (0.0003)	**0.0000** (0.0001)	**0.0000** (0.0003)
depth	Mean coefficient (SE)	0.0106 (0.0071)	0.0044 (0.0030)	0.0019 (0.0030)	0.0121 (0.0156)
	Std Dev of coefficient (SE)	-0.0067 (0.0114)	0.0090 (0.0038)	-0.0056 (0.0044)	0.0500 (0.0169)
dist_den	Mean coefficient (SE)	0.0570 (0.0067)	-0.0013 (0.0037)	-0.0165 (0.0034)	0.0350 (0.0125)
	Std Dev of coefficient (SE)	0.0404 (0.0070)	0.0227 (0.0037)	0.0153 (0.0035)	0.0733 (0.0106)
dist_coast	Mean coefficient (SE)	0.0510 (0.0083)	-0.0100 (0.0025)	-0.0042 (0.0030)	-0.0609 (0.0162)
	Std Dev of coefficient (SE)	0.0504 (0.0090)	-0.0022 (0.0052)	0.0065 (0.0060)	-0.0115 (0.0146)
dist_0	Mean coefficient (SE)	0.0376 (0.0053)	0.0005 (0.0004)	-0.0019 (0.0002)	-0.0235 (0.0044)
	Std Dev of coefficient (SE)	0.0207 (0.0036)	0.0001 (0.0006)	0.0001 (0.0004)	0.0085 (0.0030)
dist_50	Mean coefficient (SE)	0.0097 (0.0016)	0.0002 (0.0002)	-0.0011 (0.0002)	-0.0128 (0.0060)
	Std Dev of coefficient (SE)	0.0048 (0.0011)	**0.0000** (0.0002)	**0.0000** (0.0004)	0.0147 (0.0089)
dist_60	Mean coefficient (SE)	-0.0032 (0.0017)	-0.0001 (0.0001)	-0.0012 (0.0003)	0.0117 (0.0071)
	Std Dev of coefficient (SE)	0.0133 (0.0046)	**0.0000** (0.0001)	-0.0009 (0.0004)	0.0094 (0.0113)
dist_75	Mean coefficient (SE)	-0.0053 (0.0015)	0.0005 (0.0002)	-0.0022 (0.0004)	0.0078 (0.0056)
	Std Dev of coefficient (SE)	0.0016 (0.0022)	**0.0000** (0.0003)	-0.0001 (0.0006)	0.0090 (0.0079)
dist_85	Mean coefficient (SE)	0.0085 (0.0019)	-0.0007 (0.0004)	-0.0017 (0.0007)	-0.0009 (0.0009)
	Std Dev of coefficient (SE)	0.0063 (0.0022)	-0.0001 (0.0007)	0.0002 (0.0009)	0.0002 (0.0011)
dist_100	Mean coefficient (SE)	0.0000 (0.0019)	-0.0002 (0.0007)	-0.0043 (0.0043)	0.0202 (0.0069)
	Std Dev of coefficient (SE)	0.0004 (0.0022)	-0.0002 (0.0008)	-0.0017 (0.0079)	0.0016 (0.0097)

The freeze-up and break-up seasons had larger mean coefficient magnitudes compared to the two winter seasons (Figure 3.2). For almost all covariates, early and late winter values were low, near zero in some cases, indicating that polar bears were not reacting to many variables other than the ice concentrations within the mean step length.

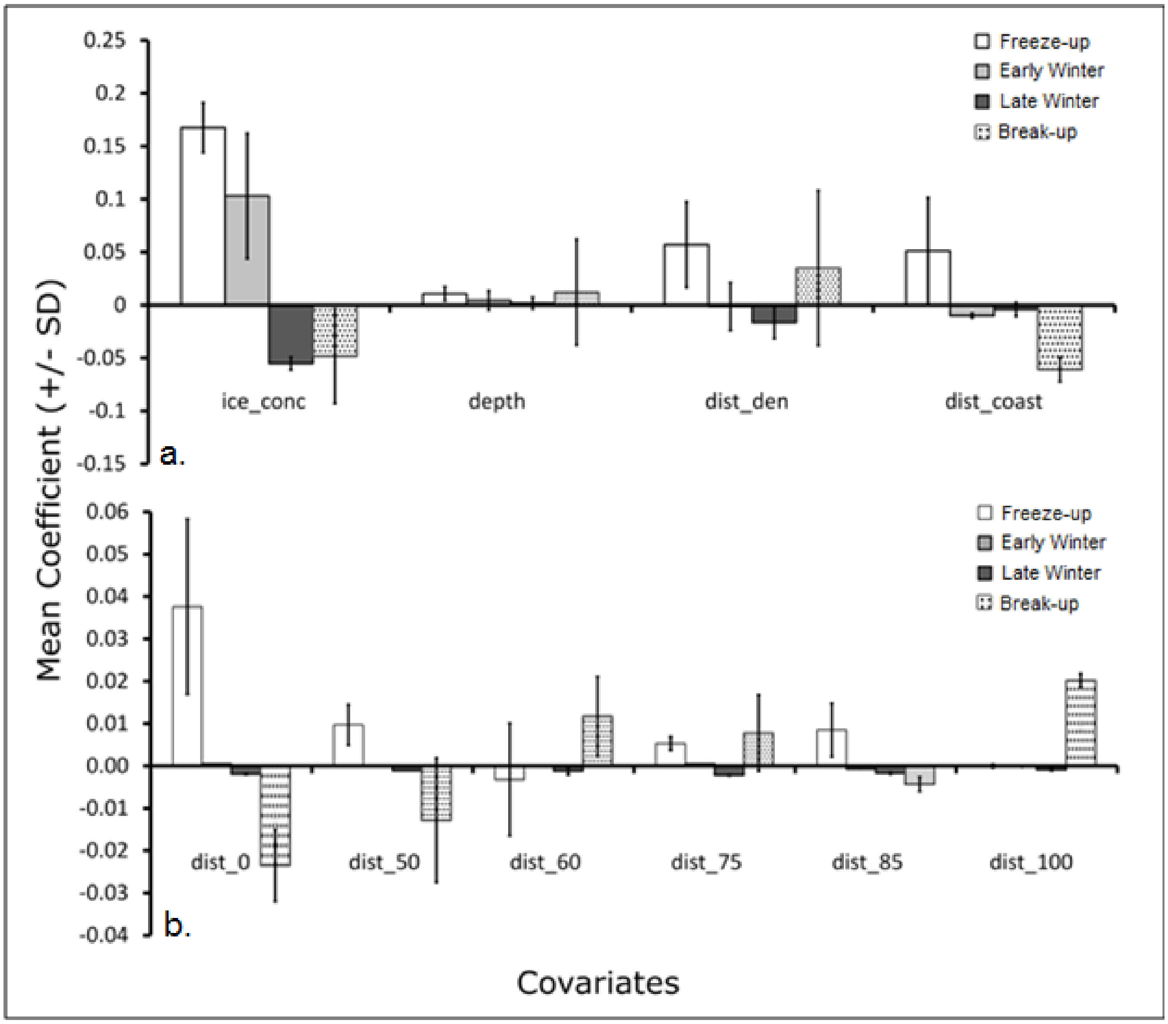

Figure 3.2. Differences in the magnitude of the mean coefficient (± SD) across habitat covariates for polar bears in four seasons: a = various habitat covariates, b = distances to different SSM/I contour values. For each variable, non-significant variation within the population is indicated where the SD overlaps 0.

Selection for ice concentration was positive in freeze-up and early winter, but negative in late winter and break-up (Figure 3.2a). Deeper water was overall positively selected for in all seasons, yet during break-up 62% of bears selected for deep waters while 38% selected to be closer to shallower water. Polar bears selected to be far from the denning area during freeze-up, and selected to be closer to the denning region in late winter, though the magnitude was weaker during the winter period. The standard deviation for distance to the denning area spanned zero in both early winter and break, indicating no individual variation in selection. During early winter, 47% of bears selected to be farther from the coast and 53% selected to be closer to the coast, while during break-up 74% of bears selected to be close to the denning area and 26% were further away. Polar bears preferred to be far from the west coast during freeze-up, but preferred to be closer to the coast during break-up. No strong selection for distance to the coast was evident in the winter periods.

During break-up there was high positive selection for dist_100 (i.e., the farther away from this contour the higher the selection), indicating bears avoided the highest concentrations of ice, instead selecting to be close to open water and 50% ice (Figure 3.2b). This 50% ice concentration was not an important factor in other seasons. During freeze-up, polar bears stayed far away from open water preferring to be close to mid-range ice concentrations.

RSF maps show higher selection along the western coast of Hudson Bay in early winter, late winter, and break. During freeze-up (Figure 3.3a), selection was highest at the far edges of the study area, reflecting the polar bear preference to be as far as possible from the coast and open water during ice formation. Early winter (Figure 3.3b) showed highest selection along the west coast, most strongly along the denning region, reflecting that distance to denning was the strongest driving for the model. Local ice concentration was also important during this season but the magnitudes of selection for other covariates were small.

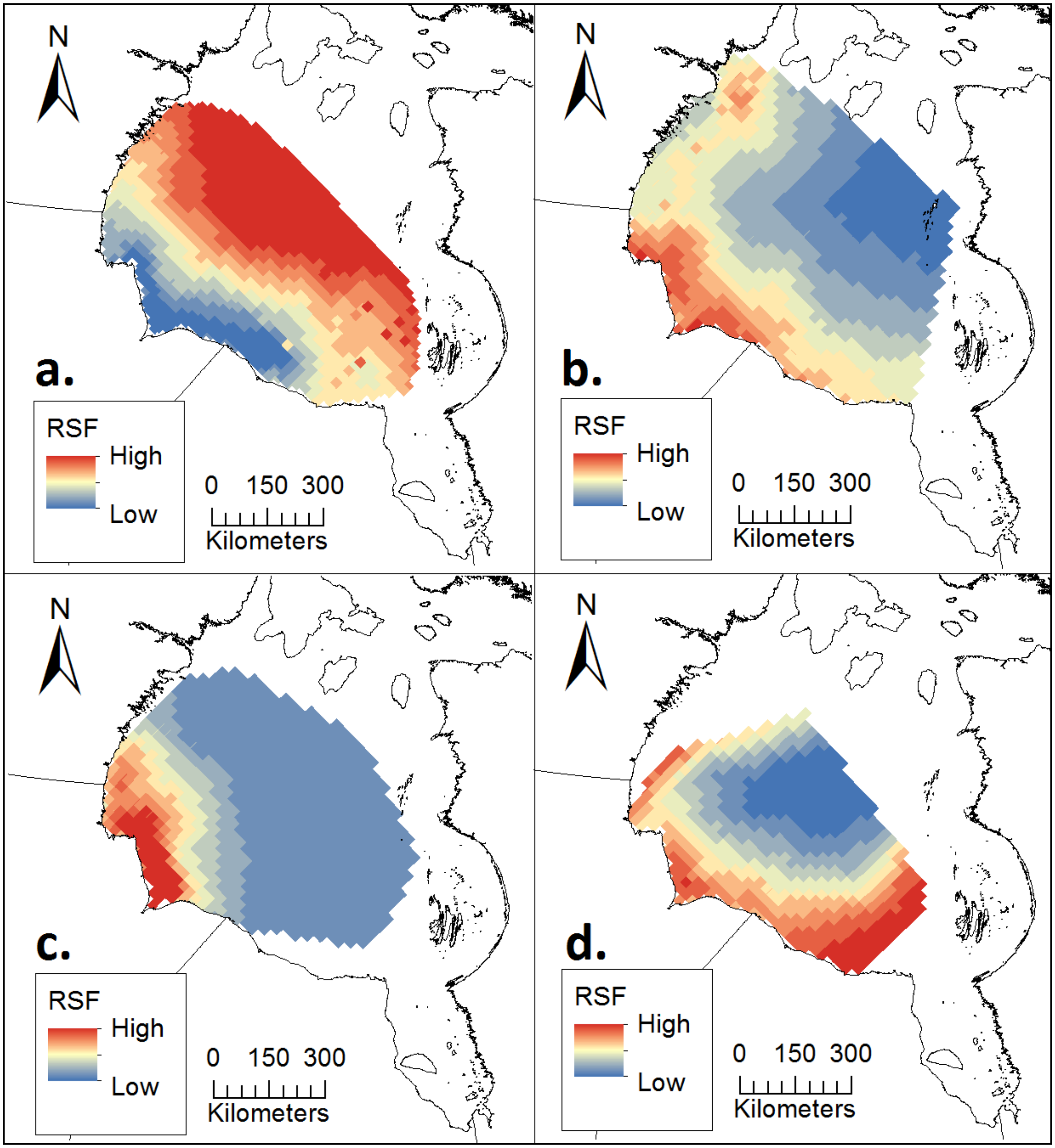

Figure 3.3. Examples of seasonal Resource Selection Functions for Western Hudson Bay polar bears represented by the same day averaged across four years (2006, 2007, 2008, and 2009) for each season. Each seasonal model was constrained to the 100% MCP of all bear locations in that season (including all years): a = freeze-up (December 7); b = early winter (February 1); c = late winter (May 5); d = break-up (June 27).

Late winter (Figure 3.3c), which had a low magnitude of selection and the least amount of individual variation, showed the highest selection near the western Hudson Bay coast, reflecting the strongest driving habitat covariates of distance to the denning area and local ice concentrations for this season. In the break-up season (Figure 3.3d), high selection was seen nearer Ontario and along the coast, reflecting selection for mid-range ice concentrations and avoidance of 100% ice.

Discussion

This is the first habitat selection model for the WH polar bear population. While a similar study has not been conducted in this region, research in other regions demonstrated that distance to land was an important covariate for polar bear populations during winter, as was habitat partially covered by ice (Durner et al. 2009). This is similar to my study in that WH polar bears showed strong selection to be closer to their denning area and avoided both open water and the highest concentration of ice. Durner et al. (2009) noted differences in magnitudes of selection between the autumn and spring/summer compared to winter, which was also seen in my study. Ferguson et al. (2000) modeled polar bear habitat selection in the Arctic Archipelago and Baffin Bay and found seasonal changes in habitat with selection for ice edges in spring in advance of break-up, also reflected in this WH study. Ice types used by these populations likely represented areas where most seal pupping occurred for each region, but polar bear density could not be directly related to prey density. Lacking data for the seal populations in Hudson Bay, I also cannot link my results directly to prey density.

Seals depend on sea ice as a platform on which they can give birth to and nurse their pups (Smith et al. 1991; Kovacs et al. 1996) and their distribution is influenced by shore leads, polynyas, bathymetry, ice thickness, floe size, and the patterns of freeze-up and break-up (Smith

1975; Stirling and Øritsland 1995; Stirling 2002). Studies have documented lower ringed seal pup survival due to reduced snow depth, increased rain, and early break-up in spring (Smith and Harwood 2001; Stirling and Smith 2004; Ferguson et al. 2005). While the relationship between the breeding and moulting populations is unknown for ringed seals, Kelly et al. (2010) showed that ringed seals hauled out on the ice in the spring close to their breeding lairs. Chambellant et al. (2012b) found that western Hudson Bay ringed seals preferred to haul out on land-fast ice, whereas bearded seals preferred unconsolidated pack ice. These documented areas of ringed seal activity and habitat preference along the coast of Hudson Bay correspond to areas of high WH polar bear habitat selection during winter and break-up. For example, late winter, the season with the least amount of individual variation and the smallest magnitudes of selection, bears showed strong selection for a time and place where Hudson Bay ringed seals give birth. Polar bears in Hudson Bay presumably select habitats that yield the best seal hunting opportunities, which vary by season. However, the patterns of habitat selection may be at least partially based on individual behaviours.

This was a population level study, but by using a random effects model I was able to examine individual differences. Spatial variation in the relative availability of different habitat types may lead to dissimilar habitat selection among similar individuals (Boyce et al. 2003; Godvik et al. 2009; Hansen et al. 2009; Herfindal et al. 2009), known as a functional response in habitat selection (Mysterud and Ims 1998). Mechanisms that result in a functional response may be related to trade-offs in the allocation of time and energy to different activities, especially when resources required for different activities are segregated spatially (Mysterud and Ims 1998; Godvik et al. 2009). Identifying the factors that lead to variation in resource selection is central to understanding animal behaviour and distribution: a functional response can describe how this variability influences resource utilization (Holling 1959). Individuals might vary in their patterns of resource selection due to differences in preferences of habitat types or because of a difference in availability of resources due to demographic groups segregating (Miquelle et al. 1992). Resource selection may also differ temporally for certain individuals in a population. For example, Thiemann et al. (2011) found that in Hudson Bay, 23% of male polar bears demonstrated dietary flexibility, switching from one main prey species to another, while the other males and all the females in the same population maintained narrower, less variable, diets.

Resources have both costs and benefits (Schoener 1971; McNamara and Houston 1994), and these can vary according to sex or reproductive status when there are demographical differences in cost or benefits associated with visiting a habitat (Main 2008). For example, in sexually dimorphic ungulates, males tend to select more strongly for good foraging conditions and may use larger areas due to their greater nutritional needs compared to females (Harestad and Bunnell 1979; Herfindal et al. 2009). Furthermore, females with young offspring may have limited mobility, and as such, space use or selection of a given resource can be expected to vary between males and females or females of different reproductive status (Main 2008; Van Beest et al. 2011). In polar bears, the presence of cubs affects a female’s space-use strategies in that females have higher energy demands when accompanied by dependent offspring, affecting their abilities and choices when travelling (Amstrup et al. 2000; Mauritzen et al. 2001). In the Barents Sea population, solitary females were closer to and used land more than females with cubs (Mauritzen et al. 2003). In the WH population in the 1990s, solitary females had significantly lower annual mean displacements compared to other reproductive classes (Parks et al. 2006). Due to the energy transfer through lactation and food-sharing when caring for young, female mammals can have a daily energy expenditure of approximately four times their basal metabolic rate (Ricklefs et al. 1996); thus, female polar bears with cubs would need to eat more than other females and their den emergence coincides with seal pupping and moulting, thus maximizing the energetic returns (Ramsay and Andriashek 1986; Amstrup and Gardner 1994). Changes in the ecosystem that affect the timing of sea ice and the hunting period can have major impacts on the distribution of females with cubs, arguably the most important demographic group in a population. Nielsen et al. (2013) found that habitat selection in grizzly bears is partly learned from their mothers, a finding that could have implications for polar bears. For example, the condition and status of females could significantly impact their habitat selection patterns, and in turn, the future habitat selection patterns of their offspring. Though reproductive classes were not explicitly examined here, this could be an important source of variation in this study.

I found clear differences in the magnitudes of selection for the multiple habitat covariates across the four different seasons, indicating that the degree of selection changed as availability changed (i.e., a functional response) (Mauritzen et al. 2003; Godvik et al. 2009). In particular, the transitional seasons of freeze-up and break-up had stronger responses to habitat variables than in the early and late winter seasons. This reflects the dynamic nature of the freeze-up and break-up seasons, periods of rapidly changing habitat resources where polar bears must make many decisions. The freeze-up season showed the most variation in selection among individuals, indicating that during this time of year, different polar bears may make different choices about where to move. My model was least improved in late winter, the season when seals are pupping, suggesting that there is less individual variation in choices at this time and, as such, most polar bears have similar preferences for habitat conditions during late winter. During the winter seasons, the regional ice concentration (i.e., ice within the mean step length) was important; the habitat covariates that were important in the freeze-up and break-up seasons, such as distances to different ice contours, were not nearly as important during the more stable, ice-covered winter seasons of Hudson Bay.

Strong responses to multiple habitat covariates during freeze-up and break-up reflect the dynamic conditions during the seasons that include the land/ice transition. WH polar bears exhibit site fidelity where they come ashore along specific sections of coast (Stirling et al. 2004; Cherry et al. 2013). My model shows that during freeze-up, WH polar bears move far offshore, while during break-up they are closer to the west coast. When Hudson Bay starts freezing up, WH polar bears follow the ice as it forms, travelling along the edges of newly formed ice and making their way out onto Hudson Bay as soon as they are able perhaps encountering naïve seals unaccustomed to predators following the long ice-free period. However, when the ice starts breaking up, the bears must either stay out long enough to have extra hunting time, but not so long that they end up having to swim long distances to shore. Stirling et al. (1999) suggest that there is a balance between the length of time that bears remain on the ice (hunting seals to accumulate fat) before it is no longer energetically cost-effective, and the amount of energy the bears would expend walking back along the coast if they were carried southward on the drifting pack ice away from the study area. This cost-benefit decision could explain why some polar bears may choose to be far from Wapusk but close to the west coast as a whole during the break-up season: they prefer to remain on the ice to hunt even if it takes them away from their denning area. By sticking closer to the west coast, it may be easier to get off on land and walk back to the denning region rather than swim a long distance to shore. It is clear that the population is divided with respect to the preferred distance to the denning area.

In Hudson Bay, freeze-up has been increasingly delayed (Gagnon and Gough 2005; Hochheim and Barber 2010) and the break-up season now starts three weeks earlier than it did 30 years ago (Stirling and Parkinson 2006). One consequence is that the WH population is now arriving on land earlier during break-up than in recent years (Cherry et al. 2013). Earlier break-up in this region has negatively affected polar bear body condition, reproduction, survival, and population abundance (Stirling et al. 1993; Derocher et al. 2004; Stirling and Parkinson 2006; Regehr et al. 2007). Bears forced off the sea ice earlier have a reduced ability to build up enough fat reserves to survive the summer and must endure a prolonged fasting period (Stirling and Derocher 1993; Stirling et al. 1999). As the dates of ice freeze-up and break-up continue to change in response to increased temperatures, polar bear responses to habitat will change and their survival and reproduction abilities will be further challenged (Stirling and Parkinson 2006; Molnár et al. 2010; Castro de la Guardia et al. 2013).

For effective natural resource management, it is important to have a good understanding of the relationship between wildlife and their habitat (Morrison 2001). Identifying patterns of habitat selection and how it changes as landscapes are altered over time can provide insights into mechanisms underlying the observed demographic trends in large mammal populations (Anderson et al. 2012). There is growing interest in quantifying functional responses in habitat selection for ecosystem management and wildlife conservation (Fortin et al. 2008; Hebblewhite and Merrill 2008; Herfindal et al. 2009; Houle et al. 2010) and conservation planning can benefit from considering individual variations in behaviour instead of assuming all individuals behave alike (Gillies and St. Clair 2009). In a rapidly changing environment, individual differences will drive population changes; monitoring habitat use and selection may provide insights into the mechanisms of change. If the climate, sea ice, and/or the seal population change, it is likely based on these results that polar bear habitat selection will experience concurrent changes.

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CHAPTER 4- DISCUSSION

Hudson Bay is changing as a result of climate change, including a significant increase in air and water temperatures and a decrease in sea ice extent (including land-fast ice) and snow depth (Skinner et al. 1998; Ferguson et al. 2005; Gagnon and Gough 2005a, b; Hochheim et al. 2010). Due to these increasing temperatures, sea ice break-up in western Hudson Bay now occurs ~10 days per decade earlier than it did in the 1970s (Gagnon and Gough 2005b; Stirling and Parkinson 2006). Predictions based on climate change scenarios indicate that these trends will continue and even intensify, possibly resulting in remarkable changes in the sea ice cycle in Hudson Bay (Gough and Wolfe 2001; Gagnon and Gough 2005b; Castro de la Guardia et al. 2013). Sea ice reductions will cause habitat loss for sea ice dependent species, affecting their distribution, nutrition, reproduction and ultimately survival, eventually affecting the distribution and availability of prey, and even an increase in predation and competition pressures (Tynan and DeMaster 1997; Laidre et al. 2008; Post et al. 2009; Chambellant 2012a). Already there is evidence of impacts of climate warming on top marine predator populations Hudson Bay, in particular the Western Hudson Bay (WH) polar bear population (Stirling et al. 1999; Regehr et al. 2007).

The WH polar bear population has been studied for more than forty years, but only recently scientists have gained the technology to get a better understanding of how these animals use their main habitat, sea ice. With changing climate conditions in Hudson Bay expected to continue (Holland et al. 2006; Stroeve et al. 2007), it is more important than ever to gain knowledge of how WH polar bears use their habitat, how they select for habitat, and how this may change over time. My research is the first to examine on-ice movements of WH bears using high-quality location data. This is the first comparison of WH distribution in the 1990s to distribution in the 2000s, the first examination of WH seasonal home ranges of different reproductive classes using GPS data, and the first model of WH habitat selection on sea ice. Knowledge gained from WH bears may help us to predict what other, more northern, populations may experience as the environment continues to change. It is important to understand the threats to polar bear viability in Hudson Bay, as those threats may soon be faced by the species throughout its range.

Projected changes in the Hudson Bay ecosystem are complex but the biggest concern for polar bears is simply the loss of their primary habitat, sea ice. If ice changes occur as predicted and the on-shore period continues to increase, the WH population will be critically threatened or extirpated. A recent analysis of sea ice in Hudson Bay suggests that WH polar bear habitat will deteriorate in the 21st century and that the polar bear population may struggle to persist after ~2050 if there is no reduction in greenhouse gas emissions (Castro de la Guardia et al. 2013). Successful reproduction may stop altogether if break-up was to occur in early June, a 2-month increase in the fasting period (Molnár 2009). Though the Southern Hudson Bay population is currently considered to be stable, it is expected to eventually parallel WH population (Stirling and Parkinson 2006; Obbard et al. 2007). Further, the declining ice habitat in Foxe Basin has generated similar predictions for polar bear there (Stirling and Parkinson 2006; Sahanatien and Derocher 2012). Predicting the future is difficult, but predicting future ecosystem structure is especially complex. For a specialized predator that relies on the same diminishing habitat as its prey, the outlook is bleak.

Polar bears have a highly specialized diet (Stirling 1974; Stirling and McEwan 1975; Thiemann et al. 2008, 2011): they evolved to exploit an energy rich habitat, the sea ice, to hunt their main prey, seals. Though polar bears will feed opportunistically on a variety of terrestrial species (Russell 1975; Smith and Hill 1996) ranging from blueberries to kelp to seabirds to geese to caribou (*Rangifer tarandus*), the importance of terrestrial food items is considered to be minimal overall (Ramsay and Hobson 1991; Hobson et al. 2009). Despite some suggestions that polar bears might make greater use of terrestrial resources if the sea ice conditions undergo further deterioration in Hudson Bay (Dyck and Kebreab 2009; Rockwell and Gormezano 2009), there is little indication that there are sufficient resources, in either abundance and nutritive value, to support viable populations of polar bears forced to live on land (Rode et al. 2010). Based on fatty acid analysis, WH bears eat mostly ringed seals (*Pusa hispida*) (~70%), followed by equal proportions of bearded seal (*Erignathus barbatus*) and harbour seals (*Phoca vitulina*) (~10–15%) with only about 5% of their diet coming from harp seals (*Pagophilus groenlandicus*) (Thiemann et al. 2008). If climate warming continues as expected, ringed seals and bearded seals face critical challenges as they have evolved to exploit the sea ice habitat for reproduction and survival. Studies have shown that reduced snow depth, increased rain and early break-up in the spring have negative effects on seal pup survival (Smith and Harwood 2001; Stirling and Smith 2004; Ferguson et al. 2005; Hezel et al. 2012), but these climate patterns may be part of a long-term shift.

Polar bears of WH are experiencing negative effects of climate change, evident through their declining body condition (Atkinson et al. 1996; Stirling et al. 1999; Stirling and Parkinson 2006; Regehr et al. 2007), and both long-term and short-term changes in the Bay may affect these bears and how they are distributed. Decadal fluctuations, especially in the sea ice regime through atmospheric forcing (e.g., North Atlantic Oscillation), were described in the Arctic environment (Mysak and Manak 1989; Hurrell 1995; Mysak et al. 1996), and fluctuations in life-history parameters or abundance of several Arctic species were linked to variations in environmental conditions (Skinner et al. 1998; Ottersen et al. 2001; Post and Forchhammer

2002; Irons et al. 2008), such as the Arctic Oscillation or North Atlantic Oscillation (Serreze et al. 2000; Gong et al. 2007; Turner et al. 2007). My research found a link between some home range sizes and the Arctic Oscillation. Furthermore, at the end of the 1990s I found that annual home range size for WH polar bears had steadily declined, agreeing with a previous study in the same region (Parks et al. 2006). The decreased movement as well as the poor bear condition also recorded in the 1990s is thought to be related to changes in ice cover, ice extent, and the duration of the ice season in Hudson Bay, all of which affected seal recruitment and distribution. Previous findings on ringed seal reproduction and survival in western Hudson Bay suggest an approximate 11-year period cycle of ringed seal density estimates in western Hudson Bay, with a decline in density in the 1990s and an apparent recovery in the 2000s (Stirling 2005; Ferguson et al. 2005; Chambellant et al. 2012b). However, in the 2000s WH bears covered greater distances and though the seal population may have rebounded, polar bear body conditions remained poor, if not poorer (Stirling et al. 1999). The poorer body conditions are likely from reduced hunting time, but it would be beneficial to have a greater understanding of the seal population in Hudson Bay. Currently, we lack detailed information on the status of seals in this region but this type of knowledge could increase our understanding of what polar bears are doing in Hudson Bay and what types of habitat are most critical. Changes in polar bear ecology and recent unidirectional climatic trends suggest that long-term modifications may be happening in the Hudson Bay ecosystem (Gagnon and Gough 2005a; Castro de la Guardia et al. 2013; Hoover et al. 2013a, 2013b). While long-term (i.e. decadal) effects are important to monitor, it may be easier and still informative to monitor fluctuations on a shorter-term basis (i.e. seasonal).

On a shorter-term scale, polar bears have to adjust their movements seasonally as the sea ice habitat may change rapidly (Durner et al. 2004, 2009). Polar bears exhibit a functional response to their environment, adjusting their selection as the habitat changes (Mauritzen et al. 2003; Chapter 3). Short-term changes were seen in my research, evident through both the shifting distributions between seasons and years, and different patterns of habitat selection between seasons. Though polar bear selection was slightly different for every season in my study, the biggest differences were seen during the ice freeze-up and break-up periods.

The sea ice freeze-up and break-up seasons of Hudson Bay have fast-changing habitat conditions; the largest magnitudes of selection in my model were calculated during these periods. The highest level of variation in selection among individuals was recorded during freeze-up, indicating that during this time of year individual polar bears may make different choices about habitat; this habitat selection is critical as the bears are coming off months of fasting. The lowest variation in selection occurred during late winter when seals are pupping, suggesting that there is less individual variation in choices at this time and, as such, most polar bears have similar preferences for habitat conditions during late winter. It is also worth considering that, because Hudson Bay is relatively shallow, seals have more widely available habitat during this time, and thus polar bears may not have as much pressure to select habitat as during the transition seasons. Habitat covariates important during freeze-up and break-up, such as distances to particular ice contours, were not nearly as important during the more stable, ice-covered winter seasons of Hudson Bay. Responses to changing habitat covariates during freeze-up and break-up reflect the dynamic conditions during the seasons that include the land to ice transition and may reflect the critical nature of the periods relative to costs and benefits, highlighting differences between individuals in the population.

Variations in reproductive status, age, and experience can affect how animals disperse on a landscape. For example, mothers with offspring face many demands that mothers without offspring do not have (Ricklefs et al. 1996). A female with cubs has a higher energy demand than a solitary female, and as such her abilities and space-use strategies, are influenced by her dependent offspring when travelling (Amstrup et al. 2000; Mauritzen et al. 2001). Thus, solitary females may make different movements than females with offspring (Mauritzen et al. 2003; Parks et al. 2006; Chapters 2 and 3). Movements may also be influenced by the distribution of resources (e.g. food or breeding habitat) and the physical structure of the landscape (Kareiva 1982; McIntyre and Wiens 1999). Individual differences were evident in how WH polar bears select habitat based on resources and habitat structure. For example, about three-quarters of the population selected to be close to the denning area while the other quarter selected to be farther away. Polar bear distribution shifted by season, as expected based on ice conditions, and differed depending on reproductive classes. Furthermore, these bears showed different patterns of habitat selection based on the time of year and the corresponding ice conditions, demonstrating that selection changed as availability changed (Mauritzen et al. 2003; Godvik et al. 2009), similar to other populations and indicative of a functional response, demonstrating that polar bears change their behaviour as the ice conditions change.

For polar bears, habitat availability changes daily as the sea ice shifts; in such a dynamic habitat, animals must select their habitat often, and as such, individual differences may became apparent as the outcome of constant selection becomes more clear. Polar bears likely select habitat in a way that allows them to search for seals, an animal whose presence may change based on ice conditions. Habitat selection by polar bears may reflect a trade-off between hunting and retreat as a result of energy-saving or risk-aversive behaviour (Mauritzen et al. 2003). The changing environment is forcing polar bears to constantly select habitat, and it is the variation in those decisions among individuals that may drive population change long-term. An understanding of the habitat characteristics that polar bears select for is important for managers. The periods of ice freeze-up and break-up are critical: if these continue to shift later and earlier, respectively, polar bears will likely continue to experience negative effects. As the climate changes in Hudson Bay, we can predict that polar bear habitat use and selection will change as well. Individual differences and variances drive changes in populations. From the large variances in many of my analyses, it is clear that there is a wide spectrum of individuals in this population and as such, it is hard to predict how WH polar bears will be distributed in the future. It is possible that some patterns or behavioural traits may be more successful over time, thus studying how movement patterns and habitat use affect body condition, survival, and reproduction could help predict how populations may shift in the future. It has become clear that collaring efforts need to be maintained and potentially increased in this area if we are to learn more about which patterns lead to more successful bears. By tracking the same individuals over multiple years, tracking the offspring of previously followed bears, or simply tracking more bears in general, much more can be learned about individual variation among polar bears in this region including if their habitat selection is based mostly on instinct or is at least partly learned, as it is in grizzly bears (Nielsen et al. 2013). Such individual variation will be one of many challenges that managers face when deciding how to best conserve this population and others.

While the decline of sea ice is the main concern for polar bear conservation, Hudson Bay bears face three additional immediate challenges. First of all, terrestrial and aquatic development in Hudson Bay is currently increasing, bringing increased commercial shipping during both ice-free and ice seasons, increased oil, gas, and mineral exploration, and newly opened waterways (Arctic Council 2009). Accordingly, shipping to the Port of Churchill is expected to increase and, while it is unclear how this will affect polar bears and their prey, it is likely that it will affect particular ice types that polar bears may rely on (Ferguson et al. 1998, 2000, 2001; Mauritzen et al. 2001, 2003; Chapter 2) and will increase the risk of an oil-spill, something polar bears are very sensitive to (Øritsland et al. 1981; Hurst and Øritsland 1982; Stirling 1990). Secondly, the disturbance of the denning area for WH bears has the potential to become a major issue through development, noise, and seismic disturbance, which could lead to den abandonment (Amstrup 1993; Lunn et al. 2004). At present, Wapusk National Park provides protection to some denning areas in Hudson Bay, but it is unknown how denning locations will change with climate change. One prediction suggests a 50% reduction in permafrost in the Hudson Bay lowlands by 2100 if temperatures increase as predicted (Gough and Leung 2002), potentially reducing den habitat. Finally, the effective use of deterrence programs to reduce human–bear conflict and defense kills is important for the management of WH bears (Peacock et al. 2010). It has been predicted that polar bear defense kills will increase as polar bears spend increasing amounts of time on land due to the lengthening of the ice-free season in Hudson Bay (Stirling and Derocher 1993; Derocher et al. 2004) and the number of problem bears in Churchill has increased with the earlier break-up of ice (Towns et al. 2009). The fact that land fast ice is declining in expanse during the ice season (Gagnon and Gough 2005a, b; Sahanatien and Derocher 2007) means that polar bears may occur at higher localized densities and closer to land during the winter months when they historically would be far out on Hudson Bay. My results show that home range centroids during the freeze-up season are shifting closer to land. If polar bear interactions with humans increase there may be an increase in problem bear kills if appropriate deterrent programs are not in place (Peacock et al. 2010). The shifting ice conditions (Gough et al. 2004; Gagnon and Gough 2005b), declining ice habitat (Sahanatien and Derocher 2007; Castro de la Guardia et al. 2013), links between sea ice and polar bear productivity make for a challenging future for polar bears in Hudson Bay.

However, the conservation of sea ice has unique conservation challenges that are difficult to address.

Unlike the management practices for many other species, it is difficult or impossible for those who manage polar bears to manipulate or protect important habitat. Sea ice as a habitat presents many novel conservation challenges: one cannot draw a boundary around ice to prevent it from melting nor get it to freeze again whenever desired. Consequently, there are few good options to protect important foraging and mating areas for polar bears and their prey in Hudson Bay. However one possible strategy is to designate a *Marine Protected Areas* under the *Oceans Act* of Canada, which could be designed to accommodate the predicted climate-induced spatial change (Prowse et al. 2009; Peacock et al. 2010). Still, designating a protected area does not guarantee that the sea ice will form predictably with the quality and quantity that would be necessary for polar bear population viability. As such, protecting essential areas (i.e., ice habitat in the intermediate and terrestrial habitat) can only mitigate declines and does not address the primary conservation concern for the species (Ragen et al. 2008). So far, little has been done to map, much less protect key marine regions for polar bears (Peacock et al. 2010). To better conserve this population in the face of the impending risks, advances are needed in our knowledge of what areas exactly to protect and the best way to go about implementing such protection. This will come with a better understanding of sea ice conditions in Hudson Bay, future sea ice projections in the bay, and polar bear and seal habitat requirements. Unfortunately, such progress is expensive and time consuming and the government would need to understand the import of the situation and act accordingly, which has not happened to date (CPAWS 2013). Though designating a protected area would be a difficult task, technological improvements can increase our knowledge at a faster rate than ever and help policy-makers make better informed decisions. If no steps are taken toward identifying and preserving important habitat in Hudson Bay in the next 10-20 years, the number of polar bear interactions with communities may increase (Towns et al. 2009) and polar bears may struggle to persist in the area as the ice conditions change (Castro de la Guardia et al. 2013).

A better understanding of Hudson Bay polar bear habitat requirements can be gained through mark-recapture and GPS collar studies, but it is the recent advancements in genetic research that will allow scientists to ask a whole host of new questions about these animals. We will be able to understand who WH polar bears are mating with, where their offspring disperse, who their offspring mate with, if their offspring follow movement patterns learned from the mother, and if paternity plays a role in dispersal. Moreover, the multiyear tracking of individuals will be imperative to determine the importance of areas that are used repeatedly and whether this use is continued by subsequent generations. Furthermore, the continued tracking of WH bears will be important to assess whether the current population boundaries are appropriate. The present boundaries between populations in Hudson Bay are thought to reflect learned patterns of ice movement relative to food availability and accessibility (Peacock et al. 2010), so if boundaries have changed it stands to reason that food availability has too. These boundaries need to be reassessed in the near future in accordance with the changing climate, and my research indicates that already there are times of the years where the majority of WH locations are outside of the WH boundary. Increasingly fuzzy population boundary lines may indicate increased genetic flow between the WH, SH, and FB populations, a better understanding of which would be useful for managers. If WH bears are going farther and farther outside their historical region to find food, we may start to see fewer bears on land in the summer due to poorer health caused by excess energy expense or simply relocation to another region. Obtaining more data on males would be hugely beneficial: population boundaries in Hudson Bay are based on harvest quotas and roughly 2/3 of this harvest is male (N. Lunn, pers. communication), yet we only have movement information for females. Currently, we are missing out on critically important information from the male demographic, information that could potentially change how we look at polar bear habitat requirements.

From both a scientific and educational perspective, polar bears of western Hudson Bay are an important resource. Polar bear tourism in Churchill has grown into a business of CDN$10 million/year (Manitoba Conservation), in turn increasing public education of the species and research support. It is important that scientists continue to monitor this population, as their condition may foretell the future of other polar bear populations. The springtime foraging period is of the utmost concern, so other regions in Hudson Bay need to be assessed and identified for their importance to polar bears during this time (Peacock et al. 2010). Also, if ice habitats continue to change in quantity and quality, it is crucial to recognize that individual polar bears may exhibit different preferences in habitat selection as their habitat changes, and reproductive status may be important to consider for management plans as females with cubs tend to act differently than females without cubs (Parks et al. 2006; Chapter 2). Sea ice habitat in Hudson Bay needs to be protected, but protection measures must consider both the spatial and temporal dynamic nature of sea ice (Prowse et al. 2009). More robust data is needed on the seal populations in Hudson Bay; without this, the links between the predator and its prey will remain speculative. For example, are the declines in polar bear body condition a function of reduced prey abundance, reduced prey availability or vulnerability, a decline in prey body condition, or a function of increased energetic demands?

Though polar bears are still relatively abundant in Hudson Bay, their future is unclear but extirpation appears likely. The earlier break-up and later formation of sea ice will push the capabilities of polar bears, and it is unknown whether they will be able to persist and thrive in a heavily altered ecosystem. Further conservation efforts in this region should be encouraged and appropriately funded. Polar bears will continue to adjust their habitat use and selection as the climate changes, and science must have the best data possible if conservation efforts are to be effective. Better ideas to preserve ice habitat in the face of increasing temperatures are needed, a complicated task and one that will involve multiple disciplines and policy-makers taking action in the near future.

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