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Sea ice dynamics influence movement patterns of adult female polar bears in southern Hudson Bay

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Abstract: To access seals (Pinnipedia), polar bears (*Ursus maritimus*) move large distances over the sea ice in winter. Already documented declines in ice duration for Hudson Bay, Canada, are predicted to continue, likely affecting polar bear movement patterns. Using data from global positioning system (GPS) collars, 2007–2011, we describe movement patterns of adult female polar bears of the Southern Hudson Bay (SH) subpopulation. We tested effects of season and reproductive class on movement rates, distance travelled, displacement distance and direction, and home range size. Except for denning females, reproductive class had no effect on movement rates, which were greatest during freeze-up and least during summer. Across all reproductive classes and seasons, mean hourly movement rate was 0.63 km/hour. Mean annual distance moved by nondenning females was 4,771 km. During freeze-up, bears moved north-easterly from the Ontario coast toward the Belcher Islands and Québec following the forming ice edge. During breakup, bears moved southerly toward the Ontario coast and away from the residual ice that occurs north of the Ontario coast. In autumn, denning females moved southerly and inland to den. Mean annual minimum convex polygon (MCP) home-range size was 153,866 km^2, with no effect of reproductive class nor change over time. Home range estimates from kernel density estimators and Brownian bridge movement models (BBMM) varied by reproductive class and were smaller than MCP ones. The BBMM estimates likely yield more realistic patterns of space use by polar bears. Using data from satellite collars, 1997–2003, we compared travel distance and home range size between periods (1997–2003; 2007–2011). We found weak evidence of a difference in distance moved between periods, perhaps due to a period of ice stability in the 2000s. Our results identified patterns of use of extensive areas of Hudson Bay by SH bears in winter, and results provide benchmarks for future studies of movement patterns.

Key words: home range, movement patterns, polar bear, sea ice, seasonal movements, Southern Hudson Bay, space use, *Ursus maritimus*

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The Southern Hudson Bay (SH) subpopulation of polar bears (*Ursus maritimus*) inhabits eastern Hudson Bay and James Bay (Canada), the most southerly continuously occupied portion of the world-wide range of polar bears (Obbard et al. 2010, Obbard and Middel 2012). Every year, Hudson Bay and James Bay undergo a complete cryogenic cycle with sea ice melting completely each summer and reforming in late autumn (Markham 1988, Etkin 1991). After spending about 7 months on the sea ice, in July or August polar bears in this region are forced ashore for up to 4–5 months. While on land they are without access to their main prey, ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*; Stirling and Archibald 1977).

Ecological change in the Arctic via changing duration and distribution of sea ice resulting from climate warming (Stirling and Derocher 2012) is currently considered the greatest threat to the conservation of polar bears (Atwood et al. 2016, Regehr et al. 2016). The duration of sea ice has declined across much of polar bear range (Stirling and Parkinson 2006, Stern and Laidre 2016), especially in seasonal sea ice regions (Amstrup et al. 2008) such as Hudson Bay (Gagnon and Gough 2005, Scott and Marshall 2010). In fact, sea ice duration has changed greatly in eastern Hudson Bay

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and James Bay since the 1980s (Gagnon and Gough 2005, Hochheim and Barber 2014, Stern and Laidre 2016). Depending on criteria used to define breakup and freeze-up dates, breakup has advanced 3.0–5.0 days/decade, and freeze-up has been delayed by 3.6–5.0 days/decade since 1980 (Obbard et al. 2016, Stern and Laidre 2016). There is annual variability, but polar bears in the region now spend up to a month longer on land than they did in the early 1980s (Obbard et al. 2016).

Analysis of movement behavior can reveal important information about foraging strategies, space use choice, intraspecific interactions, and resource preferences (Gurarie et al. 2009, 2016; Morelle et al. 2017). Documenting information on movement patterns and behavior for polar bears of differing subpopulations is important to establish a baseline against which future studies can be compared (Amstrup et al. 2000). Seasonal changes in ice distribution and concentration are known to affect the movement patterns of polar bears (Mauritzen et al. 2003, Parks et al. 2006, Sahanatien et al. 2015, Castro De La Guardia et al. 2017, Lone et al. 2017). Therefore, the objectives of this study were to describe movement behavior and home range use by polar bears of the Southern Hudson Bay subpopulation in relation to annual and long-term changes in sea ice using data obtained via global positioning system (GPS) telemetry. We report traditional movement parameters used in previous studies on polar bears (Garner et al. 1990, Amstrup et al. 2000, Wiig et al. 2003, Parks et al. 2006, Andersen et al. 2008) both to enable comparison with other subpopulations and to establish a baseline of information for this subpopulation. Information relevant to understanding the ecology and behavior of polar bears in a region deemed to be among the most at risk to climate change (Stirling and Derocher 1993) will assist future studies in assessing the impacts of a warming climate and continued reductions in ice duration and extent. Understanding the effects on the subpopulations at most risk from climate warming may help with early detection of behavioral shifts in more northern subpopulations where early detection may assist with mitigation and conservation efforts.

Seasonal variation in ice cover can dramatically alter the available prey abundance and distribution, potentially affecting polar bear movements and space use (Ferguson et al. 1999). Therefore, we used biologically relevant seasons to compare both seasonal and annual movements. As in similar studies (Amstrup et al. 2000, Parks et al. 2006), we recognized the different energetic demands of cubs (<1 yr old) and yearlings (1–2 yr old) on adult females so we separated bears at different stages of their reproductive cycle throughout the analysis. Previous studies have found little effect of reproductive status on movement of polar bears. Nevertheless, we hypothesized that younger cubs would constrain the movements of their mothers so we distinguished females by reproductive status in this analysis; and we reasoned that our data, with much higher fix frequency and location accuracy, might reveal differences that were undetected by earlier studies using coarser data. We tested the effects of season and reproductive class on movement rates, distance travelled, displacement distance and direction, and home range size. We used previously collected Argos Platform Transmitter Terminal (PTT) collar data (Obbard and Middel 2012) to enable us to test for temporal changes in annual travel distance and home range size between 2 study periods (1998–2003; 2007–2011).

Study area

The boundary of SH extends from just east of the Ontario–Manitoba border of Canada (89°W) to the Québec shore of Hudson Bay and James Bay (~73°W), and extends from 60°N latitude to the southern tip of James Bay (49.5°N; Obbard and Middel 2012 [Fig. 1]). During the ice-free season, most bears in this subpopulation are concentrated along the Ontario coast and on Akimiski Island in James Bay (Obbard et al. 2015, 2018). Though some bears spend the summer on smaller offshore islands in James Bay, on islands in eastern Hudson Bay, and along the Québec coast (Obbard et al. 2015, 2018), the melt patterns of the sea ice cause most bears to leave the ice to come ashore along the Ontario coast where they remain until freeze-up in the autumn (Prevett and Kolenosky 1982, Obbard and Walton 2004).

Methods

Animal capture and data sources

From mid-September to mid-October, 2007–2009, we captured encumbered adult females (i.e., accompanied either by cubs of the year or yearlings) along the Hudson Bay and James Bay coasts of Ontario and in areas up to 30 km inland, and on Akimiski Island in Nunavut (Fig. 1). We chemically immobilized bears from either a Bell 206L Long Ranger (Bell Textron, Fort Worth, Texas, USA) or Eurocopter EC-130 helicopter (Airbus Helicopters SAS [formerly Eurocopter Group], Marseille Provence Airport, Marignane, France) by remote drug delivery (Palmer Cap-Chur Inc., Powder Springs, Georgia, USA; or PneuDart,

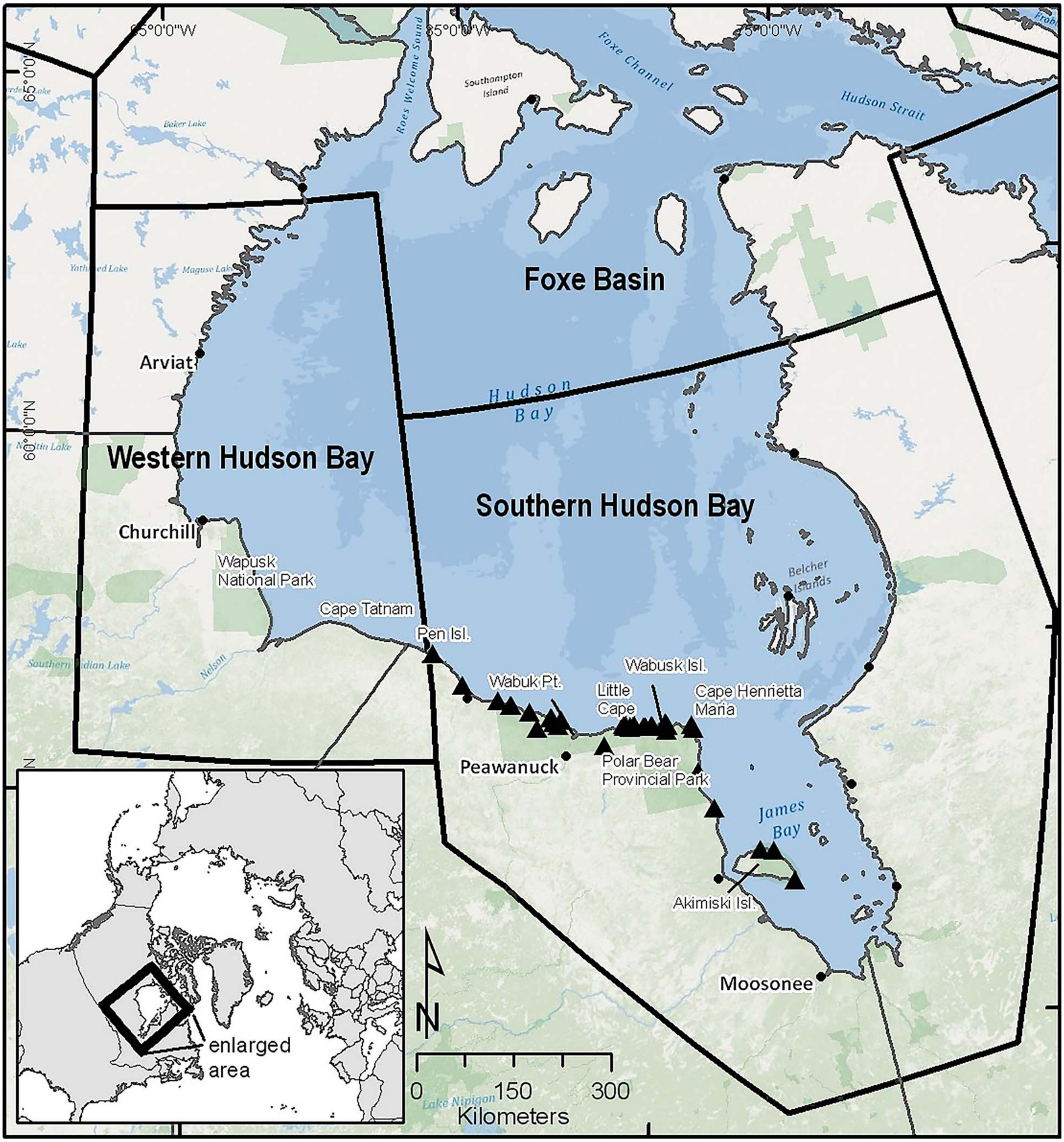

Fig. 1. Study area showing capture locations (solid triangles) of 38 global positioning system (GPS) -collared female polar bears (*Ursus maritimus*) in the Southern Hudson Bay subpopulation, 2007–2009, subpopulation boundaries, and locations mentioned in the text.

Inc., Williamsport, Pennsylvania, USA). We immobilized bears <1 year old by pole syringe. We used a combination of xylazine and zolazepam–tiletamine (XZT) administered intramuscularly as xylazine at 2 mg/kg (Cervizine 300®; Wildlife Pharmaceuticals, Inc., Fort Collins, Colorado, USA) and Telazol® at 3 mg/kg (Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA) estimated body mass (Cattet et al. 2003), or a combination of medetomidine and zolazepam–tiletamine (MZT) administered as medetomidine at 0.06 mg/kg (Bow River Pharmaceuticals, Bow River, Alberta, Canada) and Telazol® at 2 mg/kg (Cattet et al. 1997). At the conclusion of handling, we administered atipamezole (Antisedan®; Pfizer Bio-Pharmaceuticals and Animal Health, Mississauga, Ontario, Canada) intramuscularly at 0.20 mg/kg to reverse effects of xylazine or 0.30 mg/kg to reverse medetomidine (Cattet et al. 1997, 2003). Handling protocols were approved annually by the Animal Care Committee of the Ontario Ministry of Natural Resources (Protocols 99-07, 99-08, 99-09) and by Wildlife Research Permits issued by the Nunavut Department of the Environment, and we followed the general guidelines of the Canadian Council for Animal Care (CCAC 2003) and the American Society of Mammalogists (Sikes et al. 2011).

Each year we deployed Telonics Gen III or Gen IV GPS telemetry collars (Telonics Inc., Mesa, Arizona, USA) programmed to record a GPS position every 4 hours (i.e., 6 locations/day) on a sample of encumbered females. Data were delivered at least every 2 days via e-mail through the Argos Direct Automatic Distribution Service (ADS). All collars also stored locations in memory, which could be downloaded upon recovery. Collars were fitted with timed release mechanisms (CR-2A; Telonics Inc.) programmed to drop off after either 1 (Gen III) or 2 (Gen IV) years on 1 December of the year when bears were expected to be in maternity dens. We did not deploy collars on males because their necks are typically larger than their heads and collars would not be retained.

To analyze longer term changes, we incorporated previously collected Argos satellite collar data acquired for 26 female adult polar bears monitored from 1998 to 2003, with relocation data being collected every 6 days. Additional details on these data are provided in Obbard and Middel (2012), including capture dates and methodologies.

Data analysis

We collected location data in latitude and longitude coordinates and reprojected them to a modified Lambert Conformal projection commonly used to map the province of Ontario so that travel and displacement distances could be readily calculated in metric units. Although the GPS collars used in this study were highly accurate (30-m error [Tomkiewicz et al. 2010]) and reliable, erroneous points occasionally occurred (i.e., future dates, or positions hundreds of kilometers from a previous location) Therefore, prior to analysis, we manually filtered data to remove such obviously erroneous points.

We report all movement data using biologically relevant seasons based on 5 ice conditions: Summer, Freeze-up, Winter, Breakup, and Annually. For displacement and site fidelity analysis we used 2 additional periods: the period from beginning of freeze-up until the end of breakup (on-ice displacement), and the period from first capture until the subsequent autumn (autumn–autumn displacement). Periods of analysis and parameters reported largely follow those used for an earlier study on female polar bears in the Western Hudson Bay subpopulation (Parks et al. 2006). We defined ‘Summer’ as the period that included all the onshore, nondenning locations from full ice melt to the beginning of freeze-up. We defined ‘Freeze-up’ as the period from the bear’s first location on ice in November or December until the date that the average ice concentration in the Southern Hudson Bay management unit (SH subpopulation boundary + 100-km buffer) reached and remained above 90%. We chose an average ice concentration threshold of 90% because at that point all potential ice-habitat should be accessible to any bear with no restrictions to its movement. We defined ‘Winter’ as the period between the end of freeze-up and the beginning of breakup. We defined ‘Break-up’ as extending from the date the average ice concentration dropped below 90% and remained $<90\%$ for ≥ 5 consecutive days to the date the bears reached shore and remained on shore. We used a standard ice concentration metric to delineate our seasons rather than ordinal dates because ice formation and disappearance patterns vary among years (Hochheim et al. 2010).

We downloaded daily ice concentration data, estimated using the Advanced Microwave Scanning Radiometer – EOS (AMSR-E) satellite sensor at 6.25-km resolution through the University of Hamburg website (Spreen et al. 2008, Spreen and Kaleschke 2011). We analyzed ice concentration separately for each year, resulting in differing freeze-up lengths from one year to the next, depending on how rapidly the Bay froze over. We defined all seasonal periods based on an individual’s movement and annual timing on and off the ice, so they were not consistent among individuals. We based the transition between seasons on actual ice concentration and bear locations on ice to facilitate future comparisons under changing climatic conditions (i.e., later freeze-up or earlier breakup dates in the future), but report dates corresponding to the start and end of each season (Table 1).

Table 1. Calendar dates denoting the start of each season used in movement and home range analyses for Southern Hudson Bay polar bears (*Ursus maritimus*), 2007–2011. Ordinal date in parentheses.

Year	Freeze-up	Winter	Breakup	Summer
2007–2008	27 Nov (331)	12 Dec (346)	06 May (127)	16 Jul (198)
2008–2009	29 Nov (334)	17 Dec (352)	15 Jun (166)	20 Aug (232)
2009–2010	07 Dec (341)	25 Dec (359)	23 Apr (113)	18 Jul (199)
2010–2011	25 Nov (329)	16 Jan (16)	16 May (136)	26 Jul (207)
Overall mean date	02 Dec (336)	26 Dec (360)	16 May (136)	29 Jul (210)

Nothing has been reported on the ice conditions when SH bears first move out onto the ice in the autumn, or when they finally return to shore in the summer; therefore, we used Canadian Ice Service (CIS) weekly ice chart data to summarize the proportion of the defined subpopulation area with ≥50% ice concentration at the mean date of return to either ice or shore for each year. We used a threshold of 50% concentration because it was used previously to indicate freeze-up and breakup in Hudson Bay (Etkin 1991, Gough et al. 2004, Gagnon and Gough 2005) and in earlier studies analyzing ice trends with respect to polar bears in Hudson Bay (Stirling et al. 1999, 2004). We used CIS data rather than AMSR-E data, despite the coarser spatial and temporal resolution, because the satellite data alone tend to underestimate ice concentration during breakup. This underestimation in ice extent and concentration during breakup is due to ponding of water on top of the ice and the short wavelength of the sensor, resulting in water-covered ice being classified as open water (Etkin and Ramseier 1993, Agnew and Howell 2003). We summarized ice cover based on the SH subpopulation boundary because this was the first ice available to the bears in the autumn, and previous work has shown that adult females of this subpopulation largely remain within the subpopulation boundaries (Obbard and Middel 2012).

For temporal analysis of home range size and distance moved (i.e., 1998–2003 vs. 2007–2011), we used daily passive microwave ice concentration data collected by the Special Sensor Microwave/Imager (SSM/I) and the Scanning Multichannel Microwave Radiometer (SMMR), made available through the National Snow and Ice Data Center (Cavalieri et al. 1996) at a spatial resolution of 25 km. We used these data for the longer term analysis because the period of observation begins in 1978. Similar to the AMSR-E data, this sensor is sensitive to the ponding effect of water on ice.

Within each season, we included data for analysis provided the collar collected data for ≥40 days, had ≥100 locations, and had a successful fix acquisition rate >25%. The freeze-up season is typically quite short, so the requirement for this season was only 10 days or 50 fixes and a successful fix acquisition rate >25%. For annual analysis, a 'bear year' included data that began at the start of the summer season (or at initialization of the collar upon first capture) and ran to the end of breakup of the following year. The numerical year assigned was the year in which January fell (i.e., bear year 2008 was from August 2007 to July 2008). We included data from an individual bear in the annual analysis provided the collar was retained for ≥240 days, returned ≥100 locations and had a >25% fix rate.

We assigned reproductive class to bears at the time of collaring in the autumn, classifying them as either bears with yearlings (Y; aged 1–2 yr) or bears with cubs of the year (C; aged <1 yr). The reproductive status remained the same throughout the designated bear year. For bears with collar data exceeding 1 year, the reproductive status of the female progressed accordingly, so females with cubs became females with yearlings, and females with yearlings became solitary (S) or pregnant (P) the following summer, depending on whether or not they entered a maternity den in the autumn. We confirmed denning based on stationary telemetry locations for an extended period until late winter, and verified there was an occupied den by a site visit the following summer. Females that entered a den and returned to the ice in the spring with newborn cubs were classed as denning (D) for the period from freeze-up through the rest of the winter and breakup to separate them from bears accompanied by cubs in the autumn. Categorizing bears using this scheme assumes survival of the cubs through the first year for them to be classed as with yearlings the following year. Estimated survival rates of individual cubs (0–1 yr) range from 0.49 to 0.64 in Southern Hudson Bay (Obbard et al. 2007), giving some support for this assumption, given that some loss of cubs is from litters >1 (i.e., a female losing 1 cub from a litter of 2 would still progress to being a female accompanied by yearlings). Additionally, based on aerial surveys, the litter size of family groups of cubs in SH in autumn is about 1.5 and litter size of family groups of yearlings is about 1.4 (Obbard et al. 2015, 2018), suggesting low mortality of cubs older than 10 months. We did not have the ability to confirm reproductive status for every bear over the course of the year, and recapture or resight rates of collared bears in subsequent years was low. Nevertheless, only one bear denned earlier than expected, suggesting it had lost its entire litter of cubs, and this bear was classified as denning for the subsequent year, rather than with yearlings.

We calculated mean hourly movement rates as the distance (in km) between successive locations, divided by the time (in hours) between relocations. Unless otherwise specified, effects of reproductive status and season on movement rates were evaluated using a 2-way analysis of variance (ANOVA) with multiple comparisons among mean factor levels made using Tukey's Unequal N Honest Significant Difference (HSD) post-hoc test (Zar 1999:212). Data that did not meet the assumptions of normality or homogeneity of variance were transformed using a natural log or square root transformation, or effects were tested using a nonparametric Kruskal–Wallis test.

We calculated total distance traveled annually and seasonally as the sum of all straight-line distances between successive relocations for each bear. We tested the null hypothesis that total distance moved was independent of reproductive class and season using a 2-way ANOVA. To enable comparison to previously collected Argos PTT data (Obbard and Middel 2012), we subsampled recent GPS telemetry data to the same resolution as the earlier Argos data (i.e., 1 location every 6 days). Subsampling was necessary because the more frequent relocation data from GPS collars provide more detailed movement information and hence greater estimates of total distance moved (Parks et al. 2006, Rowcliffe et al. 2012). For all temporal analyses, we used linear regression to test for significant changes in distance travelled and tested for a possible correlation between distance and sea-ice duration. We calculated sea-ice duration and breakup dates using the average ice concentration within the SH subpopulation boundaries based on the SMMR and SSM/I daily ice concentration data (Cavalieri et al. 1996).

We measured net seasonal displacement as the straight-line distance between the first and last location in that season. We calculated the displacement for each bear individually and report the mean displacement length and direction by season and reproductive class. We used annual displacement as a measure of site fidelity and calculated it as the straight-line distance between the mean autumn (Sep–Oct) location of the first year of collaring and the mean autumn location of the subsequent year(s; autumn–autumn period). We calculated net on-ice displacement as the distance between the first and last location on ice, and report direction of that displacement. We report displacements according to the presumed reproductive status of the bear following breakup: solitary females, female bears accompanied by cubs born that winter, and female bears accompanied by yearlings. Small sample sizes reduced our ability to make statistical inferences about differences in reproductive status, but we report mean ± standard error, minimum, and maximum displacement distances in addition to mean displacement direction by reproductive class.

We used circular statistics to assess displacement direction of bears seasonally, annually, and between their on- and off-ice locations. We used the Watson–Williams test for multiple samples (Zar 1999:625) to test for effects of reproductive class on direction for all time periods. Prior to conducting the Watson–Williams test, we tested circular data to ensure a von Mises distribution (circular normal distribution) and, if necessary, transformed data using a cosine transformation. We evaluated circular mean direction (θ) and strength of directionality (r) using Rayleigh's Z-test (Zar 1999:616) and report both.

To enable comparison with other studies, we evaluated general use areas using 2 commonly used home range metrics: the minimum convex polygon (MCP) and the kernel density estimator (KDE; Anderson 1982, Kernohan et al. 1998, Laver and Kelly 2008). We also calculated a less commonly used metric, the Brownian bridge movement model (BBMM; Bullard 1991, Horne et al. 2007), which more precisely describes movement patterns and so may better take advantage of frequently acquired, high-accuracy data from GPS collars. We generated all home range estimates using Program R software for statistical computing (R Development Core Team 2012) and the suite of packages associated with *adehabitat* (Calenge 2006). We calculated the smoothing parameter (bandwidth, or h) for kernel density estimation independently in both the X and Y directions using the plug-in equation method (Wand and Jones 1993, 1995; Herrmann et al. 1995) in the R package *KernSmooth* (Wand 2011). We used the average of these X and Y estimates to give a single bandwidth estimate for each bear within a season, which we used to create each utilization distribution (UD). The Brownian motion variance is related to the animal's mobility (Horne et al. 2007) and was calculated separately for each individual within each season using a maximum likelihood approach implemented in the R package *adehabitat* (Calenge 2006), following the approach developed by Horne et al. (2007). The second parameter required to estimate a Brownian bridge UD is the location error estimate, which we calculated using data from dropped collars that we recovered on land. For all 3 home range methods we generated 95% contours, both seasonally and annually, and compared the mean home-range size between reproductive classes within each period using an ANOVA. We used the same criteria for inclusion to the home range estimate as we used for the movement behavior analysis, restricting inclusion to only those bears that had a suitably representative set of relocation data.

To evaluate temporal change in home range and compare earlier Argos-tracked bear home ranges with more current GPS-tracked bears, we resampled the GPS data to the same fix frequency as that of the earlier data. We used 95% annual home-range estimates created using the MCP method to determine whether there had been a change in mean annual home-range size over the previous 10 years. We used MCP methods to compare our results with an earlier study in the neighboring Western Hudson Bay subpopulation (Parks et al. 2006). Prior to comparing home ranges among years and reproductive classes, all MCP home-range area estimates were transformed using a square root transformation to achieve a normal data distribution. We used a factorial ANOVA to test for a potential effect of year on seasonal and annual MCP home-range size, and to test for interaction between year and reproductive class. We were unable to use KDE methods to compare home range sizes over time because the sparse resampled data combined with the large movements of bears made the selection of an appropriate bandwidth difficult and resulted in either unrealistically large kernel estimates using the plug-in equation method, or very restricted kernel surfaces with numerous small peaks using the least squares cross-validation method. For annual home-range analysis, we removed any bears that were denning in the current year, as well as any bears that were collared on Akimiski Island ($n = 3$ in 1998; and $n = 1$ in 2008), because these bears had movements largely contained within James Bay (Crompton et al. 2008, Obbard and Middel 2012).

We used R version 2.15 (R Development Core Team 2012) and Statistica V 10 (Statsoft Inc. 2011 [TIBCO Software, Stanford Research Park, Palo Alto, California, USA; www.tibco.com/data-science-and-streaming) for statistical analysis, and a combination of Environmental Systems Research Institute (ESRI) ArcGIS 9.3.1 (ESRI 2009) and R for spatial analyses. We created plots using Statistica V 10. We analyzed movement and home range estimates using the package *adehabitatHR* (Calenge 2006) and calculated circular statistics using the package *circular* (Agostinelli and Lund 2011), both within the R statistical environment.

Results

In total, we fitted 38 different adult female polar bears with GPS collars during 2007–2009 (9 in 2007, 13 in 2008, and 16 in 2009). We received data either through the Argos ADS, or through direct download of recovered collars, obtaining 45,630 locations between September 2007 and August 2011. Of the collars deployed, 1 failed to initialize, 5 were shed by the bear within the first week of deployment, and 2 had GPS unit failures within the first 30 days of operation, leaving 30 bears carrying collars for up to 2 years. After filtering for obviously erroneous points and removing bears with insufficient data, we retained 45,098 locations. Inconsistencies in collar functionality and variation in the collar end-date resulted in the number of locations and bears included in the analysis varying depending on the season (Table 2). Many collars released prematurely or were dropped by the bear and not recovered; however, we retrieved 8 collars that successfully released on land on the scheduled date. Data downloads from recovered collars always returned more data than that received through the Argos ADS. The volume of data transmitted through ADS was 50–60% of the actual data stored on the Gen III collars ($n = 4$) but was close to 90% for Gen IV collars ($n = 4$).

On-ice and off-ice dates

Season length varied among years depending on when the Bay began to freeze over, and when the end of melt occurred (Table 1). Analysis of Canadian Ice Service data showed that the bears moved onto the ice during freeze-up when 6–9% ($\bar{x} = 7.1\%$) of the total SH portion of the Bay had ice with a concentration of $\geq$50%. Bears returned to shore during breakup when the proportion of the SH region with $\geq$50% ice ranged from 2% to 35% ($\bar{x} = 5.2\%$). The 35% value for the entire SH management unit is an outlier not included in the

Table 2. Number of active collars deployed on adult female polar bears (*Ursus maritimus*) in Southern Hudson Bay, by season, year, and reproductive class, which were used in movement and home range analysis. Reproductive classes: C = Females accompanied by cubs, Y = Females accompanied by yearlings, and D = Females that entered maternity dens in the autumn.

	2008				2009				2010				2011				
Period	C	Y	D	Total	C	Y	D	Total	C	Y	D	Total	C	Y	D	Total	Total
Summer	0	6	0	6	6	4	0	10	6	8	2	16	0	2	5	7	39
Freeze-up	0	3	0	3	3	2	1	6	6	6	3	15	0	2	5	7	31
Winter	0	5	0	5	4	4	1	9	4	9	0	13	0	2	2	4	31
Breakup	0	3	0	3	2	3	0	5	3	8	1	12	0	2	3	5	25
Annual	0	4	0	4	4	3	1	8	4	7	3	14	0	2	3	5	31

mean (Table 3); it occurred in 2008 when only a single bear was still collared at breakup and it returned to Akimiski Island in James Bay where ice melts sooner than in the Hudson Bay portion of the management unit. Mean dates on ice and the proportion of the SH section of the Bay covered with ice of ≥50% concentration are shown in Table 3.

Daily and seasonal movement rates

Time between relocations ranged from 4 to 1,617 hours, with a median interval of 4 hours. Despite a programmed 4-hour interval between fix attempts, both natural and technical factors (e.g., transmitter failure, weather, bear swimming, substrate cover during denning) resulted in considerable variability in fix acquisition. We excluded locations separated by >8 hours from our analysis of movement rates (<5% of locations). This interval enabled a comparison with short-term movement rates used in other studies on polar bears.

The maximum movement rate recorded during any season was 6.53 km/hour by a female accompanied by a single yearling during the freeze-up season of 2007. Across all reproductive classes and seasons, the mean hourly movement rate was 0.63 km/hour (Table 4). A 2-way ANOVA indicated that there was very strong evidence (sensu Muff et al. 2022) of the effect of season on movement rate ($F_{3,114} = 152.7$, $P < 0.0001$), and of the effect of reproductive class on movement rate ($F_{2,114} = 49.4$, $P < 0.0001$; Table 4). There was very strong evidence of a significant interaction between the main effects ($F_{6,114} = 41.2$, $P < 0.0001$). This interaction was influenced by denning females during the freeze-up period (Fig. 2) because these bears were localized at a den site while all other bears were moving rapidly out onto the ice. Therefore, we repeated the analysis to exclude denning females. This removed the interaction between main effects so that there was no longer any evidence that reproductive class had an effect on movement rates ($F_{1,95} = 0.93$, $P = 0.34$), though there was very strong evidence that season remained an important factor ($F_{3,95} = 182.5$, $P < 0.0001$). Post-hoc analysis, excluding denning females, showed that movement rates during the summer were significantly lower than those of any other season. Movement rates during freeze-up were significantly higher than in any other season, except for the class of females with cubs during breakup, which had a small

Table 3. Mean calendar dates on and off sea-ice for radiocollared adult female polar bears (*Ursus maritimus*) in the Southern Hudson Bay subpopulation, 2007–2011. Ordinal dates ± standard errors provided in parentheses; *n* = sample size, and percent area >50% refers to the area with ≥50% ice concentration as defined by the Canadian Ice Service ice chart closest in time to the mean on- or off-ice date. “n/a” is Not applicable.

Year	Mean off-ice date	*n*	Percent area >50%	Mean on-ice date	*n*	Percent area >50%
2007	n/a	n/a	n/a	27 Nov (331 ± 1.9)	5	9.3
2008	16 Jul (198 ± 0)	1	35.0	29 Nov (334 ± 2.2)	9	6.7
2009	20 Aug (232 ± 1.9)	4	6.9	07 Dec (341 ± 0.8)	14	6.2
2010	18 Jul (199 ± 2.3)	7	6.3	25 Nov (329 ± 5.0)	2	6.2
2011	26 Jul (207 ± 0.7)	6	2.3	n/a	n/a	n/a
Overall mean	29 Jul (210 ± 3.3)	17	5.2[a]	02 Dec (336 ± 1.2)	30	7.1

[a] Overall Mean Off-ice Date does not include 35% ice concentration value observed in 2008 when only one bear was still collared during breakup, and it was resident in James Bay.

Table 4. Mean movement rates (km/hr ± standard error [SE]) by season and reproductive class for radiocollared adult female polar bears (*Ursus maritimus*) in the Southern Hudson Bay subpopulation, 2007–2011. Annual movement rates were calculated using bears that retained their collars for ≥240 days. Reproductive classes are as follows: accompanied by cubs in autumn (Cubs), accompanied by yearlings in autumn (Yearlings), denning females (Denning), and all classes combined (Overall).

	Cubs			Yearlings			Denning			Overall		
Period	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*
Summer	0.14	0.01	12	0.14	0.02	20	0.06	0.01	7	0.13	0.01	39
Freeze-up	1.47	0.13	9	1.38	0.12	13	0.02	0.01	9	1.01	0.13	31
Winter	0.82	0.07	8	0.85	0.05	20	0.8	0.14	3	0.84	0.04	31
Breakup	1.11	0.14	5	0.92	0.06	16	0.88	0.06	4	0.95	0.05	25
Overall	0.79	0.1	34	0.76	0.06	69	0.28	0.08	23	0.68	0.05	126
Annual	0.73	0.06	8	0.69	0.03	16	0.38	0.06	7	0.63	0.03	31

sample size and consequently high variance. Rates of movement during winter and breakup were similar across all reproductive classes (Table 4, Fig. 2).

As a supplementary test of the effect of reproductive status, we performed a separate annual analysis (1-way ANOVA) on bears with data for ≥240 days, ensuring bears contributed data for all seasons. This indicated that there was very strong evidence that reproductive status affected movement rates ($F_{2,28} = 16.25$, $P < 0.0001$); females that entered maternity dens during the year had much lower mean annual movement rates than did either bears accompanied by cubs of the year in autumn or bears accompanied by yearlings in autumn (Table 4).

Total seasonal and annual distance traveled

There was very strong evidence that both season ($F_{3,114} = 72.3$, $P < 0.0001$) and reproductive class

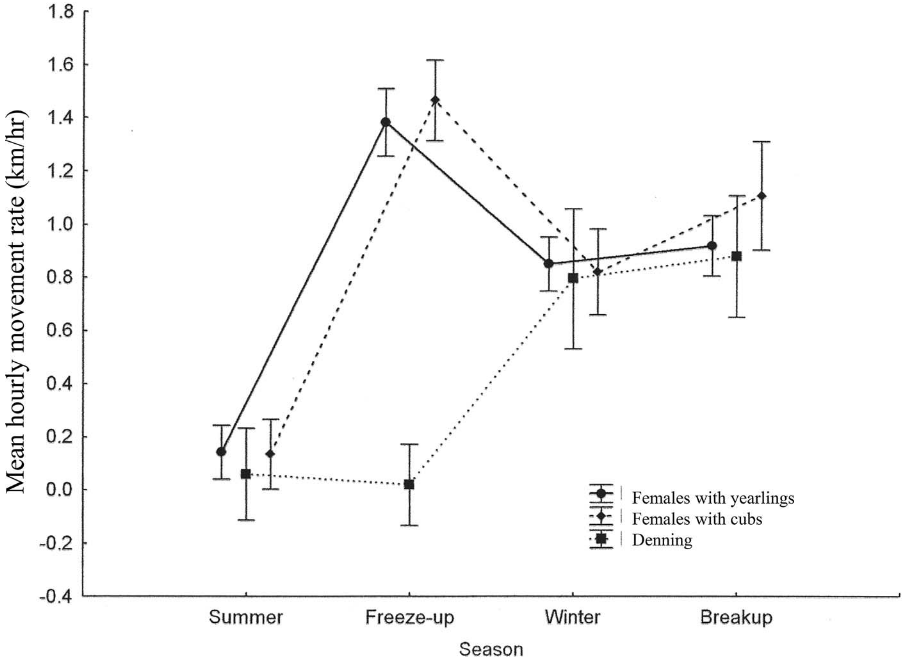

Fig. 2. Mean (±0.95 confidence interval) hourly movement rates (km/hr) by season and by reproductive class for radiocollared adult female polar bears (*Ursus maritimus*) in the Southern Hudson Bay subpopulation, 2007–2011.

Table 5. Mean (± standard error [SE]) total seasonal and annual distances traveled (km) by radiocollared adult female polar bears (*Ursus maritimus*) in the Southern Hudson Bay subpopulation, 2007–2011. Annual values were calculated using bears that retained their collars for ≥240 days. Reproductive classes are as follows: accompanied by cubs in autumn (Cubs), accompanied by yearlings in autumn (Yearlings), denning females (Denning), and all classes combined (Overall).

	Cubs			Yearlings			Denning			Overall		
Period	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*
Summer	215	23.2	12	235	25.3	20	135	35.9	7	211	16.9	39
Freeze-up	658	75.1	9	792	133.4	13	32.8	7.7	9	533	83.3	31
Winter	2,543	325.8	8	2,489	149.2	20	1,197	301.9	3	2,378	145.2	31
Breakup	1,772	334.4	5	1,314	141.2	16	1,138	244.5	4	1,378	121.2	25
Overall	1,109	185.8	34	1,244	122.5	69	408	119.0	23	1,055	90.3	126
Annual	4,798	539.6	8	4,744	290.8	16	2,297	555.7	7	4,206	297.9	31

($F_{2,114} = 13.3$, $P < 0.0001$) affected total distance travelled (Table 5), with denning females travelling shorter distances during the freeze-up season. There was no difference in distance moved between females accompanied by cubs and females accompanied by yearlings, regardless of season. Following removal of denning females from the analysis, there was very strong evidence that total distance moved by nondenning females varied with season ($F_{3,95} = 94.7$, $P < 0.0001$), but there was no evidence that distance moved varied with reproductive class (Table 5, Fig. 3). Seasonally, the greatest mean distance moved by all nondenning females combined occurred during winter ($\bar{x} = 2{,}504$ km, $n = 28$), followed by breakup ($\bar{x} = 1{,}423$ km, $n = 21$), freeze-up ($\bar{x} = 737$ km, $n = 22$), and summer ($\bar{x} = 227$ km, $n = 32$; Table 5, Fig. 3).

The mean total annual distance travelled was 4,206 ± 297.9 km ($n = 31$) across all reproductive classes (Table 5). However, there was very strong evidence that females

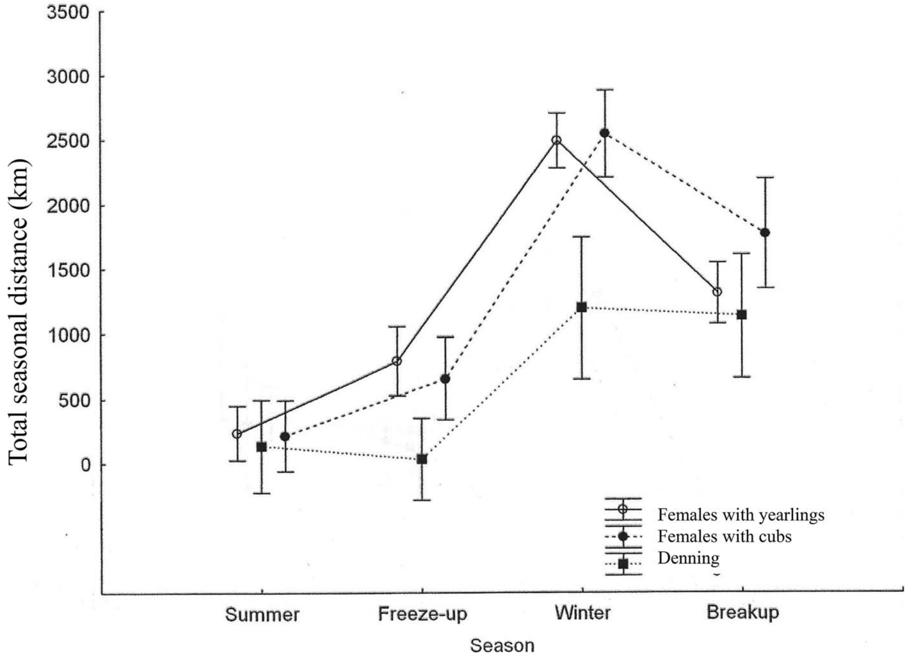

Fig. 3. Mean (±0.95 confidence interval) distances (km) travelled by season and reproductive class for radiocollared adult female polar bears (*Ursus maritimus*) in the Southern Hudson Bay subpopulation, 2007–2011.

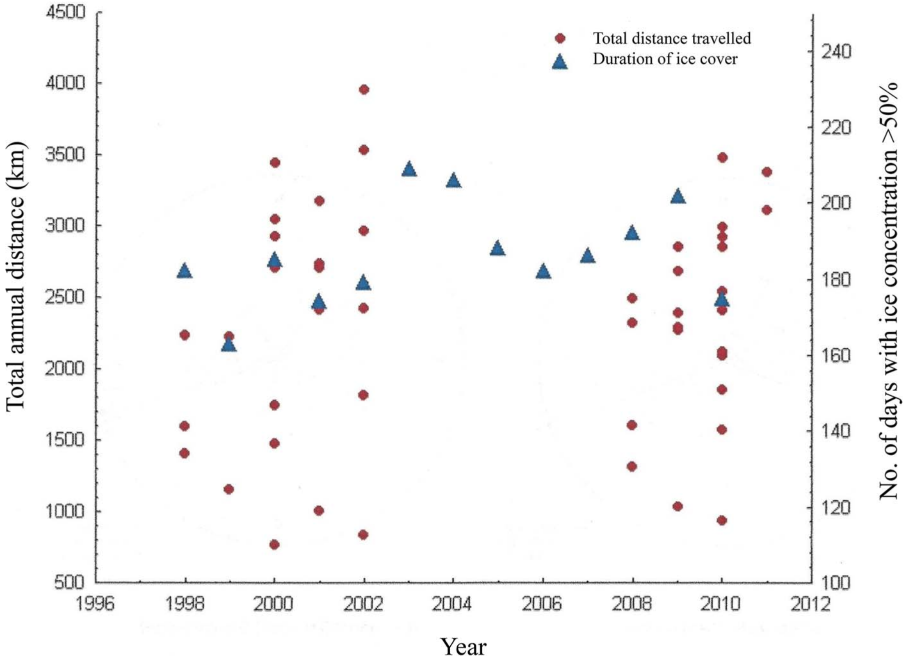

Fig. 4. Temporal trend of total annual distance travelled for nondenning adult female polar bears (*Ursus maritimus*) fitted with either Argos Platform Transmitter Terminal (1998–2002) or global positioning system collars (2007–2011) in the Southern Hudson Bay subpopulation. Annual distances (●) are plotted with annual ice duration (▲).

entering maternity dens moved shorter distances over the course of the year ($F_{2,28} = 9.3$, $P = 0.0008$). There was no evidence that annual distance travelled differed between females accompanied by cubs in the autumn and females accompanied by yearlings in the autumn ($t_{22} = -0.095$, $P = 0.92$; Table 5). The mean annual distance traveled by nondenning females was twice that of denning females (Table 5). The maximum distance traveled was 6,774 km by a female accompanied by 2 yearlings in 2011, whereas the minimum distance was just 681 km by a denning female in 2009. Minimum annual distance traveled by a nondenning bear was 2,323 km by a female accompanied by 2 yearlings in 2010.

The median fix interval for the Argos data was 7.5 days, so we resampled more recent GPS data to match. There was no evidence that ice duration at 50% concentration affected total distance travelled over the period 1998–2010 ($r_{46} = -0.063$, $P = 0.67$). Also, there was no evidence that the annual distance travelled changed between the two study periods ($\overline{x}_{(1998\text{–}2002)} = 2{,}287$ km, $\overline{x}_{(2008\text{–}2011)} = 2{,}327$ km; $t_{46} = -0.177$, $P = 0.198$). Further, there was only weak evidence that ice duration changed over the period 1998–2010 ($b = 0.24$, $t_{46} = 1.72$, $P = 0.09$; Fig. 4).

Displacement distances and direction

The mean straight line distance between a bear's first location on ice in autumn and its last location on ice the following summer was 155.7 ± 27.5 km ($n = 17$; Table 6). Although the median was close to the mean (median = 170 km), displacement distances varied greatly among individuals (min. = 7.4 km, max. = 373.6 km). There was moderate evidence of an effect of reproductive status on net on-ice displacement distances ($F_{2,14} = 4.008$, $P = 0.042$). Few bears with first year cubs retained their collars long enough to document their return to land the summer following parturition; but of those that did, displacement distances were small compared with bears accompanied by yearlings or solitary females (Table 6). A Tukey's post-hoc test indicated that bears arriving on shore with yearlings returned from the ice significantly farther from their first position on ice the previous autumn than did bears accompanied by cubs of the year. High variability among individuals (Fig. 5A) resulted in there being no evidence that direction of net ice displacement between first location on ice during freeze-up and last location on ice during breakup deviated from being uniformly distributed (Rayleigh's $z = 0.026$, $P = 0.978$), and

Table 6. Mean (± standard error [SE]) displacement distances (km) for radiocollared adult female polar bears (*Ursus maritimus*) in the Southern Hudson Bay subpopulation 2007–2011, measured as the straight line distance between the first and last location on ice (Net on-ice) and the straight line distance between mean autumn locations in subsequent years (Annual). Displacement direction (θ) in degrees, strength of directionality (*r*), and sample size (*n*) are reported for each reproductive class and period. Reproductive classes are as follows: accompanied by young cubs in winter (Cubs), accompanied by yearlings in autumn (Yearlings), denning females (Denning), and all classes combined (Overall).

	Net on-ice (Autumn–Summer)					Annual Autumn–Autumn				
Reproductive class	Mean	SE	θ	*r*	*n*	Mean	SE	θ	*r*	*n*
Denning	167.6	31.2	298	0.37	10	106.6	28.4	243	0.58	10
Cubs	51.2	39.7	96	0.11	4	62.5	35.4	32	0.38	4
Yearlings	255.3	63.6	111	0.98	3	208	73.2	107	0.99	2
Overall	155.7	27.5	353	0.04	17	108.3	22.9	233	0.19	16

there was no evidence of an effect of reproductive class on the mean direction of displacement (Watson–Williams test $F_{2,14} = 1.12$ $P = 0.36$).

Annual autumn to autumn displacement distances (i.e., straight line distance between mean Sep–Oct locations in consecutive years) were similar to net on-ice displacement distances (Table 6). Annual and net on-ice displacement directions were similar for females accompanied by yearlings, but solitary females had a more south-westerly mean autumn direction and females accompanied by cubs had a more north-easterly direction (Fig. 5B). Again, high inter-individual variability resulted in there being no evidence that annual autumn displacement directions deviated from being uniformly distributed (Rayleigh's $z = 0.63$, $P = 0.54$), and there was little evidence of an effect of reproductive class on the mean direction of displacement (Watson–William test $F_{2,13} = 1.7$, $P = 0.22$; Fig. 5B). Further, there was little evidence of an effect of reproductive status on the mean annual displacement distances ($F_{2,13} = 1.881$, $P = 0.192$).

There was very strong evidence of a seasonal effect on displacement distances ($F_{3,114} = 15.6$, $P = <0.0001$) for all reproductive classes, with summer displacements being much shorter than those of any other season (Table 7). Within each season, reproductive class had an effect only during Freeze-up, with

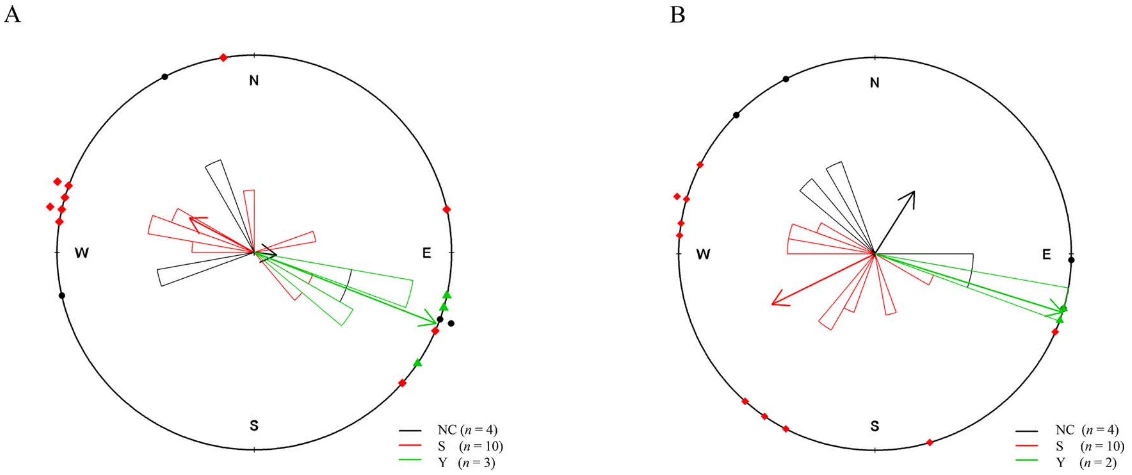

Fig. 5. Rose plots showing the direction of displacement for (A) the net on-ice (freeze-up to breakup) and (B) the annual (autumn–autumn) periods of radiocollared female polar bears (*Ursus maritimus*) in Southern Hudson Bay, 2007–2011. Direction of arrows indicates direction of travel; length of the arrow indicates the strength of the directionality (*r*), and points around the circle represent individual bears (● = females returning to the ice in late winter with new cubs (NC), ▲ = females accompanied by yearlings (Y), ♦ = solitary females (S).

Table 7. Mean (± standard error [SE]) total seasonal and annual displacement distances (km) and displacement direction (θ) by reproductive class for radiocollared adult female polar bears (*Ursus maritimus*) in the Southern Hudson Bay subpopulation, 2007–2011. Strength of direction is given by the *r*-value (range = 0–1); *n* indicates sample size.

	Cubs					Yearlings					Denning					Overall				
Period	Mean	SE	θ	*r*	*n*	Mean	SE	θ	*r*	*n*	Mean	SE	θ	*r*	*n*	Mean	SE	θ	*r*	*n*
Summer	76.5	20.8	332	0.56	12	71.9	15.7	303	0.63	20	67.9	14.9	187	0.59	6	72.7	10.5	304	0.4	38
Freeze-up	342.3	42.8	64	0.95	9	307.1	48.6	69	0.89	13	22.4	6.7	47	0.51	9	234.6	34.1	63	0.79	31
Winter	271.2	63.6	326	0.71	8	291.7	37.6	318	0.74	20	347.5	126.6	6	0.89	3	291.8	30.6	325	0.72	31
Breakup	339.7	60	189	0.91	5	292.4	48.5	193	0.64	16	317.5	46.3	206	0.89	4	305.9	33.4	194	0.73	25
Overall	231.4	29.2	4	0.29	34	231.0	22.0	315	0.24	69	132.8	34.2	119	0.08	22	213.8	16.0	335	0.19	125

denning females having a short displacement distance (Table 7). When we considered only females actively moving while Hudson Bay was ice covered (Freeze-up through Breakup), there was no evidence of an effect of reproductive class ($F_{1,65} = 0.21$, $P = 0.65$) or season ($F_{2,65} = 0.39$, $P = 0.67$) on displacement distances.

There was very strong evidence that direction of movements varied by season (Watson–Williams test, $F_{3,2} = 34.9$, $P < 0.0001$; Table 7, Fig. 6). Within seasons, there was very strong evidence that reproductive class had an effect only during the Summer period ($F_{2,2} = 13.84$, $P < 0.0001$), when denning females had a mean southerly movement direction ($\theta = 187°$), whereas females accompanied by cubs and females accompanied by yearlings traveled primarily northwesterly ($\theta = 332°$ and 303°, respectively). In the other seasons, reproductive class had little effect on displacement direction, with bears travelling generally northeast in the general direction of the Belcher Islands and the Québec shore during Freeze-up ($\theta = 63°$), south toward the Ontario coast through Breakup ($\theta = 194°$), and having a general northwest movement during Winter ($\theta = 325°$; Table 7, Fig. 6).

Approximately one-third ($n = 11$) of GPS-collared bears underwent a large-scale autumn movement travelling westerly and north-westerly along the Ontario coast just prior to freeze-up. Two bears collared along the James Bay coast of Ontario made a northward long-distance movement to Cape Henrietta Maria, which enabled them to move out onto the ice sooner than if they had stayed in more southerly reaches of James Bay. Few bears moved east to Cape Henrietta Maria, and of those that did, the movements were shorter and much less directed than those moving west or north. Of the bears making the west or northwest movements, the mean distance traveled from their core summer areas was 166 km; however, 6 of the 11 bears travelled >200 km in as few as 12 days to reach the early ice. Such movements typically started during the second week of November (7 Nov–16 Nov), ending when they reached the first land-fast ice (anywhere from 20 Nov to 6 Dec). The longest movement (246 km in 23 days) was made in 2008 by a female accompanied by a single cub when she travelled from just northwest of Fort Severn (87.7°W) to the Cape Tatnam vicinity in Manitoba (91°W).

Home ranges

There was moderate evidence of an effect of year on the annual MCP home-range size ($F_{3,22} = 3.725$, $P = 0.023$), but no interaction, so we used a mixed effects model to test for effect of reproductive class on home range size. We treated reproductive status as the fixed effect and year as the random effect and found only weak evidence of an effect of reproductive class on MCP annual home-range size ($F_{2,3} = 7.95$, $P = 0.11$).

Within seasons, there was no significant effect of year on MCP home-range size so we pooled all home range estimates across years for analysis. Similar to the annual MCP estimates, there was no evidence of an effect of reproductive class on home range size in any season (Table 8), but there was very strong evidence of an effect of season ($F_{3,113} = 64.9$, $P < 0.0001$). A Tukey's HSD test showed no significant difference between home range sizes during Breakup and Freeze-up ($\bar{x} = 38{,}103$ km^2, $\bar{x} = 28{,}266$ km^2, respectively), but showed that home range sizes in the Winter ($\bar{x} = 66{,}664$ km^2) and Summer ($\bar{x} = 900$ km^2) were significantly larger and smaller, respectively, than in other seasons. Mean annual MCP home-range size was 153,866 km^2 (±18,984 km^2; Table 8).

Regression analysis (Fig. 7) showed only weak evidence for a change in annual MCP home-range size over time ($t_{42} = 1.94$, $P = 0.059$). There was little

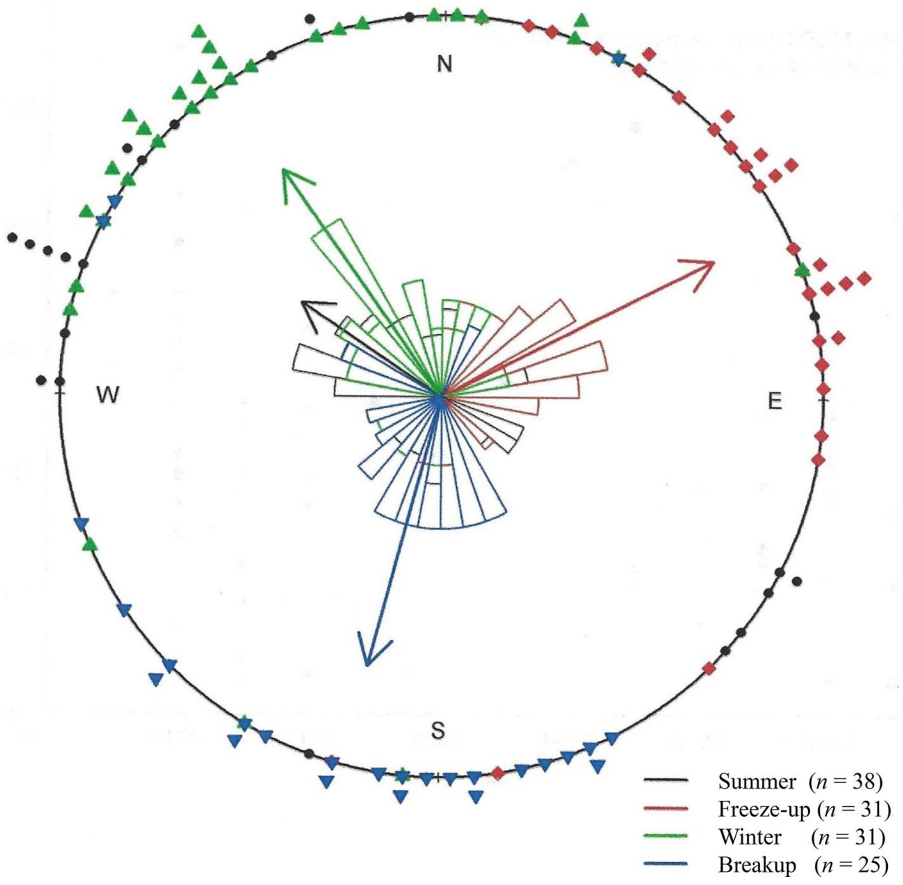

Fig. 6. Rose plot showing mean direction of seasonal displacements for radiocollared adult female polar bears (*Ursus maritimus*) in the Southern Hudson Bay subpopulation, 2007–2011. Direction of arrows indicates direction of travel, length of the arrow indicates the strength of the directionality (*r*), and points around the circle represent individual bears (● = Summer season, ♦ = Freeze-up season, ▲ = Winter season, ▼ = Breakup season).

evidence of a correlation between ice duration at 50% concentration and mean home-range size over the period 1998–2010 ($r_{58} = -0.20$, $P = 0.119$), and no significant change in the distance travelled between the two study periods. Lastly, we compared mean home-range size in Period 1 (1999–2003; 89,081 km^2) to that of Period 2 (2008–2011; 124,959 km^2) and found only weak evidence of an effect of period on home range size ($t_{42} = -1.68$, $P = 0.099$).

Using the kernel density estimation method to generate annual home ranges, we found no significant year effect on home range size; so we pooled data for all years to assess the effects of reproductive class on home range size (Table 8). Annual KDE home-range sizes were normally distributed and there was strong evidence that home range size varied by reproductive class (ANOVA, $F_{2,23} = 5.14$, $P = 0.01$); Tukey's HSD test provided strong evidence that denning females had smaller home ranges ($\bar{x} = 24{,}823$ km^2) than did females with cubs ($\bar{x} = 105{,}028$ km^2; $P = 0.012$), and moderate evidence that they had smaller home range areas than did females with yearlings ($\bar{x} = 77{,}520$ km^2; $P = 0.057$). When subdivided into seasonal home ranges, there was little evidence that reproductive status had an effect on home range size in any season, though females that entered maternity dens in the autumn and returned to the ice with newborn cubs had consistently smaller home ranges than either of the other two reproductive classes (Table 8).

Using Brownian bridge movement models (BBMM), both Summer and Freeze-up home-range estimates were nonnormally distributed, so we transformed them

Table 8. Mean ± Standard Error (SE) annual and seasonal home range areas (km^2) by reproductive class and home-range estimation technique (95% minimum convex polygon [MCP]; 95% kernel density estimator [KDE]; and 95% Brownian bridge movement model [BBMM]) for radiocollared adult female polar bears (*Ursus maritimus*) in Southern Hudson Bay, 2007–2011.

95% MCP home range areas

	Females with cubs			Females with yearlings			Denning			Overall		
Period	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***
Summer	947	298	12	1,032	290	20	441	180	7	900	178	39
Freeze-up	28,855	6,570	9	27,858	6,861	13	n/a	n/a	n/a	28,266	4,757	22
Winter	74,653	22,610	8	68,190	8,816	20	35,194	14,321	3	66,664	8,225	31
Breakup	51,157	11,927	5	36,889	8,021	16	26,640	7,544	4	38,103	5,826	25
Annual	215,957	44,449	6	161,877	21,554	15	55,325	15,446	5	153,866	18,984	26

95% KDE home range areas

	Females with cubs			Females with yearlings			Denning			Overall		
Period	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***
Summer	490	155	12	739	329	20	172	83	7	561	177	39
Freeze-up	38,641	8,804	9	28,928	5,629	13	n/a	n/a	n/a	32,901	4,885	22
Winter	48,431	14,128	8	49,921	6,254	20	27,023	11,823	3	47,321	5,512	31
Breakup	50,667	10,673	5	29,117	5,263	16	23,726	2,277	4	32,564	4,307	25
Annual	105,028	24,546	6	77,520	9,979	15	24,823	8,237	5	73,734	9,478	26

95% BBMM home range areas

	Females with cubs			Females with yearlings			Denning			Overall		
Period	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***
Summer	96	18	12	198	67	20	232	92	7	172	38	39
Freeze-up	2,952	441	9	4,506	893	13	n/a	n/a	n/a	3,871	572	22
Winter	7,922	1,254	8	11,086	1,178	20	3,930	1,406	3	9,577	921	31
Breakup	9,035	2,227	5	8,287	1,241	16	5,128	1,033	4	7,931	932	25
Annual	16,452	2,826	6	19,247	1,598	15	5,975	1,682	5	16,050	1,516	26

using a natural log transformation prior to analysis. Home range estimates for other seasons, including the annual estimates of home range, were normally distributed. There was no effect of year on home range size, so we pooled data across years within each season. There was strong evidence that annual BBMM home-range size varied with reproductive class (ANOVA, $F_{2,23} = 9.13$, $P = 0.001$). Tukey's HSD test indicated that denning females had significantly smaller annual home ranges, approximately one-third the size of females in other reproductive classes (Table 8). Reproductive class had an effect on home range size during Winter, though the Tukey unequal *n* HSD pairwise comparison failed to find a significant difference between classes, likely due to the small sample size of females returning to the ice from dens ($n = 3$). Females returning to the ice from maternity dens tended to have smaller home ranges during Winter. During Summer, pregnant females entering maternity dens tended to have larger home ranges than females with cubs, or females with yearlings (Table 8). For illustrative purposes we compare results from the 3 home range estimators in Figure 8 using data from a single bear for each of the 4 seasons.

Discussion

This study is the first to document movement patterns of polar bears in the Southern Hudson Bay subpopulation. Our results enable a comparison with the neighboring Western Hudson Bay (WH) subpopulation, and establish a baseline against which results of future studies of the Southern Hudson Bay subpopulation can be compared in the context of ongoing and future climate warming (Castro de la Guardia et al. 2013), and the resultant lengthening of the open water season

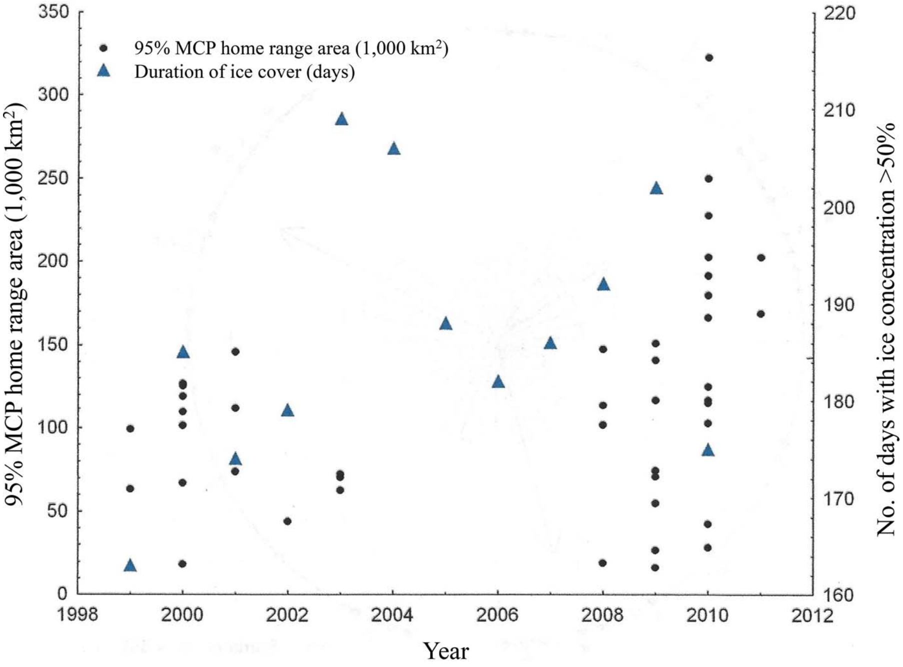

Fig. 7. Annual 95% minimum convex polygon (MCP) home range sizes (●) of individual radiocollared adult female polar bears (*Ursus maritimus*) from the Southern Hudson Bay subpopulation, 1999–2010, for encumbered, nondenning females plotted with ice duration (▲) at 50% concentration in the Southern Hudson Bay management unit.

(Andrews et al. 2018). Annual sea ice patterns are similar in areas occupied by the WH and SH subpopulations; however, patterns in the two areas are out of synchrony because freeze-up begins earlier in WH in each year (Andrews et al. 2018, Gupta et al. 2022). Also, despite breakup beginning earlier in SH (Andrews et al. 2018, Gupta et al. 2022), counterclockwise ocean currents and patterns of wind forcing (predominantly northwesterly winds) mean that the last ice of the season persists off the northern coast of Ontario when areas off the Manitoba coast are ice-free (Hochheim et al. 2010, Hochheim and Barber 2014).

Changes in the annual duration of sea ice started earlier in WH than in SH, despite SH being farther south because increases in seasonal air temperatures are greater in northern and western areas of Hudson Bay (Hochheim et al. 2010, Hochheim and Barber 2014). The consequence of these sea ice trends for polar bears is that declines in body condition and eventually abundance began earlier in WH than in SH, but they have occurred in both subpopulations (Stirling et al. 1999; Regehr et al. 2007; Obbard et al. 2016, 2018).

Implications of ice patterns in Hudson Bay

General movement patterns shown by SH bears in our study are similar to those of WH bears (Parks et al. 2006), though there are differences that reflect the differing sea ice regimes such as when bears can access the ice in autumn and when they depart the ice in spring. From 2008 to 2011, the mean date SH bears left the ice in spring was 29 July (range 16 Jul–20 Aug). For a similar period (2005–2009) the mean date that WH bears began to move toward shore was 13 July and it took on average 5.8 days for bears to reach land (Cherry et al. 2016), suggesting that the average date that WH bears left the ice was 19 July. The mean date that SH bears moved onto the ice was 2 December (range 27 Nov–7 Dec). Using data from 1991 to 1997 and 2004 to 2010, the timing of WH bears moving on or off the ice showed a trend toward earlier arrival on shore and later departure from land—trends driven by declines in the duration of sea ice (Cherry et al. 2013). Pooling data from 1991 to 2019, the mean departure date onto the ice for WH bears was 23 November (Miller et al. 2022). The pattern shown by this longer dataset differed from Cherry et al. (2013) in that departure date did not

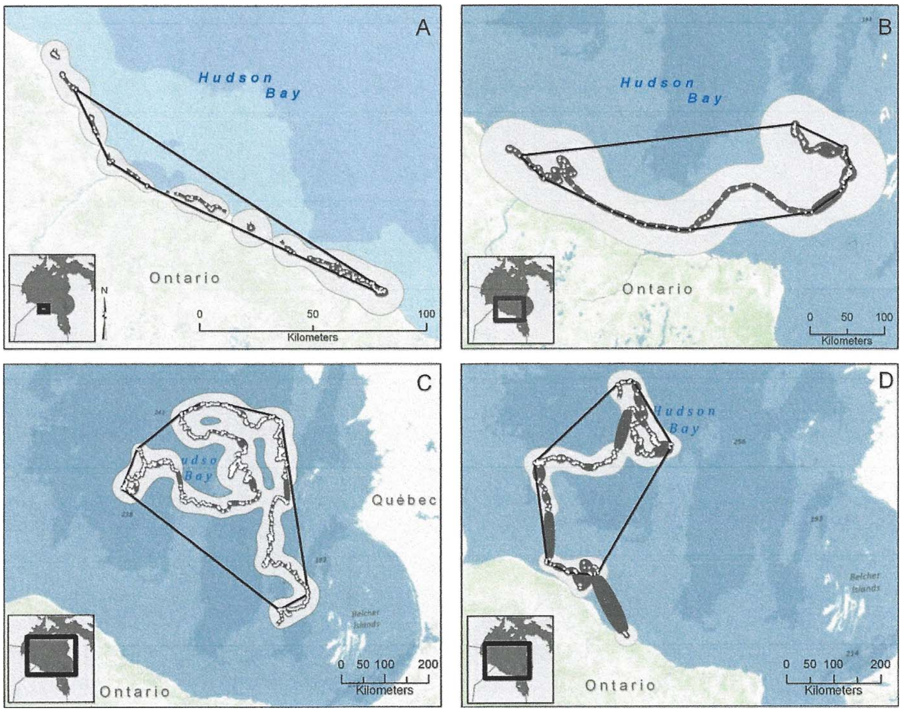

Fig. 8. Home range estimates for a 13-year-old female polar bear (*Ursus maritimus*; X16508) accompanied by 2 yearlings through Summer (A), Freeze-up (B); Winter (C); and Breakup (D) in Southern Hudson Bay, October 2009–July 2010. Each panel shows the 95% minimum convex polygon (MCP; solid outline), kernel density estimate (light grey polygon), and Brownian bridge estimate (darker grey polygon) along with point locations (white dots).

change over time, even though freeze-up dates were delayed (Miller et al. 2022). Regardless, SH bears were able to access the first landfast ice about 9 days later in the year than were bears in WH, but they were able to remain on the ice about 10 days longer in spring. Therefore, on average, bears from both subpopulations spend the same number of days on the sea ice, though the seasonal timing of departing for and leaving the ice is shifted later in the year in SH. On average, during 2007–2011, SH bears spent 239 days on ice and 126 days ashore. Similarly, on average, WH bears spent 238 days on ice and 127 days ashore. This is considerably longer than the number of days bears in High Arctic subpopulations currently spend ashore (e.g., 95 days, Baffin Bay subpopulation; Laidre et al. 2020) and substantially more than such bears spent ashore in the past (84 days [Ferguson et al. 1997]; 75 d [Laidre et al. 2020]). The current average number of days ashore for both SH and WH bears could already be affecting survival rates. 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. The duration of the ice-free season in Hudson Bay is expected to increase even more in the future (Castro de la Guardia et al. 2013, Stern and Laidre 2016). Ultimately, a longer ice-free season will have major negative effects on reproductive success via declines in the fat stores of pregnant females, which greatly influences litter weight and survival (Atkinson and Ramsay 1995), and on survival of all age classes (Molnár et al. 2010, 2011, 2020).

Movement patterns

Bears in SH had the lowest hourly movement rates while on land during the ice-free period. This is consistent with earlier studies in SH (Knudsen 1978) and in the neighboring WH subpopulation (Derocher and Stirling 1990, Parks et al. 2006), which showed that bears have low levels of activity at this time. While on land, polar bears largely live off their stored reserves (Ramsay and Hobson 1991, Rode et al. 2015), and adopt strategies to maximize energy conservation, such as being inactive (Ware et al. 2017). This strategy will be even more important in the future as polar bears come under increasing energetic stress as a result of the lengthening ice-free season (Molnár et al. 2020). Hourly movement rates were greatest during Freeze-up, averaging 1.38 km/hour when bears moved out rapidly onto the ice and many seemed to follow the advancing ice edge as it swept across Hudson Bay.

Other than the low movement rates of denning females during Summer and Freeze-up periods when they headed inland to a denning area and eventually were in a maternity den, in contrast to our hypothesis we found no effect of reproductive class on movement rates (i.e., females accompanied by cubs or yearlings moved at the same rates). Cubs in the autumn are close to 1 year old when the family returns to the ice, so likely are capable of movement rates on the ice that do not impede their mother's movement rate. The general pattern of highest movement rates during Freeze-up and lower movement rates during Winter and Breakup are consistent with patterns reported for the WH subpopulation (Parks et al. 2006). These authors interpreted the more rapid movement during freeze-up as evidence of traveling behavior, whereas the lower movement rates during winter and breakup suggested hunting behavior (Parks et al. 2006). For example, WH bears spent nearly half of their time budget during winter in 'sedentary drift behavior' characterized by stalking or still hunting, prey handling, and resting (Togunov et al. 2022). The style of rapid directed movement that SH bears exhibited during freeze-up is described as traveling behavior for other animals (Pyke 1978, Kareiva and Shigesada 1983, Gurarie et al. 2009). Austin et al. (2004) classified grey seals (*Halichoerus grypus*) exhibiting this type of behavior as 'directed movers,' characterized by many long, similarly sized movement lengths, and suggested that this style of movement is necessary to reduce travel time to distant feeding areas. This movement behavior is consistent with optimal foraging theory, which predicts that animals should minimize travel time between resource areas to increase time spent foraging (Pyke 1978), assuming that there is a high likelihood of reward at distant locations. Southern Hudson Bay polar bears appear to follow this strategy because they move rapidly along the landfast ice, then across the pack ice to presumably richer hunting grounds near and north of the Belcher Islands.

Pagano et al. (2018a) showed that movement rates of polar bears on ice in the Beaufort Sea averaged 3.4 km/hour during 10-minute intervals with only 3% of movements >5.4 km/hour. Movement rates we report (<1.5 km/hr) were averaged over much longer time intervals (median 4 hr), so likely included periods when bears moved little, perhaps because they were resting or hunting seals either by stalking or as sit-and-wait predators (Stirling 1974, Pagano et al. 2018b, Togunov et al. 2022). Movement rates <5.4 km/hour were shown to be energetically economical for polar bears despite their heavy limbs and plantigrade gait (Pagano et al. 2018a), an important adaptation for an animal that undergoes extensive movements in search of prey.

Within seasons, reproductive class had an effect on direction of movement only during the Summer period when denning females had a mean southerly movement direction as they moved inland to find a suitable area for a maternity den. In contrast, about half of females accompanied by cubs and females accompanied by yearlings traveled northwesterly during this time toward the Pen Islands and Cape Tatnam areas in the vicinity of the Ontario–Manitoba border. Several bears made rapid north-westerly movements of about 20 km/day ($\bar{x} = 166$ km total distance moved) in the 2–3 weeks prior to freeze-up. Other bears moved easterly toward Cape Henrietta Maria. Hudson Bay typically freezes over in from 3 to 4 weeks (Hochheim and Barber 2010, Hochheim et al. 2010, Stewart and Barber 2010) and the pattern of freeze-up is largely consistent from year to year with the north and west freezing first, followed by the formation of landfast ice along the northern Ontario coast eastward toward James Bay, and lastly along the Québec coast (Gupta et al. 2022). Ice formation progresses from west to east through the central portion of Hudson Bay with the area between the Belcher Islands and the Québec coast being the last to freeze (Hochheim and Barber 2010, Hochheim et al. 2010, Stewart and Barber 2010). Landfast ice initially forms in shallow water areas along the shoreline, often starting near headlands, points, spits, and offshore islands (Gupta et al. 2022). In the autumn, prior to freeze-up, SH bears tend to be distributed in highest concentration along the shoreline, with points, peninsulas, offshore islands, and raised beach ridges being favored (Prevett and Kolenosky 1982; Obbard et al. 2015, 2018). Presumably, these areas are preferred by bears because this enables them to move out onto the earliest forming landfast ice. Concentrations of bears can often be found at Cape Henrietta Maria, Wabusk Island, Little Cape, Wabuk Point, and the Pen Islands and Cape Tatnam areas (Fig. 1). Given the pattern of formation of landfast ice (Gupta et al. 2022), these bears moved toward areas where ice would form first, suggesting accumulated knowledge of ice formation patterns. Bears in WH also move in autumn to areas where the ice forms first, such as the Cape Churchill area (Derocher and Stirling 1990, Cherry et al. 2013, Togunov et al. 2017, Miller et al. 2022). Locomotion is fairly energetically efficient for polar bears, especially at low speeds (Pagano et al. 2018a), so the trade-off that some bears appear to make is the energetic cost incurred by walking to where the first ice forms versus the energetic gain from killing a seal from newly formed landfast ice. In an earlier study to delineate the SH population boundary using data from 1998 to 2003 (Obbard and Middel 2012), we found only 1 bear of 26 made a long distance (>100-km) move along the coast, whereas 11 of 39 bears monitored in the current study (2007–2011) made moves >100 km. Future work on this subpopulation should include a component to monitor mid- to late-summer migration patterns.

When first on the newly formed landfast ice during Freeze-up, bears often traveled along the ice edge, which presumably provided bears with their first opportunities to capture seals. Once out on the pack ice, SH bears generally moved in a north-easterly direction. As a result, many bears ended up close to the Québec shore or in the vicinity of the Belcher Islands by late in the Freeze-up period or early in the Winter period. Flaw leads that form close to the Québec coast and west of the Belcher Islands, and polynyas near the Belcher Islands, would provide hunting opportunities for polar bears (Gilchrist and Robertson 2000, Stewart and Barber 2010). Predictable open water areas such as polynyas and shore leads or flaw leads are important foraging areas for a variety of Arctic birds and mammals, including polar bears (Stirling 1980, Stirling et al. 1981, Heide-Jørgensen et al. 2013), and SH bears appear to exploit these in the early winter. Western Hudson Bay bears followed a similar pattern during freeze-up—as they followed the advancing sea ice edge, they headed easterly toward the center of the Bay (Togunov et al. 2017).

During Winter, SH bears generally moved in a northwesterly direction, and movement rates during winter and breakup were lower than during freeze-up. Movement of WH bears in winter was more variable and influenced by wind direction and speed and by ice drift but bears continued to head out on the Bay (Togunov et al. 2017). By late winter bears from both subpopulations are widely spread out across the surface of Hudson Bay where ice floes are kept moving by the wind (Markham 1986, Stewart and Barber 2010). Such areas of moving consolidated pack ice also provide hunting opportunities for polar bears (Stirling et al. 1993). In much of Hudson Bay a broad coastal shelf <80 m deep extends well offshore and average depth of the Bay is about 250 m (Stewart and Barber 2010), providing suitable habitat for ringed seals and bearded seals (Kingsley et al. 1985). Therefore, seals are likely distributed across the entire Bay. By March and April, polar bears may focus more on seal pups born in areas of landfast ice (Stirling and Archibald 1977, Smith 1980, Pilfold et al. 2014), though ringed seals will also breed in pack ice (Pilfold et al. 2014). In Hudson Bay, the band of landfast ice is generally <10 km wide, whereas consolidated and unconsolidated pack ice covers the rest of the Bay (Chambellant et al. 2012), explaining the wide distribution of bears across Hudson Bay at that time. Landfast ice and consolidated pack ice are favored haulout habitat for molting ringed and bearded seals in May–June and polar bears hunt there for seals (Smith 1975, Lunn et al. 1997, Chambellant 2010, Chambellant et al. 2012). During Breakup, SH bears tended to remain on the residual ice north of the Ontario coast. As a result, direction of movement during Breakup was southerly toward land. During Breakup, movement patterns of bears in the two subpopulations reflected the general orientation of the shore of Hudson Bay in Manitoba and Ontario (Fig. 1). The WH bears moved generally southwesterly toward the Manitoba coast (Parks et al. 2006, Togunov et al. 2017), whereas SH bears moved south to return to the Ontario shore.

During Summer, denning females showed overall large displacement distances measured from their first position on shore, but overall low movement rates. Pregnant bears moved little after leaving the ice until they moved inland to a denning area, so most of the displacement distance reflects southerly movements to an area where they constructed a maternity den. Maternity dens have been detected up to 118 km inland from the northern coast of Ontario (Kolenosky and Prevett 1983, Obbard and Walton 2004). Denning bears showed little east–west displacement during these inland movements, suggesting they returned to shore north of their preferred denning area. Known den locations or tracks of family groups returning to the ice in late winter were broadly distributed from near James Bay to the Manitoba border (Kolenosky and Prevett 1983, Obbard and Walton 2004). A similar extensive area where polar bears den occurs in Manitoba, where females den up to 80 km or more inland (Clark et al. 1997, Richardson et al. 2005). Female polar bears in WH show a high degree of fidelity to the denning area (Ramsay and Stirling 1990), and there is evidence that the population has used this denning area for several hundred years, including reuse of specific den sites (Scott and Stirling 2002). Females in both SH and WH tend to den much farther inland than do bears in other subpopulations such as those from the South Beaufort Sea ($\bar{x} = 1.7$ km, range 0–24.7 km; Durner et al. 2003), Viscount Melville Sound ($\bar{x} = 8.6$ km, range 0.4–24.8 km; Messier et al. 1994), and in Svalbard ($\bar{x} = 1.17$ km, range = 0.01–18.74 km; Andersen et al. 2012).

Females in SH entered maternity dens in the late autumn around mid- to late November. This contrasts with the situation in WH where pregnant females typically head inland shortly after coming ashore in summer and are settled at inland den sites by August or September (Lunn et al. 2004). Actual den entry and exit dates varied from year to year in SH but bears typically remained in or around the den for about 4 months, thus extending their fasting period up to 8 months. Of the collared bears, the longest period on land was 242 days, but on average, denning females were on land for 212 days before returning to the sea ice. This duration of time on land approaches the fasting limit for bears to reproduce successfully. Models using WH bears and sea ice data predicted between 40% and 73% pregnancy failure if date of arrival on shore during breakup approached 1 July, about 1 month earlier than that of the 1990s (Molnár et al. 2011).

Annual movement rates and distances travelled in SH were similar to rates reported for WH (Parks et al. 2006), provided their estimate of GPS data reporting distances 2–3 times greater than that of Argos data is accurate. That is, our mean annual distance moved of about 4,771 km for nondenning females is comparable to the Parks et al. (2006) estimate of 2,080 km based on Argos collar data if that estimate is doubled. Movement rates of bears in SH were lower than the monthly short-term rates (<8-hr fix interval) reported for the Northern and Southern Beaufort Sea subpopulations of about 2 km/hour across all reproductive classes, and were more similar to the mean long-term (>8-hr fix interval) movement rates of <1 km/hour (Amstrup et al. 2000, 2001). Total distances travelled by bears in the South Beaufort Sea and North Beaufort Sea subpopulations were about 1,000 km and 2,000 km less, respectively, than that of bears in SH (Amstrup et al. 2000). However, these data were derived from Argos PTT collars, so actual distances moved by bears in the Beaufort Sea may have been 2–3 time greater as suggested by Parks et al. (2006) based on their comparison of Argos PTT and GPS-collar data. Annual movements of 2 GPS-collared bears (4-hr fix interval) in the Svalbard region were 4,109 km and 5,095 km (Andersen et al. 2008), which is similar to the mean annual distance of 4,771 km that we found for encumbered females. Mean movement rates of the Svalbard bears ranged from 0.01 to 1.48 km/hour with a maximum movement rate of 4.58 km/hour (Andersen et al. 2008), which is similar to the rates found for bears in SH. Data from GPS collars with their higher temporal resolution and greater accuracy and precision (Tomkiewicz et al. 2010) likely provide more reliable estimates of distances moved and movement rates.

Displacement patterns

The displacement distance between a bear's first location on ice in autumn and its last location on ice the following summer was greater for females accompanied by yearlings (i.e., those that went on the ice accompanied by 11-month-old cubs and came off the ice accompanied by 19-month-old yearlings) and for pregnant females (i.e., those that went on the ice accompanied by 23-month-old yearlings and came off the ice pregnant) than for females accompanied by new cubs. These latter females had only a short period on the ice between leaving the maternity den and breakup, yet they moved similar total distances during the breakup period. It is unclear why they appeared to show greater fidelity to a stretch of coastline than did other females. Pregnant females tended to leave the ice northwest of where they went on the ice in autumn, whereas females accompanied by yearlings tended to leave the ice east of where they went on the ice the previous autumn. We have no explanation for this pattern and there was considerable variation in displacement direction. It is possible that the pattern for individual bears had more to do with that particular year's ice melt pattern and movement of residual ice under the influence of currents and winds than with fidelity to a particular area of the coast.

For females accompanied by either cubs or yearlings in autumn, annual autumn to autumn net displacement distances were greater for SH bears ($\bar{x} = 157.5$ km) than for WH ($\bar{x} = 112.5$ km; Parks et al. 2006). The larger displacement distances for females accompanied by cubs or yearlings in the autumn in SH suggests bears tended to remain on the residual ice for as long as possible over the tendency to return to a particular spot along the coast. The distance between capture locations in consecutive years (displacement) has been considered a measure of fidelity in the neighboring WH subpopulation, where bears often return to locations close to each other from one year to the next even though there is considerable variation in the position and date of ice breakup (Stirling et al. 2004, Parks et al. 2006). For both subpopulations females returning to land with new cubs showed much lower net displacement from their location the previous autumn when they were pregnant (SH, $\bar{x} = 62.5$ km; WH, $\bar{x} = 34$ km), and they also returned from the ice at a similar longitude to their original denning area, further suggesting that these females show greater fidelity to a section of the coast. This is consistent with the hypothesis that bears will return to the coast opposite their preferred denning area to familiarize new cubs with preferred denning habitat (Stirling et al. 2004). Solitary females and females with yearlings did not show the same degree of site fidelity but seemed to remain on the ice until forced ashore by the melt, with females accompanied by yearlings returning and spending the summer a considerable distance ($\bar{x} = 208$ km) from their location the previous year.

Home ranges

We used 3 home range estimators to evaluate space use by SH polar bears, with each method providing a very different picture of space use. Each method has advantages and disadvantages described in detail elsewhere (Kernohan et al. 2001, Laver and Kelly 2008, Walter et al. 2011), which should be weighed against the objectives of any particular study to determine which is most suitable. Kernel density estimator methods are highly sensitive to the selection of the smoothing parameter (*h* or bandwidth; Worton 1995, Seaman and Powell 1996, Kernohan et al. 2001, Hemson et al. 2005), so we used the less subjective and more robust plug-in equation method (Wand and Jones 1995) to estimate *h*. We include KDE because it is an increasingly popular method for estimating space use in animals and has been shown to represent home ranges much better than MCP methods (Worton 1987, Kernohan et al. 2001, Borger et al. 2006). Kernel density estimators not only provide an estimate of an animal's home range, but create a utilization distribution (UD), which predicts an animal's probability of occurrence at each point in space (Kernohan et al. 2001). Use of UD estimates (KDE or BBMM) sets the framework for further space use research such as resource selection and proportional overlap between home ranges. Similar to KDE, Brownian bridge estimators also create a UD but incorporate a temporal component into the UD estimation, allowing the interpolation of paths between successive locations that otherwise would be underrepresented or missing from kernel estimates. The ability to represent paths as well as high use areas is particularly well-suited for animals that have serially correlated data and migrate or travel long distances (Walter et al. 2011). Although uncertainty exists as to what processes a polar bear uses to find prey that are sparsely distributed, they likely use a combination of visual and olfactory cues (Stirling 1974, Smith 1980), they do not defend a territory, and bears of Hudson Bay travel very large distances, often covering much of the available habitat throughout their time on the ice. This type of behavior is well-represented by BBMM estimates, which are likely a more appropriate method of representing space use by polar bears both seasonally and annually.

Minimum convex polygon (95%) home-range estimates for SH polar bears were similar to those of other subpopulations, though bears inhabiting active or highly fluctuating offshore ice have been noted as having larger home ranges than do bears inhabiting landfast ice (Amstrup et al. 2000, Mauritzen et al. 2001, Wiig et al. 2003). Our home range estimates were smaller than those for subpopulations occupying more open ocean habitats such as those of the Bering and Chukchi seas (Garner et al. 1990) or east Greenland pack ice (Wiig et al. 2003), but were similar to those of the Svalbard area, specifically bears that ventured into the Russian territory (Wiig 1995). However, SH home ranges were considerably larger than those for Svalbard bears in a later study (Mauritzen et al. 2001), and unlike that study, we did not find an effect of reproductive status on home range size. Within the Hudson Bay complex, MCP-based SH annual home ranges (153,866 ± 18,984 km^2) tended to be larger than those in WH (106,613 ± 12,314 km^2; Parks et al. 2006).

Regardless of the method used to calculate home range area, we did not find a difference in area based on reproductive class when looking at encumbered females. As expected, females that spent time in a maternity den had reduced home range areas as reported elsewhere (Mauritzen et al. 2001, Parks et al. 2006).

The use of older Argos PTT data allowed us to compare annual movement distances and changes in home range sizes over time, but the long fix interval of Argos PTT data (6 days) and small sample sizes resulted in inability to reliably assess seasonal patterns. Unlike Parks et al. (2006), we did not find a significant trend in the total annual distance moved over time and did not see a significant trend in the average annual home-range size. Despite trends to earlier breakup and later freeze-up prior to 2000 in WH, during 2001–2010 there was a period of ice stability with no significant trend in either freeze-up or breakup date (Lunn et al. 2016). We noted a similar lack of trend in sea ice conditions in SH during the 2000s. Apart from the shorter interval between periods in our study than in Parks et al. (2006), the lack of trend in sea ice duration in the 2000s may explain why we found no differences in annual distance moved or in home range size.

Management implications

That bears from SH and WH currently spend the same amount of time on ice and on land is ecologically interesting because bears from both subpopulations have exhibited declines in body condition since the 1980s (Stirling et al. 1999, Obbard et al. 2016); however, it confounds interpretations of recent trends in abundance. Evidence suggests a decline in abundance in WH since the late 1980s is likely (Regehr et al. 2007, Lunn et al. 2016, Atkinson et al. 2022), but the situation in SH is less clear. Obbard et al. (2018) suggested a decline of 17% between 2011 and 2016, but results of a 2021 survey suggest that the subpopulation may have increased since 2016 (Northrup et al. 2022). It may be that it is more important for SH bears to have access to seals later in the breakup season when molting seals may be more available because they are resting on the ice surface than for WH bears to have access earlier during freeze-up when seals may be less available. Nevertheless, factors other than time on ice and access to prey may be at play and affecting these neighboring subpopulations in different ways.

Monitoring trends in polar bear habitat and ecosystem change, including polar bear use of sea ice, was identified as an important component of a circumpolar monitoring framework for polar bears (Vongraven et al. 2012). The length of time polar bears can spend on the sea ice is critical to population persistence via the link to body condition and survival (Stirling et al. 1999, Regehr et al. 2007, Rode et al. 2010, Obbard et al. 2016). In a Bayesian network model, overall sea ice conditions had the greatest influence on polar bear population outcomes, with ice-free periods lengthening and resulting in reduced availability of marine mammal prey (Atwood et al. 2016). Given the evidence of declines in body condition in SH bears since the 1980s (Obbard et al. 2016), the evidence of declines in abundance (Obbard et al. 2018), and the possibility that recent increases in abundance may reflect changes in distribution of bears in the region (Northrup et al. 2022), continued monitoring of this subpopulation is warranted. Building on the baseline data presented here, understanding trends in polar bear use of sea ice including monitoring on-ice and off-ice dates, total time spent ashore, movement patterns, and home ranges should be a focus of future research in SH. Recent technological innovations (Ross et al. 2024) could enable the study of movement patterns of subadults and adult males to evaluate whether their movement patterns differ from those of adult females.

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Literature cited

AGNEW, T., AND S. HOWELL. 2003. The use of operational ice charts for evaluating passive microwave ice concentration data. Atmosphere-Ocean 41:317–331.

AGOSTINELLI, C., AND U. LUND. 2011. R Package "circular": Circular statistics. Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University, Venice, Italy; Department of Statistics, California Polytechnic State University, San Luis Obispo, California, USA. https://r-forge.r-project.org/projects/circular/. Accessed 1 Oct 2011.

AMSTRUP, S.C., G.M. DURNER, T.L. MCDONALD, D.M. MULCAHY, AND G.W. GARNER. 2001. Comparing movement patterns of satellite-tagged male and female polar bears. Canadian Journal of Zoology 79:2147–2158.

———, ———, I. STIRLING, N.J. LUNN, AND F. MESSIER. 2000. Movements and distribution of polar bears in the Beaufort Sea. Canadian Journal of Zoology 78:948–966.

———, B.G. MARCOT, AND D.C. DOUGLAS. 2008. A Bayesian network modeling approach to forecasting the 21st century worldwide status of polar bears. Pages 213–268 in E.T. DeWeaver, C.M. Bitz, and L.-B. Tremblay, editors. Arctic sea ice decline: Observations, projections, mechanisms, and implications. Geophysical Monographs 180. American Geophysical Union, Washington, DC, USA.

ANDERSEN, D.J. 1982. The home range: A new nonparametric estimation technique. Ecology 63:103–112.

ANDERSEN, M., A.E. DEROCHER, Ø. WIIG, AND J. AARS. 2008. Movements of two Svalbard polar bears recorded using geographical positioning system satellite transmitters. Polar Biology 31:905–911.

———, ———, ———, AND ———. 2012. Polar bear (*Ursus maritimus*) maternity den distribution in Svalbard, Norway. Polar Biology 35:499–508.

ANDREWS, J., D. BABB, AND D.G. BARBER. 2018. Climate change and sea ice: Shipping in Hudson Bay, Hudson Strait, and Foxe Basin (1980–2016). Elementa: Science of the Anthropocene 6:19.

ATKINSON, S.N., J. BOULANGER, M. CAMPBELL, V. TRIM, J. WARE, AND A. ROBERTO-CHARRON. 2022. 2021 aerial survey of the Western Hudson Bay polar bear subpopulation. Final report. Government of Nunavut, Department of Environment, Wildlife Research Section, Iqaluit, Nunavut, Canada.

———, AND M.A. RAMSAY. 1995. The effects of prolonged fasting of the body composition and reproductive success of female polar bears (*Ursus maritimus*). Functional Ecology 9:559–567.

ATWOOD, T.C., B.G. MARCOT, D.C. DOUGLAS, S.C. AMSTRUP, K.D. RODE, G.M. DURNER, AND J.F. BROMAGHIN. 2016. Forecasting the relative influence of environmental and anthropogenic stressors on polar bears. Ecosphere 7:e01370.

AUSTIN, D., W.D. BOWEN, AND J.I. MCMILLAN. 2004. Intraspecific variation in movement patterns: Modeling individual behaviour in a large marine predator. Oikos 105:15–30.

BORGER, L., N. FRANCONI, G. DE MICHELE, A. GANTZ, F. MESCHI, A. MANICA, S. LOVARI, AND T. COULSON. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75: 1393–1405.

BULLARD, F. 1991. Estimating the home range of an animal: A Brownian bridge approach. University of North Carolina, Chapel Hill, North Carolina, USA.

CALENGE, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

CANADIAN COUNCIL ON ANIMAL CARE [CCAC]. 2003. CCAC guidelines on the care and use of wildlife. Canadian Council on Animal Care, Ottawa, Ontario, Canada.

CASTRO DE LA GUARDIA, L., A.E. DEROCHER, P.G. MYERS, A.D. TERWISSCHA VAN SCHELTINGA, AND N.J. LUNN. 2013. Future sea ice conditions in Western Hudson Bay and consequences for polar bears in the 21st century. Global Change Biology 19:2675–2687.

———, P.G. MYERS, A.E. DEROCHER, N.J. LUNN, AND A.D. TERWISSCHA VAN SCHELTINGA. 2017. Sea ice cycle in western Hudson Bay, Canada, from a polar bear perspective. Marine Ecology Progress Series 564:225–233.

CATTET, M.R.L., N.A. CAULKETT, AND N.J. LUNN. 2003. Anesthesia of polar bears using xylazine–zolazepam–tiletamine or zolazepam–tiletamine. Journal of Wildlife Diseases 39:655–664.

———, ———, S.C. POLISCHUK, AND M.A. RAMSAY. 1997. Reversible immobilization of free-ranging polar bears with medetomidine–zolazepam–tiletamine and atipamezole. Journal of Wildlife Diseases 33:611–617.

CAVALIERI, D., C.L. PARKINSON, P. GLOERSEN, AND H.J. ZWALLY. 1996. Sea ice concentration from Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave data 1979–2010. NASA National Snow and Ice Data Center Distributed Active Archive Center, Boulder, Colorado, USA. https://doi.org/10.5067/8GQ8LZQVL0VL. Accessed 15 Sep 2011.

CHAMBELLANT, M. 2010. Hudson Bay ringed seal: Ecology in a warming climate. Pages 137–158 in S.H. Ferguson, L. L. Loseto, and M.L. Mallory, editors. A little less Arctic: Top predators in the world's largest northern inland sea, Hudson Bay. Springer, New York, New York, USA.

———, N.J. LUNN, AND S.H. FERGUSON. 2012. Temporal variation in distribution and density of ice-obligated seals in western Hudson Bay, Canada. Polar Biology 35:1105–1117.

CHERRY, S.G., A.E. DEROCHER, AND N.J. LUNN. 2016. Habitat-mediated timing of migration in polar bears: An individual perspective. Ecology and Evolution 6:5032–5042.

———, ———, G.W. THIEMANN, AND N.J. LUNN. 2013. Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. Journal of Animal Ecology 82:912–921.

CLARK, D.A., I. STIRLING, AND W. CALVERT. 1997. Distribution, characteristics, and use of earth dens and related excavations by polar bears on the western Hudson Bay Lowlands. Arctic 50:158–166.

CROMPTON, A.E., M.E. OBBARD, S.D. PETERSEN, AND P.J. WILSON. 2008. Population genetic structure in polar bears (*Ursus maritimus*) from Hudson Bay, Canada: Implications of future climate change. Biological Conservation 141:2528–2539.

DEROCHER, A.E., AND I. STIRLING. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. Canadian Journal of Zoology 68: 1395–1403.

DURNER, G.M., S.C. AMSTRUP, AND A.S. FISCHBACH. 2003. Habitat characteristics of polar bear terrestrial maternal den sites in northern Alaska. Arctic 56:55–62.

ESRI. 2009. ArcGIS desktop: Release 9.3.1. Environmental Systems Research Institute, Redlands, California, USA.

ETKIN, D.A. 1991. Break-up in Hudson Bay: Its sensitivity to air temperatures and implications for climate warming. Climatological Bulletin 25:21–34.

———, AND R.O. RAMSEIER. 1993. A comparison of conventional and passive microwave sea-ice datasets for Hudson Bay. Atmosphere-Ocean 31:359–378.

FERGUSON, S.H., F. MESSIER, AND M.K. TAYLOR. 1997. Space use by polar bears in and around Auyuittuq National Park, Northwest Territories, during the ice-free period. Canadian Journal of Zoology 75:1585–1594.

———, M.K. TAYLOR, E.W. BORN, A. ROSING-ASVID, AND F. MESSIER. 1999. Determinants of home range size for polar bears (*Ursus maritimus*). Ecology Letters 2:311–318.

GAGNON, A.S., AND W.A. GOUGH. 2005. Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. Arctic 58:370–382.

GARNER, G.W., S.T. KNICK, AND D.C. DOUGLAS. 1990. Seasonal movements of adult female polar bears in the Bering and Chukchi Seas. International Conference on Bear Research and Management 8:219–226.

GILCHRIST, H.G., AND G.J. ROBERTSON. 2000. Observations of marine birds and mammals wintering at polynyas and ice edges in the Belcher Islands, Nunavut, Canada. Arctic 53:61–68.

GOUGH, W.A., A.R. CORNWELL, AND L.J.S. TSUJI. 2004. Trends in seasonal ice duration in Southwestern Hudson Bay. Arctic 57:299–305.

GUPTA, K., A. MUKHOPADHYAY, D.G. BABB, D.G. BARBER, AND J.K. EHN. 2022. Landfast sea ice in Hudson Bay and James Bay: Annual cycle, variability and trends, 2000–2019. Elementa: Science of the Anthropocene 10:0073.

GURARIE, E., R.D. ANDREWS, AND K.L. LAIDRE. 2009. A novel method for identifying behavioural changes in animal movement data. Ecology Letters 12:395–408.

———, C. BRACIS, M. DELGADO, T.D. MECKLEY, I. KOJOLA, AND C.M. WAGNER. 2016. What is the animal doing? Tools for exploring behavioural structure in animal movements. Journal of Animal Ecology 85:69–84.

HEIDE-JØRGENSEN, M.P., L.M. BURT, R.G. HANSEN, N.H. NIELSEN, M. RASMUSSEN, S. FOSSETTE, AND H. STERN. 2013. The significance of the north water polynya to Arctic top predators. Ambio 42:596–610.

HEMSON, G., P. JOHNSON, A. SOUTH, R. KENWARD, R. RIPLEY, AND D. MACDONALD. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analysis with least squares cross validation. Journal of Animal Ecology 74:455–463.

HERRMANN, E., J. ENGEL, M.P. WAND, AND T. GASSER. 1995. A bandwidth selector for bivariate kernel regression. Journal of the Royal Statistical Society 57:171–180.

HOCHHEIM, K., D.G. BARBER, AND J.V. LUKOVICH. 2010. Changing sea ice conditions in Hudson Bay, 1980–2005. Pages 39–51 in S.H. Ferguson, L.L. Loseto, and M.L. Mallory, editors. A little less Arctic: Top predators in the world's largest northern inland sea, Hudson Bay. Springer, New York, New York, USA.

HOCHHEIM, K.P., AND D.G. BARBER. 2010. Atmospheric forcing of sea ice in Hudson Bay during the fall period, 1980–2005. Journal of Geophysical Research 115:C05009.

———, AND ———. 2014. An update on the ice climatology of the Hudson Bay system. Arctic, Antarctic, and Alpine Research 46:66–83.

HORNE, J.S., E.O. GARTON, S.M. KRONE, AND J.S. LEWIS. 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363.

KAREIVA, P.M., AND N. SHIGESADA. 1983. Analyzing insect movement as a correlated random walk. Oecologia 56: 234–238.

KERNOHAN, B.J., R.A. GITZEN, AND J.J. MILLSPAUGH. 2001. Analysis of animal space use and movements. Pages 125–166 in J.J. Millspaugh and J.M. Marzluff, editors. Radiotracking and animal populations. Academic Press, San Diego, California, USA.

———, J.J. MILLSPAUGH, J.A. JENKS, AND D.E. NAUGLE. 1998. Use of an adaptive kernel home-range estimator in a GIS environment to calculate habitat use. Journal of Environmental Management 53:83–89.

KINGSLEY, M.C.S., I. STIRLING, AND W. CALVERT. 1985. The distribution and abundance of seals in the Canadian High Arctic, 1980–82. Canadian Journal of Fisheries and Aquatic Sciences 42:1189–1210.

KNUDSEN, B. 1978. Time budget of polar bears (*Ursus maritimus*) on North Twin Island, James Bay, during summer. Canadian Journal of Zoology 56:1627–1628.

KOLENOSKY, G.B., AND J.P. PREVETT. 1983. Productivity and maternity denning of polar bears in Ontario. International Conference on Bear Research and Management 5:238–245.

LAIDRE, K.L., S. ATKINSON, E.V. REGEHR, H.L. STERN, E.W. BORN, Ø. WIIG, N.J. LUNN, AND M. DYCK. 2020. Interrelated ecological impacts of climate change on an apex predator. Ecological Applications 30:e02071.

LAVER, P.N., AND M.J. KELLY. 2008. A critical review of home range studies. Journal of Wildlife Management 72: 290–298.

LONE, K., B. MERKEL, C. LYDERSEN, K.M. KOVACS, AND J. AARS. 2017. Sea ice resource selection models for polar bears in the Barents Sea subpopulation. Ecography 41: 567–578.

LUNN, N.J., S. SERVANTY, E.V. REGEHR, S.J. CONVERSE, E. RICHARDSON, AND I. STIRLING. 2016. Demography of an apex predator at the edge of its range: Impacts of changing sea ice on polar bears in Hudson Bay. Ecological Applications 26:1302–1320.

———, I. STIRLING, D. ANDRIASHEK, AND E. RICHARDSON. 2004. Selection of maternity dens by female polar bears in western Hudson Bay, Canada and the effects of human disturbance. Polar Biology 27:350–356.

———, ———, AND S.N. NOWICKI. 1997. Distribution and abundance of ringed (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) in western Hudson Bay. Canadian Journal of Fisheries and Aquatic Sciences 54:914–921.

MARKHAM, W.E. 1986. The ice cover. Pages 101–116 in I.P. Martini, editor. Canadian inland seas. Elsevier Science, Amsterdam, The Netherlands.

———. 1988. Ice atlas: Hudson Bay and approaches. Environment Canada, Atmospheric Services Division, Downsview, Ontario, Canada.

MAURITZEN, M., A.E. DEROCHER, O. PAVLOVA, AND Ø. WIIG. 2003. Female polar bears, *Ursus maritimus*, on the Barents Sea drift ice: Walking the treadmill. Animal Behaviour 66:107–113.

———, ———, AND Ø. WIIG. 2001. Space-use strategies of female polar bears in a dynamic sea ice habitat. Canadian Journal of Zoology 79:1704–1713.

MESSIER, F., M.K. TAYLOR, AND M.A. RAMSAY. 1994. Denning ecology of polar bears in the Canadian Arctic archipelago. Journal of Mammalogy 75:420–430.

MILLER, E.N., N.J. LUNN, D. MCGEACHY, AND A.E. DEROCHER. 2022. Autumn migration phenology of polar bears (*Ursus maritimus*) in Hudson Bay, Canada. Polar Biology 45:1023–1034.

MOLNÁR, P.K., C.M. BITZ, M.M. HOLLAND, J.E. KAY, S.R. PENK, AND S.C. AMSTRUP. 2020. Fasting season length sets temporal limits for global polar bear persistence. Nature Climate Change 10:732–738.

———, A.E. DEROCHER, T. KLANJSCEK, AND M.A. LEWIS. 2011. Predicting climate change impacts on polar bear litter size. Nature Communications 2:186.

———, ———, G.W. THIEMANN, AND M.A. LEWIS. 2010. Predicting survival, reproduction and abundance of polar bears under climate change. Biological Conservation 143: 1612–1622.

MORELLE, K., N. BUNNEFELD, P. LEJEUNE, AND S.A. OSWALD. 2017. From animal tracks to fine-scale movement modes: A straightforward approach for identifying multiple spatial movement patterns. Methods in Ecology and Evolution 8:1488–1498.

MUFF, S., E.B. NILSEN, R.B. O'HARA, AND C.R. NATER. 2022. Rewriting results sections in the language of evidence. Trends in Ecology and Evolution 37:203-210.

NORTHRUP, J.M., E.J. HOWE, N.J. LUNN, K.R. MIDDEL, M.E. OBBARD, T.R. ROSS, G. SZOR, L.R. WALTON, AND J.V. WARE. 2022. 2021 Southern Hudson Bay polar bear subpopulation aerial survey. Ontario Ministry of Natural Resources and Forestry, Peterborough, Ontario, Canada.

OBBARD, M.E., M.R.L. CATTET, E.J. HOWE, K.R. MIDDEL, E. J. NEWTON, G.B. KOLENOSKY, K.F. ABRAHAM, AND C.J. GREENWOOD. 2016. Trends in body condition in polar bears (*Ursus maritimus*) from the Southern Hudson Bay subpopulation in relation to changes in sea ice. Arctic Science 2:15–32.

———, T.L. MCDONALD, E.J. HOWE, E.V. REGEHR, AND E. S. RICHARDSON. 2007. Polar bear population status in Southern Hudson Bay, Canada. U.S. Geological Survey, Reston, Virginia, USA.

———, AND K.R. MIDDEL. 2012. Bounding the Southern Hudson Bay polar bear subpopulation. Ursus 23:134–144.

———, S. STAPLETON, K.R. MIDDEL, I. THIBAULT, V. BRODEUR, AND C. JUTRAS. 2015. Estimating the abundance of the Southern Hudson Bay polar bear subpopulation with aerial surveys. Polar Biology 38:1713–1725.

———, ———, G. SZOR, K.R. MIDDEL, C. JUTRAS, AND M. DYCK. 2018. Re-assessing abundance of Southern Hudson Bay polar bears by aerial survey: Effects of climate change at the southern edge of the range. Arctic Science 4:634–655.

———, G.W. THIEMANN, E. PEACOCK, AND T.D. DEBRUYN, editors. 2010. Polar bears: Proceedings of the 15th working meeting of the IUCN/SCC polar bear specialist group, 29 June–3 July 2009, Copenhagen, Denmark. Occasional Paper of the IUCN Species Survival Commission No. 43. International Union for Conservation of Nature, Gland, Switzerland and Cambridge, U.K.

———, AND L.R. WALTON. 2004. The importance of Polar Bear Provincial Park to the Southern Hudson Bay polar bear population in the context of future climate change. Pages 105–116 in C.K. Rehbein, J.G. Nelson, T.J. Beechey, and R.J. Payne, editors. Parks and protected areas research in Ontario, 2004: Planning northern parks and protected areas. Proceedings of the Parks Research Forum of Ontario Annual General Meeting, 4–6 May 2004, Thunder Bay, Ontario, Canada.

PAGANO, A.M., A.M. CARNAHAN, C.T. ROBBINS, M.A. OWEN, T. BATSON, N. WAGNER, A. CUTTING, N. NICASSIO-HISKEY, A. HASH, AND T.M. WILLIAMS. 2018a. Energetic costs of locomotion in bears: Is plantigrade locomotion energetically economical? Journal of Experimental Biology 221:175372.

———, G.M. DURNER, K.D. RODE, T.C. ATWOOD, S.N. ATKINSON, E. PEACOCK, D.P. COSTA, M.A. OWEN, AND T.M. WILLIAMS. 2018b. High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. Science 359:568–572.

PARKS, E.K., A.E. DEROCHER, AND N.J. LUNN. 2006. Seasonal and annual movement patterns of polar bears on the sea ice of Hudson Bay. Canadian Journal of Zoology 84: 1281–1294.

PILFOLD, N.W., A.E. DEROCHER, I. STIRLING, AND E. RICHARDSON. 2014. Polar bear predatory behaviour reveals seascape distribution of ringed seal lairs. Population Ecology 56:129–138.

PREVETT, J.P., AND G.B. KOLENOSKY. 1982. The status of polar bears in Ontario. Naturaliste Canadien 109:933–939.

PYKE, G.H. 1978. Optimal foraging: Movement patterns of bumblebees between inflorescences. Theoretical Population Biology 13:72–98.

R DEVELOPMENT CORE TEAM. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RAMSAY, M.A., AND K.A. HOBSON. 1991. Polar bears make little use of terrestrial food webs: Evidence from stable-carbon isotope analysis. Oecologia 86:598–600.

———, AND I. STIRLING. 1990. Fidelity of female polar bears to winter-den sites. Journal of Mammalogy 71:233–236.

REGEHR, E.V., K.L. LAIDRE, H.R. AKC, S.C. AMSTRUP, T.C. ATWOOD, N.J. LUNN, M. OBBARD, H. STERN, G.W. THIEMANN, AND Ø. WIIG. 2016. Conservation status of polar bears (*Ursus maritimus*) in relation to projected sea-ice declines. Biology Letters 12:20160556. https://doi.org/10.1098/rsbl.2016.0556

———, N.J. LUNN, S.C. AMSTRUP, AND I. STIRLING. 2007. Effects of earlier sea ice breakup on survival and population size of polar bears in Western Hudson Bay. Journal of Wildlife Management 71:2673–2683.

RICHARDSON, E., I. STIRLING, AND D.S. HIK. 2005. Polar bear (*Ursus maritimus*) maternity denning habitat in western Hudson Bay: A bottom-up approach to resource selection functions. Canadian Journal of Zoology 83:860–870.

RODE, K.D., S.C. AMSTRUP, AND E.V. REGEHR. 2010. Reduced body size and cub recruitment in polar bears associated with sea ice decline. Ecological Applications 20:768–782.

———, C.T. ROBBINS, L. NELSON, AND S.C. AMSTRUP. 2015. Can polar bears use terrestrial foods to offset lost ice-based hunting opportunities? Frontiers in Ecology and the Environment 13:138–145.

ROSS, T.R., G.W. THIEMANN, B.J. KIRSCHHOFFER, J. KIRSCHHOFFER, G. YORK, A.E. DEROCHER, A.C. JOHNSON, N.J. LUNN, D. MCGEACHY, V. TRIM, AND J.M. NORTHRUP. 2024. Telemetry without collars: Performance of fur- and ear-mounted satellite tags for evaluating the movement and behaviour of polar bears. Animal Biotelemetry 12(1):18. https://doi.org/10.1186/s40317-024-00373-2

ROWCLIFFE, J.M., C. CARBONE, R. KAYS, B. KRANSTAUBER, AND P.A. JANSEN. 2012. Bias in estimating animal travel distance: The effect of sampling frequency. Methods in Ecology and Evolution 3:653–662.

SAHANATIEN, V., E. PEACOCK, AND A.E. DEROCHER. 2015. Population substructure and space use of Foxe Basin polar bears. Ecology and Evolution 5:2851–2864.

SCOTT, J.B.T., AND G.J. MARSHALL. 2010. A step-change in the date of sea-ice breakup in Western Hudson Bay. Arctic 63:155–164.

SCOTT, P.A.D., AND I. STIRLING. 2002. Chronology of terrestrial den use by polar bears in western Hudson Bay as indicated by tree growth anomalies. Arctic 55:151–166.

SEAMAN, D.E., AND R.A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

SIKES, R.S., W.L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

SMITH, T.G. 1975. Ringed seals in James Bay and Hudson Bay: Population estimates and catch statistics. Arctic 28: 170–182.

———. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Canadian Journal of Zoology 58:2201–2209.

SPREEN, G., AND L. KALESCHKE. 2011. AMSR-E ASI 6.25 km Sea Ice Concentration Data, V5.6i. Digital media. Institute of Oceanography, University of Hamburg, Germany.

———, ———, L. KALESCHKE, AND G. HEYGSTER. 2008. Sea ice remote sensing using AMSR-E 89-GHz channels. Journal of Geophysical Research 113(C2). https://doi.org/10.1029/2005JC003384

STERN, H.L., AND K.L. LAIDRE. 2016. Sea-ice indicators of polar bear habitat. The Cryosphere 10:2027–2041.

STEWART, D.B., AND D.G. BARBER. 2010. The ocean–sea ice–atmosphere system of the Hudson Bay complex. Pages 1–37 in S.H. Ferguson, L.L. Loseto, and M.L. Mallory, editors. A little less Arctic: Top predators in the world's largest northern inland sea, Hudson Bay. Springer, New York, New York, USA.

STIRLING, I. 1974. Midsummer observations on the behavior of wild polar bears (*Ursus maritimus*). Canadian Journal of Zoology 52:1191–1198.

———. 1980. The biological importance of polynyas in the Canadian Arctic. Arctic 33:303–315.

———, AND W.R. ARCHIBALD. 1977. Aspects of predation of seals by polar bears. Journal of Fisheries Research Board of Canada 34:1126–1129.

———, AND W. CALVERT. 1993. Habitat preferences of polar bears in the western Canadian Arctic in late winter and spring. Polar Record 29:13–24.

———, H. CLEATOR, AND T.G. SMITH. 1981. Marine mammals. Pages 45–58 in I. Stirling and H. Cleator, editors. Polynyas in the Canadian Arctic, Canadian Wildlife Service, Occasional Paper No. 45. Environment Canada, Ottawa, Ontario, Canada.

———, AND A.E. DEROCHER. 1993. Possible impacts of climatic warming on polar bears. Arctic 46:240–245.

———, AND ———. 2012. Effects of climate warming on polar bears: A review of the evidence. Global Change Biology 18:2694–2706.

———, N.J. LUNN, AND J. IACOZZA. 1999. Long-term trends in the population ecology of polar bears in Western Hudson Bay in relation to climate change. Arctic 52:294–306.

———, ———, ———, C. ELLIOTT, AND M. OBBARD. 2004. Polar bear distribution and abundance on the southwestern Hudson Bay coast during open water season, in relation to population trends and annual ice patterns. Arctic 57:15–26.

———, AND C.L. PARKINSON. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. Arctic 59:261–275.

TOGUNOV, R.R., A.E. DEROCHER, AND N.J. LUNN. 2017. Windscapes and olfactory foraging in a large carnivore. Scientific Reports 7:46332.

———, ————, ———, AND M. AUGER-MÉTHÉ. 2022. Drivers of polar bear behavior and the possible effects of prey availability on foraging strategy. Movement Ecology 10:1–20.

TOMKIEWICZ, S.M., M.R. FULLER, J.G. KIE, AND K.K. BATES. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2163–2176.

VONGRAVEN, D., J. AARS, S. AMSTRUP, S.N. ATKINSON, S. BELIKOV, E.W. BORN, T.D. DEBRUYN, A.E. DEROCHER, G. DURNER, M. GILL, N. LUNN, M.E. OBBARD, J. OMELAK, N. OVSYANIKOV, E. PEACOCK, E. RICHARDSON, V. SAHANATIEN, I. STIRLING, AND Ø. WIIG. 2012. A circumpolar monitoring framework for polar bears. Ursus 23: 1–66.

WALTER, W.D., J.W. FISCHER, S. BARUCH-MORDO, AND K. C. VERCAUTEREN. 2011. What is the proper method to delineate home range of an animal using today's advanced GPS telemetry systems: The initial step. Pages 249–268 in O. Krejcar, editor. Modern telemetry. InTech Open Access Publisher, London, England, U.K.

WAND, M.P. 2011. KernSmooth: Functions for kernel smoothing supporting Wand & Jones (1995). https://cran.r-project.org/web/packages/KernSmooth/index.html. Accessed 15 Sep 2011.

———, AND M.C. JONES. 1993. Comparison of smoothing parameterizations in bivariate kernel density estimation. Journal of the American Statistical Association 88:520–528.

———, AND ———. 1995. Kernel smoothing. Chapman and Hall, London, England, U.K.

WARE, J.V., K.D. RODE, J.F. BROMAGHIN, D.C. DOUGLAS, R. R. WILSON, E.V. REGEHR, S.C. AMSTRUP, G.M. DURNER, A.M. PAGANO, J. OLSON, C.T. ROBBINS, AND H.T. JANSEN. 2017. Habitat degradation affects the summer activity of polar bears. Oecologia 184:87–99.

WIIG, Ø. 1995. Distribution of polar bears (*Ursus maritimus*) in the Svalbard area. Journal of Zoology 237:515–529.

———, E.W. BORN, AND L.T. PEDERSEN. 2003. Movements of female polar bears (*Ursus maritimus*) in the East Greenland pack ice. Polar Biology 26:509–516.

WORTON, B. 1987. A review of models of home range for animal movement. Ecological modelling 38:277–298.

———. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794–800.

ZAR, J.H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

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