

Seasonal and annual movement patterns of polar bears on the sea ice of Hudson Bay

E.K. Parks, A.E. Derocher, and N.J. Lunn

Abstract: Polar bears (*Ursus maritimus* Phipps, 1774) move thousands of kilometres over sea ice searching for mates and hunting for seals, which are their primary prey. Recently, decreased sea ice extent and earlier ice break-up have been linked to shifts in seal distribution and abundance and to declines in polar bear condition and numbers in the western Hudson Bay polar bear population. We used geographic positioning system and satellite collars deployed between 1991 and 2004 to quantify movement patterns of adult female polar bears on the sea ice of Hudson Bay in relation to reproductive class and temporal variations in sea ice patterns. We tested whether reproductive status and season affected movement and whether temporal changes in movement were correlated with temporal changes in sea ice patterns in Hudson Bay. Movement patterns were not dependent on reproductive status but did change significantly with season. Annual distances moved and areas covered by bears in Hudson Bay have decreased since 1991, which suggests that measured declines in bear condition and numbers are due to reduced prey intake as opposed to increased energy output. These declines in bear movement are correlated with progressively earlier ice break-up in western Hudson Bay.

Résumé : Les ours polaires (*Ursus maritimus* Phipps, 1774) se déplacent sur des milliers de kilomètres sur la banquise à la recherche de partenaires sexuels ou en quête des phoques qui constituent leurs proies principales. Ces dernières années, on a relié la réduction de l'extension de la banquise et la débâcle précoce des glaces aux changements dans la répartition et l'abondance des phoques et au déclin dans la condition et la densité de la population d'ours polaires de l'ouest de la baie d'Hudson. Entre 1991 et 2004, nous avons utilisé un système de positionnement géographique et des colliers satellites pour quantifier les patrons de déplacement des femelles de l'ours polaire sur la banquise de la baie d'Hudson en fonction de la classe des reproducteurs et des variations temporelles de la banquise. Nous avons vérifié si les déplacements sont affectés par le statut reproductif et la saison et si les changements temporels dans les déplacements sont en corrélation avec les modifications dans le temps de la structure de la banquise dans la baie d'Hudson. Les patrons de déplacement ne sont pas reliés au statut reproductif, mais varient selon la saison. Les distances parcourues et les surfaces explorées par les ours dans la baie d'Hudson ont diminué depuis 1991, ce qui laisse croire que les déclinés observés dans la condition physique et la densité des ours sont dus plus à une ingestion réduite de proies qu'à une production accrue d'énergie. Ces diminutions des déplacements des ours sont en corrélation avec les débâcles de plus en plus hâtives dans l'ouest de la baie d'Hudson.

[Traduit par la Rédaction]

Introduction

Animal movement is influenced both by the distribution of resources, such as food or breeding habitat, and by the physical structure of the landscape (Kareiva 1982; McIntyre and Wiens 1999). Analysis of animal movement and distribution across a landscape and through time can provide insights into resource use patterns, foraging strategies, energy expenditure, and population dynamics (e.g., Jones 1977; Johnson et al. 2002; Fortin et al. 2003). The increased use of satellite and global positioning system (GPS) technology in recent years has made it easier to examine the movement patterns of large, wide-ranging animals, particularly where

their habitat is difficult to access by humans (e.g., Jouventin and Weimerskirch 1990; Fritz et al. 2003).

Polar bears (*Ursus maritimus* Phipps, 1774) are non-territorial carnivores that travel thousands of kilometres over Arctic sea ice to hunt their principal prey, ringed seals (*Pusa hispida* (Schreber, 1775)) and bearded seals (*Erignathus barbatus* (Erxleben, 1777)) (Stirling and Archibald 1977; Smith 1980). Earlier research on polar bear movement relied on mark-recapture data alone, or together with VHF telemetry when the bears were close to or on land (e.g., Stirling et al. 1980; Lentfer 1983; Derocher and Stirling 1995); however, satellite and GPS technology have improved our ability to understand the structure and dynamics of polar bear distribution, especially over vast remote areas. The circumpolar population has been divided into 19 relatively discrete populations based on satellite location data (Bethke et al. 1996; Taylor et al. 2001). Satellite-tracking studies in the Beaufort Sea, the eastern high Arctic, Greenland, and the Barents Sea have revealed a significant degree of variation in movement patterns both within and between populations (Born et al. 1997; Messier et al. 2001; Mauritzen et al. 2003a; Durner et al. 2004).

Variations within populations are likely due to differences both in the energetic demands of individual bears and in the

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local ice conditions. For example, females have greater energetic demands when they are accompanied by dependent offspring than when they are not, and therefore may adopt different space-use strategies (Amstrup et al. 2000; Mauritzen et al. 2001). In addition, seasonal changes in ice conditions create different habitats through which bears must move and hunt, and their movement rates and habitat preferences often change cyclically with the seasons (Ferguson et al. 2000a).

Variation in bear movement may also be influenced by regional differences in ocean productivity, seal distribution, and sea ice. For instance, levels of marine primary productivity vary with water depth, vertical mixing, and freshwater input, and areas of high primary productivity can support higher densities of other marine organisms (Jones and Anderson 1994). Seal distribution is dependent on local productivity, as well as on sea ice dynamics; both of which vary substantially throughout the Arctic (Kingsley et al. 1985; Lunn et al. 1997; Frost et al. 2004). Sea ice structure and dynamics are determined by regional air and water circulation patterns, temperature fluctuations, and bathymetry (Thomas and Dieckmann 2003).

In addition to this existing variability, climate change is affecting ecosystem dynamics across the Arctic (Hansell et al. 1998; Derocher et al. 2004). Sea ice extent, concentration, and thickness have all declined since the 1970s (Parkinson et al. 1999; Maslowski et al. 2001; Comiso 2002), and these changes have been attributed to large-scale climatic shifts in air temperature and global ocean and atmosphere circulation (Parkinson et al. 1999; Comiso and Parkinson 2004). Negative effects of climate change on arctic wildlife have already been documented in several species, such as declining reproductive success in geese (*Chen caerulescens* (L., 1758), *Branta canadensis* (L., 1758)), Atlantic cod (*Gadus morhua* L., 1758), and ringed seals (MacInnes et al. 1990; Portner et al. 2001; Stirling 2005). Because climate change will affect ice conditions and seal distributions differently in different regions of the Arctic (Gough and Wolfe 2001; Maslowski et al. 2001), it is likely that the responses of individual polar bear populations to climate change will also vary.

The western Hudson Bay (WH) polar bear population live close to the southern limit of polar bear distribution and are therefore expected to be affected by a warming climate sooner than other populations (Stirling and Derocher 1993; Derocher et al. 2004). Each summer, the entire sea ice cover in the Bay melts and bears are forced ashore where they spend several months on land without access to food (Stirling et al. 1977; Derocher and Stirling 1990). The WH females show strong fidelity to the terrestrial denning area and return year after year despite wide-ranging movements on the ice during winter (Derocher and Stirling 1990; Ramsay and Stirling 1990). When the ice reforms in October and November, bears move back out onto the ice to hunt, with the exception of pregnant females, who dig and enter dens (Ramsay and Stirling 1988). Cubs are born between mid-November and mid-December (Derocher et al. 1992), and family groups emerge from dens in February or March and then return to the sea ice together. The most critical hunting period for all WH bears is between April and July, when both ringed and bearded seals haul out onto the ice to moult

or pup and fat, naïve seal pups, which are 50% fat by wet mass, become abundant (Stirling and McEwan 1975; Kingsley and Stirling 1991; Stirling and Øritsland 1995). During this period, bears must acquire sufficient fat stores to sustain their metabolic requirements throughout the ice-free period when food is not available, which lasts 3–4 months for bears of most age and sex classes but 8 months for pregnant females that remain onshore after freeze-up to give birth in terrestrial dens (Ramsay and Stirling 1988; Derocher et al. 1992; Atkinson and Ramsay 1995).

Recent studies have confirmed that the break-up of the sea ice in western and southern Hudson Bay has been occurring progressively earlier over the past 30 years (Stirling et al. 1999; Gough et al. 2004; Gagnon and Gough 2005), and that this may be the cause of a measured decline in polar bear condition, because the time available to accumulate fat stores has been significantly reduced (Stirling et al. 1999). The trend toward earlier break-up is projected to continue, as well as declines in ice cover and concentration (Etkin 1991; Gagnon and Gough 2005). Patterns of polar bear movement in Hudson Bay are predicted to change as this happens, in response to changes in prey distribution, prey species, and ice structure (Derocher et al. 2004); however, little is known about the present movement patterns of bears on the sea ice of Hudson Bay when they are away from land, as well as how much they may already have changed.

The purpose of this study was to quantify the movement of satellite-collared female bears from the WH population in relation to reproductive status, season, and temporal changes in sea ice. We hypothesized that reproductive status would affect movement because females with cubs have greater energetic demands than solitary females. We expected solitary females to travel greater distances and have larger home ranges than females with dependent cubs. Furthermore, we hypothesized that movement patterns would be affected by seasonal changes in ice conditions and may also have changed in response to temporal shifts in ice break-up dates in Hudson Bay from 1991 to 2004. We expected bears to travel farther and to have larger home ranges when break-up occurred later. To test these predictions, we compared movement metrics among reproductive classes of females from the WH population both annually and seasonally and compared temporal trends in movement to changes in ice break-up dates in the western Hudson Bay area.

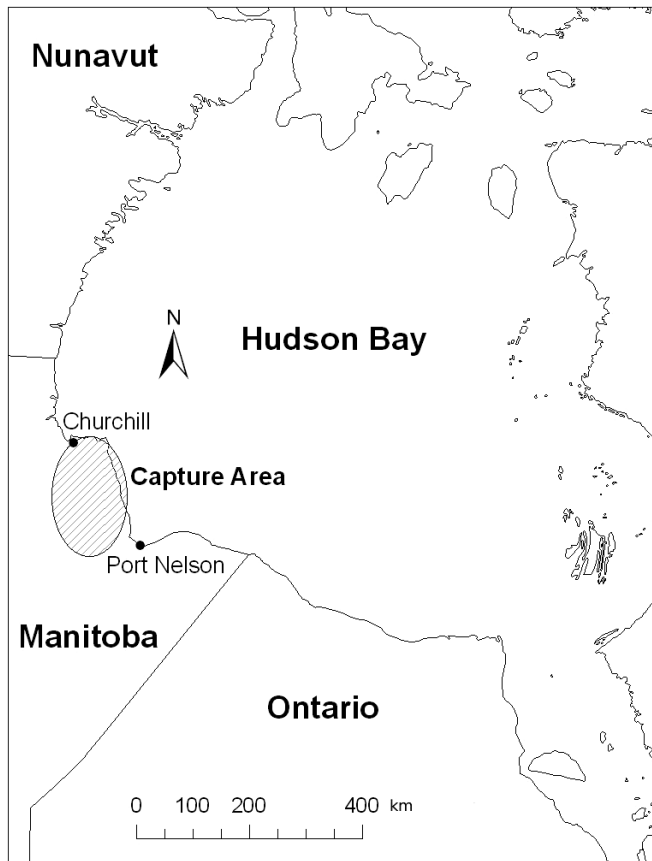
Methods

Study area

The boundary of the WH polar bear population includes coastal areas of Manitoba, Nunavut, and northwestern Ontario, and is bounded by 63°10'N and 88°30'W (Stirling et al. 1977, 1999). The capture area for this study was south of Churchill, Manitoba (Fig. 1), between 57°00'N–58°50'N and 92°25'W–94°15'W.

Hudson Bay is a shallow inland sea with a mean depth of 125 m and an area of about 10⁶ km² (Jones and Anderson 1994). Annual productivity has mainly been estimated in southeastern Hudson Bay and is 35 g of C/m², on average, with the highest levels (175 g of C/m² annually) found around the Belcher Islands (Roff and Legendre 1986). In comparison, the average annual productivity on arctic

Fig. 1. Map of the Hudson Bay region showing the area where polar bears (*Ursus maritimus*) from the western Hudson Bay population are captured by helicopter.



shelves is between 40 and 90 g of C/m² (Hill and Cota 2005), and is <7 g of C/m² in the Arctic Basin (Lee and Whitlege 2005). Ocean currents in the Bay follow a large-scale counterclockwise gyre that moves south from Foxe Basin and exits through the Hudson Strait (Prinsen-berg 1986). Ice formation begins in mid-October in the northwest and early forming ice is pushed south by the gyre along the west coast towards the northern coasts of Manitoba and Ontario. Ice velocities during freeze-up are between 0.36 and 0.54 km/h (Saucier et al. 2004). From late December until the end of April, ice cover is >9/10 throughout the Bay and the maximum extent occurs in April. Break-up occurs from May to mid-August, as the southernmost ice begins to melt, owing to warmer temperatures, and ice from the northwest is pushed south by currents along the west coast (Maxwell 1986; Saucier et al. 2004). The last ice floes are generally found along the Ontario coast of Hudson Bay and, by September, the entire Bay is ice-free (Gough et al. 2004).

Data collection

Between 1991 and 1998, 41 adult female bears from the WH population were captured and collared. No more than 10 bears were collared each year, with as few as 3 bears collared in both 1994 and 1995. Polar bears were caught in either September or March using standard helicopter capture methods (e.g., Derocher and Stirling 1996) and were immo-

bilized using Telazol[®] (Fort Dodge Laboratories, Fort Dodge, Iowa) according to Stirling et al. (1989). Animal handling procedures were approved by the University of Alberta BioSciences Animal Policy and Welfare Committee and the Animal Care Committee of the Canadian Wildlife Service (Prairie and Northern Region). Bears were classified as belonging to one of the following groups: females with cubs of the year (COYs), females with yearlings, solitary adult females 5 years or older, adult males 5 years or older, or subadult males or females (2–4 years). A sample of adult females was fitted with Telonics (Mesa, Arizona) satellite radio collars linked to the Argos[®] system (Service Argos, Inc., Lynnwood, Washington). Males were not tracked because their necks are wider than their heads and collars could not be secured. The satellite collars were programmed with different duty cycles in different years depending on immediate study objectives. Argos[®] provided quality indices for the accuracy of each location: 3, accuracy <150 m; 2, accuracy 150–350 m; 1, accuracy 350–1000 m; 0, accuracy >1000 m; and A or B, unable to estimate error but locations may be accurate.

In September 2004, 11 Telonics Gen III GPS Argos[®] satellite-linked collars were deployed in the same capture area. Accuracy of these newer collars is within 30 m (M. Edwards, personal communication). The collars were programmed to acquire 6 GPS locations per day (i.e., a fix attempt every 4 h). Only adult females accompanied by offspring were fitted with collars because solitary females might have been pregnant and would have gone into maternity dens rather than return to the sea ice. Collared bears were all classified according to reproductive status as above at the time of collaring. For all bears, status was updated if bears were recaptured; otherwise, bears were classified as “unknown reproductive status” 1 year after capture.

Statistical analysis

We used the North American Datum 1983 coordinate system for plotting bear locations in Hudson Bay. All bear locations were originally plotted as latitude north and longitude west, but were converted to universal transverse mercator (UTM) coordinates for zone 15 in ArcGIS[®] version 9.2 (Environmental Systems Research Institute, Inc. 2005) so that locations are positive and in metres for all spatial analyses.

For seasonal analyses, we divided the year into four biologically relevant seasons based on both bear behaviour and ice conditions: freeze-up, winter, break-up, and summer. Because movement and behaviour changes when bears move onto the ice from land (Ramsay and Andriashek 1986; Durner et al. 2004), freeze-up was defined as the period for each bear from its first location on the ice after summer to 31 December. The ice on Hudson Bay continues to thicken until April, at which point it reaches its maximum concentration and thickness (Saucier et al. 2004); therefore, we defined winter as the period from 1 January to 30 April. After April, ice concentration begins to decline throughout the Bay, and both ringed and bearded seals begin to pup and moult (Stirling and Øritsland 1995; Lunn et al. 1997). Therefore, we defined break-up as the period from 1 May to each bear’s last location on the ice before returning to

land. Once on land, bears move little (Knudsen 1978; Latour 1981) and we defined the period from first to last location on land as summer.

Because polar bears do not defend territories, the term “home range” in this paper refers to the general area occupied by a bear within a given time period. Annual and seasonal home-range size were estimated by the minimum convex polygon (MCP) method (Hayne 1949) using Hawth’s analysis tools for ArcGIS® version 3.21 (Beyer 2004). This method of home-range estimation was chosen both because of its simplicity and because MCP has been the most commonly used method in other populations, and it facilitates comparisons. Annual home range was estimated when there were ≥ 25 locations within a year for a given bear and where the first and last locations were ≥ 292 days apart (80% of a year). If there were data for a single bear beyond 365 days, a second bear-year was started on the 366th day. Seasonal home range was estimated when there were ≥ 20 locations in a season and if the first and last locations were ≥ 20 days apart. To make comparisons between the older satellite data and the new GPS data valid, we reduced the number of locations in the GPS data by randomly subsampling it 1000 times and calculating mean MCP sizes with the reduced data sets.

We used “displacement” to mean the net straight-line distance between the first and the last locations for an individual bear in a given period. For example, net displacements for freeze-up were calculated by measuring the straight-line distance between the first and the last locations for each bear during freeze-up. All seasonal net displacements were calculated similarly; however, net annual displacement was calculated differently. Because WH bears are known to show site fidelity when they return to land after being on the ice, we were interested in the straight-line distance between where bears left land and where they returned after break-up. For females collared on land in September, this was the distance between the first and the last locations for each bear within 1 year, September to September. However, for females collared as they emerged from dens on land in March, net annual displacement was calculated as the distance between their denning location (where they were collared in March) and their location in September, when they had returned to land.

Hourly movement rates were calculated by dividing the straight-line distance from one location to the next by the hours elapsed between them. To determine how much the interval between locations influenced the derived movement rate, we plotted the hour interval between consecutive locations against the derived mean rate for that interval and found the best fit curve to describe the relationship. We used the curve to help determine whether hourly rates should be divided into short-term and long-term rates, as well as where those divisions should occur.

We estimated total annual distance moved as the sum of all straight-line distances for a particular bear within a year. We used only bears for which there were ≥ 12 locations where no 2 locations were greater than 30 days apart, and for which the first and last locations were ≥ 292 days apart. In analyses of total seasonal distance, we used bears for which there were ≥ 4 locations in a season and ≥ 20 days between the first and the last locations. Because locations were

much more frequent in the GPS collar data set than in the satellite data set, we subsampled each season of the GPS collar data set 1000 times using the mean number of locations per season from the satellite collars. To quantify the difference between the satellite data and the GPS data, we randomly subsampled the new data and plotted the number of locations used against the derived total distance.

For all analyses, we tested the null hypothesis that measured variables were independent of reproductive class or season using one-way ANOVAs when data conformed to statistical assumptions of normality and equal variance. If data were not distributed normally, or if they showed heteroskedasticity, we used the Kruskal–Wallis H or Mann–Whitney U nonparametric test (Sokal and Rohlf 2001). We also correlated all variables with year to identify temporal relationships. When we found time trends, we tested whether these were correlated with mean ice break-up dates for western and southern Hudson Bay. Other changes in sea ice over time, such as declines in extent or concentration, may also affect bear movement, but earlier break-up dates have been identified as being closely correlated to polar bear fitness (Stirling et al. 1999). Break-up date was defined as the date by which ice concentration in western and southern coastal regions of Hudson Bay was 5/10 (for calculation methods see Stirling et al. 1999). We used Pearson’s product-moment correlation (correlation coefficient reported as r) if data were distributed normally; otherwise, we used Spearman’s rank correlation (reported as r_s), which produces a more conservative estimate but lifts the assumption of normality (Sokal and Rohlf 2001). Because the number of bears collared each year varied, and within a single year a particular bear may have locations for one season and not another, sample sizes vary for each analysis. All ANOVAs or nonparametric tests of multiple differences were followed by either Bonferroni test or nonparametric Tukey’s test (Zar 1999) to determine which variable(s) differed significantly from others. For all analyses, sample sizes are reported and values are means \pm one standard error (1 SE); a result was considered significant if its probability was ≤ 0.05 . All linear statistics were performed with SPSS® version 13.0 for Windows (SPSS Inc. 2004). Subsampling was performed using R version 2.0 (R Development Core Team 2005) and Tukey’s tests were calculated using Microsoft® Excel 2003.

Mean angles (Θ) and r (a vector between 0 and 1 that indicates strength of directionality, where 1 is perfect directionality with no variance and 0 is uniform distribution of angles) were computed for each season according to Zar (1999). The null hypothesis of uniform distribution was calculated using Rayleigh’s z test for circular uniformity. In all cases, bearings are given in true degrees north. We tested the effect of reproductive status on mean angles using the Watson–Williams multisample test of mean angles (Zar 1999, p. 625), which is a test analogous to an ANOVA in linear statistics. Circular statistics were calculated using Microsoft® Excel 2003.

Results

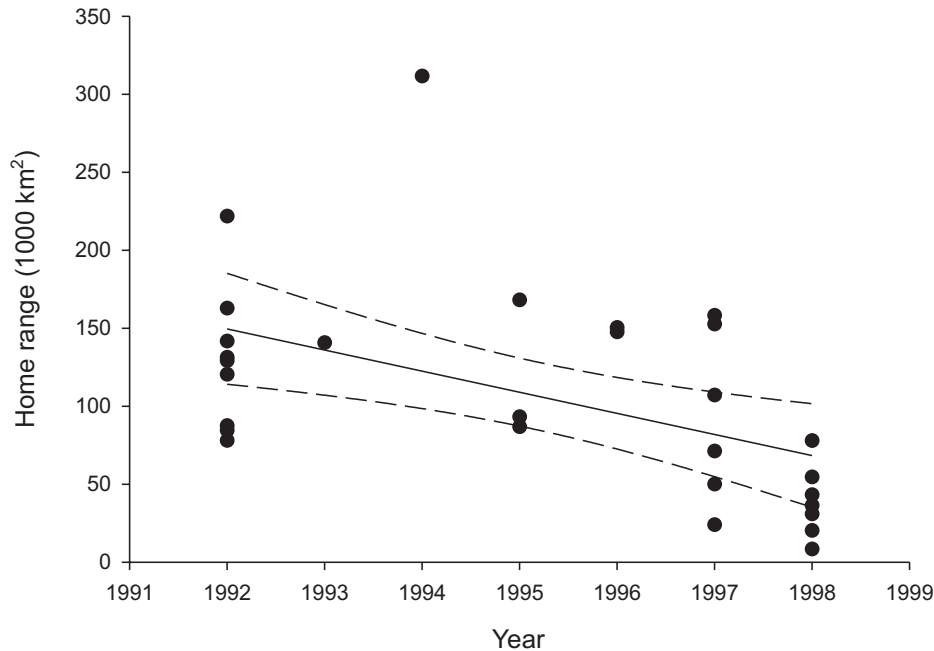
Argos® satellite collars were deployed on 46 adult females between March 1991 and September 1998 and 6083

Table 1. Annual home-range sizes of satellite-collared female polar bears (*Ursus maritimus*) from the western Hudson Bay population, 1992–1998.

Reproductive class	Mean ± SE (km ²)	<i>n</i>	Minimum (km ²)	Maximum (km ²)
Females with COYs	109 491 ± 21 255	14	8 470	311 646
Solitary females	93 428 ± 14 932	11	24 034	158 236
Females with yearlings	132 800 ± 31 102	4	86 876	221 819
Overall	106 613 ± 12 314	29	8 470	311 646

Note: COYs are cubs of the year.

Fig. 2. Annual home-range size (km²) of satellite-collared female polar bears from the western Hudson Bay population, 1992–1998. Females from all reproductive classes are pooled and the regression line (solid) is shown with 95% confidence intervals (broken lines).



locations were obtained from a total of 63 bear-years (although not all bear-years were complete 365 day-years). Of these, 16% had a quality index of 0 (>1000 m error) and were omitted from the analyses. After these were removed, 12% of locations had A or B ratings (locations with no accuracy estimate) and most of these were also removed if movement rates between locations were >10 km/h (the maximum movement rate recorded). No B locations filled this criterion, but some A locations did. The frequency of locations varied; however, the time between two locations was 195 ± 8 h (about 8 days) and the median was 117 h (5 days).

For analyses of bears with GPS collars, one good location for each fix time was used when available. Because of collar malfunctions, weather, and bear behaviour, there were commonly <6 locations/day. The number of fixes/day was 4.3 ± 0.04 and the fixes were obtained every 7.2 ± 0.3 h, 27 times more frequently than in the older data set. Life span of the 11 collars deployed in September 2004 ranged from 68 to 309 days; therefore, we did not use the 2005 data in any break-up or annual comparisons. However, seven collars transmitted consistently through freeze-up and winter, so these data were combined and compared with the satellite data.

Home ranges

Annual home-range size for WH bears was $106\,614 \pm$

$12\,314$ km² ($n = 29$). Females with COYs had both the smallest (8 470 km²) and the largest (311 646 km²) home ranges (Table 1). There were no significant differences among reproductive classes (ANOVA, $F_{[2,26]} = 0.52$, $P = 0.60$), so all bears were pooled for further analyses. Annual home-range size decreased by 55%, from 149 576 km² in 1992 to 68 321 km² in 1998 ($r = -0.51$, $P = 0.005$; Fig. 2), and was positively correlated with ice break-up date ($r_S = 0.569$, $P = 0.001$, $n = 29$). Break-up occurred very late in 1992 owing to the eruption of Mount Pinatubo in 1991 and bear home ranges may have been anomalously large during that year, so we tested the correlation between home-range size and year without the 1992 data. The relationship remained significant and was, in fact, stronger ($P = 0.0006$).

Seasonal MCPs were created from means of 38 locations in freeze-up, 33 in winter, 24 in break-up, and 38 in summer. We subsampled the 2004–2005 data and made MCPs using the appropriate number of locations per season to facilitate comparisons. However, the subsampled MCPs were not significantly different from the MCPs created for the same bears using all of the points in a season, despite the fact that there were hundreds of locations per season in the raw GPS data (Kruskal–Wallis test, $H = 0.63$, $P = 0.43$). Home ranges varied significantly with season (Table 2) for

Table 2. Seasonal minimum convex polygon home-range sizes of satellite-collared female polar bears from the western Hudson Bay population, 1992–2004.

Reproductive class	Freeze-up		Winter		Break-up		Summer	
	Mean \pm SE (km ²)	<i>n</i>	Mean \pm SE (km ²)	<i>n</i>	Mean \pm SE (km ²)	<i>n</i>	Mean \pm SE (km ²)	<i>n</i>
Females with COYs	43 552 \pm 5 033	18	29 323 \pm 5 003	27	41 039 \pm 12 452	19	733 \pm 183	22
Solitary females	26 220	1	44 875 \pm 7 931	12	15 803 \pm 5 824	4	462 \pm 301	7
Females with yearlings	13 824 \pm 4 168	11	52 808 \pm 6 482	19	18 565 \pm 3 781	7	553 \pm 148	10
Overall	28 203 \pm 3 286	23	40 234 \pm 3 759	58	32 430 \pm 8 157	30	638 \pm 121	39

Table 3. Seasonal net displacement of satellite-collared female polar bears from the western Hudson Bay population, 1991–2004.

Reproductive class	Freeze-up		Winter		Break-up		Summer	
	Mean \pm SE (km)	<i>n</i>	Mean \pm SE (km)	<i>n</i>	Mean \pm SE (km)	<i>n</i>	Mean \pm SE (km)	<i>n</i>
Females with COYs	355 \pm 22	19	354 \pm 24	27	293 \pm 42	20	44 \pm 7	29
Solitary females	na	na	195 \pm 23	14	146 \pm 23	6	12 \pm 3	7
Females with yearlings	308 \pm 31	13	195 \pm 24	18	220 \pm 37	10	51 \pm 11	20
Overall	336 \pm 19	32	268 \pm 17	59	248 \pm 27	36	42 \pm 6	43

all reproductive classes of bears (Kruskal–Wallis test, $H = 90.9$, $P < 0.0001$) and were smallest in summer. Home ranges in all other seasons were not significantly different from each other (Tukey's test for multiple comparisons).

There were no significant differences between reproductive classes for home ranges in summer (Kruskal–Wallis test, $H = 1.94$, $P = 0.38$), or break-up (Kruskal–Wallis test, $H = 1.02$, $P = 0.60$), and no changes over time (summer: $r_S = -0.14$, $P = 0.41$; break-up: $r_S = -0.07$, $P = 0.71$). During freeze-up, there were significant differences between females with COYs or yearlings, but there were not enough solitary females to include them in the analysis (Mann–Whitney U test, $U = 34.0$, $P = 0.003$). Females with COYs had larger home ranges, but this difference was dependent on an increase in freeze-up home-range size in 2004 for females with COYs ($r_S = 0.69$, $P = 0.001$, $n = 18$). There was only one female with yearlings in the 2004 data, so we could not determine whether this increase in freeze-up home-range size occurred for only females with COYs or whether it occurred for all reproductive classes of bears. In winter, reproductive class had a significant effect on home-range size (Kruskal–Wallis test, $H = 8.73$, $P = 0.013$). Tukey's test for multiple comparisons showed that females with yearlings had significantly larger winter home ranges than females with COYs, but solitary females were not significantly different from either group. There were no trends over time in winter home-range size ($r_S = -0.114$, $n = 58$, $P = 0.39$).

Net displacement

Annual net displacement was 82 ± 17 km ($n = 48$), but the data were highly skewed and median net displacement was 39 km. There were no differences between the median displacement of reproductive classes (Kruskal–Wallis test, $H = 4.38$, $P = 0.11$), although there were differences between the means (Kruskal–Wallis test, $H = 6.35$, $P = 0.04$). Females with COYs (113 ± 35 km, $n = 20$) and females with yearlings (112 ± 41 km, $n = 9$) had similar mean displacements, but solitary females had significantly lower displacements (34 ± 4 km, $n = 19$). The high means for

females with offspring were strongly influenced by two bears that had net annual displacements of 696 km in 1994, 306 km in 1995, and 406 km in 1996. When these two individuals were removed from analysis, there were no differences among classes (Kruskal–Wallis test, $H = 4.4$, $P = 0.11$) and the annual net displacement for all classes was 56 ± 7 km (median 36 km). Annual net displacement did not change over time for any reproductive class ($r_S = -0.15$, $P = 0.32$).

For all reproductive classes, net displacement depended on season (Kruskal–Wallis test, $H = 110.6$, $P < 0.0001$). Tukey's test for multiple comparisons showed that displacement in summer was significantly lower than in all other seasons and that displacement in freeze-up was higher than in winter (Table 3). During freeze-up, net displacement was 336 ± 18 km and there were no significant differences between reproductive classes (ANOVA, $F_{[1,30]} = 1.54$, $P = 0.22$) or over time ($r = 0.056$, $P = 0.76$). During winter, there were significant differences between classes (ANOVA, $F_{[2,56]} = 16.5$, $P < 0.0001$). The Bonferroni test for multiple comparisons showed that females with COYs (354 ± 23 km) had larger mean net displacements in winter than other females (solitary females 195 ± 23 ; females with yearlings 195 ± 24). There were no changes in net winter displacement over time for any reproductive class (females with COYs: $r_S = -0.15$, $P = 0.46$; solitary females: $r_S = -0.13$, $P = 0.66$; females with yearlings: $r_S = 0.14$, $P = 0.57$). There were no significant differences between classes in net displacement during break-up (Kruskal–Wallis test, $H = 4.6$, $P = 0.1$) or summer (Kruskal–Wallis test, $H = 5.7$, $P = 0.06$) and there were no changes with time in either season (break-up: $r_S = -0.80$, $P = 0.64$; summer: $r_S = 0.02$, $P = 0.91$).

Directional patterns

Bears only showed significant directional movement when they were leaving land and moving onto the ice (Table 4), and overall, reproductive class had little effect on direction of movement. During freeze-up, there were no differences between reproductive classes (Watson–Williams multisam-

Table 4. Mean seasonal direction of travel (Θ , in degrees true) and r (vector of mean direction) for satellite-collared female polar bears from the western Hudson Bay population, 1991–2004.

Reproductive class	Freeze-up			Winter			Break-up			Summer		
	Θ	n	r	Θ	n	r	Θ	n	r	Θ	n	r
Females with COYs	55	21	0.32	52	31	0.40	239	22	0.17	66	30	0.11
Solitary females	87	4	0.19	199	23	0.08	230	15	0.38	97	16	0.15
Females with yearlings	45	17	0.39	233	20	0.05	266	12	0.13	86	26	0.33
Overall	52	42	0.33	58	74	0.14	238	49	0.22	83	72	0.19

Table 5. Hourly movement rates of satellite-collared female polar bears from the western Hudson Bay population, 1991–2004, for short-term (<8 h between consecutive locations), mid-term (>8 h and <100 h between consecutive locations), and long-term (>100 h and <200 h between consecutive locations) movements.

Reproductive class	Freeze-up		Winter		Break-up		Summer	
	Mean \pm SE (km/h)	n	Mean \pm SE (km/h)	n	Mean \pm SE (km/h)	n	Mean \pm SE (km/h)	n
Short-term rates								
Females with COYs	1.8 \pm 0.3	9	3.0 \pm 1.4	4	1.6 \pm 0.2	4	0.4 \pm 0.2	10
Solitary females	na	0	2.5 \pm 0.6	4	1.4	1	0.6	1
Females with yearlings	1.7 \pm 0.3	2	1.7 \pm 0.4	11	1.0 \pm 0.3	5	1.9	2
Overall	1.8 \pm 0.3	11	2.1 \pm 0.4	19	1.3 \pm 0.2	10	0.7 \pm 0.3	13
Mid-term rates								
Females with COYs	1.1 \pm 0.2	9	0.5 \pm 0.1	10	0.5 \pm 0.1	6	0.1 \pm 0.1	9
Solitary females	0.3	1	0.9 \pm 0.2	4	0.6 \pm 0.1	4	0.1 \pm 0.02	7
Females with yearlings	1.1 \pm 0.2	4	0.9 \pm 0.1	8	0.7 \pm 0.2	6	0.2 \pm 0.1	2
Overall	1.0 \pm 0.1	14	0.7 \pm 0.1	22	0.6 \pm 0.1	16	0.1 \pm 0.03	18
Long-term rates								
Females with COYs	0.5 \pm 0.1	4	0.3 \pm 0.1	9	0.4 \pm 0.1	5	0.1 \pm 0.02	5
Solitary females	0.7 \pm 0.4	3	0.6 \pm 0.1	5	0.4 \pm 0.1	3	0.1 \pm 0.03	5
Females with yearlings	0.4 \pm 0.1	3	0.5 \pm 0.02	4	0.4 \pm 0.04	4	0.1 \pm 0.03	5
Overall	0.5 \pm 0.1	10	0.4 \pm 0.1	18	0.4 \pm 0.04	12	0.1 \pm 0.02	15

ple test, $F_{[2,32]} = 0.44$, $P > 0.25$), and bears of all classes moved significantly to the northeast (mean $\Theta = 52^\circ$, $r = 0.33$; Rayleigh's $z = 4.64$, $P < 0.01$, $n = 42$). During winter, reproductive class affected direction of movement (Watson–Williams multisample test, $F_{[2,64]} = 12.03$, $P < 0.0005$), with females with COYs moved significantly to the northeast (mean $\Theta = 52^\circ$, Rayleigh's $z = 5.1$, $P < 0.01$, $n = 31$), while all other females showed no directionality (solitary females: Rayleigh's $z = 0.14$, $P > 0.25$, $n = 23$; females with yearlings: Rayleigh's $z = 0.05$, $P > 0.25$, $n = 20$). During break-up, there were no significant differences between classes (Watson–Williams multisample test, $F_{[2,46]} = 0.26$, $P > 0.25$) and no significant directionality, although there was weak support for a mean angle of 240° (Rayleigh's $z = 2.35$, $0.05 < P < 0.1$, $n = 67$). Solitary females had the strongest directionality during break-up (mean $\Theta = 230^\circ$, $r = 0.38$); however, it was not strong enough to reject the null hypothesis of uniform distribution (Rayleigh's $z = 2.12$, $P > 0.1$). During summer, there were no significant differences between classes (Watson–Williams multisample test, $F_{[2,71]} = 0.56$, $P > 0.25$) and bears did not show significant directionality (Rayleigh's $z = 2.72$, $P > 0.25$, $n = 72$).

Rates of movement

Rate of movement was strongly dependent on the interval between successive locations until approximately 100 h sep-

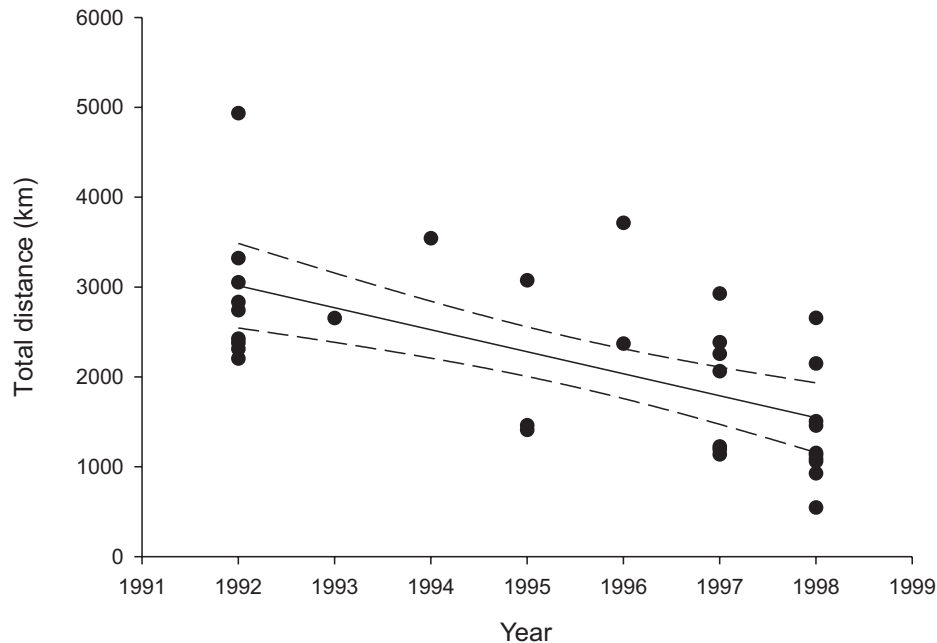
arated the two points. Because most of the 2004–2005 GPS locations were <8 h apart, and because the point separating an extremely steep slope from a lesser one appeared to occur at around 10 h, we decided to separate the rates into short-term (<8 h between locations) and mid-term (between 8 and 100 h intervals). However, because most other studies on polar bear movements have used satellite collars that provided locations only every 4–7 days (or every 96–168 h), we also calculated long-term movement rates when the consecutive location interval was between 100 and 200 h to facilitate comparison with other populations.

Long-term movement rates (100–200 h between consecutive locations) did not differ between classes (Kruskal–Wallis test, $H = 0.71$, $P = 0.70$), but did vary significantly with season (Kruskal–Wallis test, $H = 18.8$, $P < 0.0001$; Table 5). Tukey's tests for multiple comparisons showed that summer movement rates were significantly lower than those of all other seasons. During break-up and summer, movement rates did not change over time. During winter, however, there was a significant decline over time in long-term rates ($r_S = -0.061$, $P = 0.008$, $n = 18$).

Mid-range hourly movement rates (8–100 h between consecutive locations) varied significantly with season (Kruskal–Wallis test, $H = 24.5$, $P < 0.0001$; Table 5), but did not vary with reproductive class in any season (Kruskal–Wallis tests; freeze-up: $H = 1.97$, $P = 0.37$; winter: $H = 5.6$, $P =$

Table 6. Total distance moved annually by satellite-collared female polar bears from the western Hudson Bay population, 1992–1999.

Reproductive class	Mean \pm SE (km)	<i>n</i>	Minimum (km)	Maximum (km)
Females with cubs	2516 \pm 589	6	1060	4935
Solitary females	1843 \pm 210	17	547	3714
Females with yearlings	2198 \pm 269	12	674	3543
Overall	2080 \pm 170	35	547	4935

Fig. 3. Total distance traveled annually (km) by satellite-collared female polar bears from the western Hudson Bay population, 1992–1998. Females from all reproductive classes are pooled and the regression line (solid) is shown with 95% confidence intervals (broken lines).

0.06; break-up: $H = 1.47$, $P = 0.48$; summer: $H = 0.84$, $P = 0.66$). Movement rates were highest during freeze-up (1.06 ± 0.11 km/h) and lowest during summer (0.10 ± 0.02 km/h), but Tukey's tests for multiple comparisons showed that only summer movement rates were significantly different from rates in other seasons ($P < 0.0001$). There were no changes in mid-range movement rates over time in any season (freeze-up: $r_S = 0.38$, $P = 0.18$; winter: $r_S = -0.08$, $P = 0.72$; break-up: $r_S = 0.31$, $P = 0.24$; summer: $r_S = 0.28$, $P = 0.46$). The highest mid-range rate recorded was 4.12 km/h and was achieved by a solitary female in winter, but the overall rate was 0.61 ± 0.08 km/h.

Short-term movement rates (<8 h between consecutive locations) were consistently higher than longer term rates in all seasons (Table 5). There were significant differences between seasonal short-term movement rates (Kruskal–Wallis test, $H = 14.5$, $P = 0.002$), and Tukey's test for multiple comparison showed that summer was significantly lower than winter. Reproductive classes did not affect short-term movement rates in any season (Kruskal–Wallis tests; freeze-up: $H = 0.50$, $P = 0.48$; winter: $H = 1.76$, $P = 0.42$; break-up: $H = 2.59$, $P = 0.27$; summer: $H = 1.84$, $P = 0.40$). There were no changes in short-term movement rate over time in freeze-up ($r_S = -0.23$, $P = 0.50$), but rates declined in winter ($r_S = -0.74$, $n = 19$, $P < 0.0001$) and summer ($r_S = -0.79$, $n = 13$, $P = 0.001$). There was also weak evidence for a

decline in break-up movement rates ($r_S = -0.63$, $P = 0.052$). The highest calculated short-term movement rate was 10.86 km/h and was recorded for a female with yearlings in winter. There were only three instances of rates as high as 10 km/h; all three occurred when bears were on the ice and when the time between consecutive locations was less than 2 h.

Total distances

The annual distance traveled was 2080 ± 170 km ($n = 35$). The shortest distance was 547 km by a solitary female and the greatest distance was 4935 km by a female with COYs (Table 6). There were no significant differences between reproductive classes (ANOVA, $F_{[2,32]} = 1.13$, $P = 0.335$), so classes were pooled for further analyses. There was a 45% decline in total annual distance traveled over time from 2885 km in 1991 to 1581 km in 1998 ($r = -0.47$, $n = 35$, $P = 0.004$; Fig. 3). Total annual distance traveled was positively correlated with break-up date ($r_S = 0.579$, $n = 35$, $P < 0.0001$).

The total seasonal distances calculated for bears with GPS collars were two to three times greater than those calculated for bears with satellite collars, because of the much higher frequency of locations available from GPS collar data. Total seasonal distances were calculated from the satellite data using 12 locations for freeze-up, 16 for winter, 11 for break-up,

Table 7. Total distance moved per season by satellite-collared female polar bears from the western Hudson Bay population, 1991–2004.

Reproductive class	Freeze-up		Winter		Break-up		Summer	
	Mean \pm SE (km)	<i>n</i>	Mean \pm SE (km)	<i>n</i>	Mean \pm SE (km)	<i>n</i>	Mean \pm SE (km)	<i>n</i>
Females with COYs	686 \pm 35	19	568 \pm 47	27	739 \pm 91	19	84 \pm 13	26
Solitary females	792	1	898 \pm 99	17	420 \pm 77	8	70 \pm 21	8
Females with yearlings	702 \pm 48	10	1090 \pm 99	19	500 \pm 137	12	87 \pm 16	14
Overall	695 \pm 27	30	814 \pm 52	63	600 \pm 53	39	82 \pm 9	48

and 12 for summer. Once GPS data were subsampled to match these numbers of locations, distances moved were comparable. There were significant differences between seasonal distances traveled (Kruskal–Wallis test, $H = 92.12$, $P < 0.0001$) and Tukey's test for multiple comparisons showed that total distance traveled in winter was higher than during break-up and distances traveled in summer were lower than those in every other season (Table 7). During freeze-up, there was no difference between the distance traveled by females with COYs or yearlings (Mann–Whitney U test, $U = 1.11$, $P = 0.57$) and there were not enough data for solitary females in freeze-up to include them in the analysis. Distance traveled in freeze-up did not change over time ($r_S = 0.14$, $P = 0.53$). In winter, females with yearlings traveled a greater total distance (1090 \pm 99 km) than other females (solitary: 898 \pm 99 km; females with COYs: 568 \pm 47 km; Kruskal–Wallis test, $H = 17.6$, $P < 0.0001$). Total distance traveled in winter by solitary females did not change significantly over time ($r_S = -0.30$, $P = 0.24$, $n = 17$); however, there was weak evidence that total distance traveled by females with offspring in winter has declined over time (females with COYs: $r_S = -0.35$, $P = 0.071$, $n = 27$; females with yearlings: $r_S = -0.44$, $P = 0.059$, $n = 19$). During break-up, females with COYs traveled a greater total distance than did other females (Kruskal–Wallis test, $H = 7.48$, $P = 0.024$) and there were no changes in distance traveled by any class over time. There were no significant differences between reproductive classes for total distance moved in the summer (Kruskal–Wallis test, $H = 0.67$, $P = 0.72$). The total distance traveled in summer did not change over time ($r_S = -0.15$, $P = 0.31$).

Discussion

This study is the first to quantitatively examine bear movement on the ice of Hudson Bay and, because both hunting and mating occur exclusively on the ice (but see Derocher et al. 1993), this period is critical to bear survival and reproductive success (Atkinson and Ramsay 1995). Sample sizes in many analyses were small because of variation in location frequency, but in most cases, effect sizes were large relative to sample variation and results were clear. Subsampling the GPS data allowed us to combine these and the satellite data, thereby increasing our sampling period and sample sizes. Overall, we found no evidence that combining the two data sets produced any misleading results.

Effects of reproductive class and season

Polar bears from the WH population used space differently, depending on the season, with the most apparent differences in movement seen in summer. Consistent with other

studies that show Hudson Bay bears are not active while on land in summer (Knudsen 1978; Lunn and Stirling 1985; Derocher and Stirling 1990; Lunn et al. 2004), home ranges in summer were small, distances moved were minimal, and hourly movement rates were low. Although our results show high mean net displacements for females with young, these were influenced by only two bears that did not return to the Churchill area when the ice melted, and median displacements were less than 40 km for all groups, which is similar to the net annual displacements of 30–32 km found by Derocher and Stirling (1990). Despite one bear's return to land almost 700 km from where she left, this bear did return to her original denning area the following year. These results are consistent with the hypothesis that females return to the same area to familiarize their cubs with suitable denning habitat (Derocher and Stirling 1990; Scott and Stirling 2002).

During freeze-up, polar bears had high hourly movement rates, high net and total distances covered, small home ranges, and significant directionality, all of which describe travelling behaviour (Kareiva and Shigesada 1983; Fritz et al. 2003). Bears moved with a mean Θ of 52°, which agrees with the mean Θ s of 53° and 39° found by Derocher and Stirling (1990) and Ramsay and Andriashek (1986), respectively, for bears as they moved onto the ice. However, because of logistic constraints, bears in previous studies were either followed on land only or relocated up to 195 km offshore, and it is now evident that bears move more than 300 km offshore and maintain their northeast directionality until late December. Ice drift contributes to observed movement rates and directions because bears are walking on a moving platform (Mauritzen et al. 2003b). In Hudson Bay, ice drift velocities are highest during freeze-up and early winter, at 0.4–0.5 km/h in a southeast direction (Saucier et al. 2004), so bears probably move faster and in a more northerly direction than is apparent by their observed paths.

By winter, bears moved more slowly in random directions, covered less net distance, and had larger home ranges than during freeze-up, suggesting that hunting became the main activity after December. Net displacement during break-up for all classes was similar to net displacement during freeze-up, indicating that over the winter bears moved neither closer to nor farther from the Churchill capture area and only began to move toward land after 1 May. The similarity between freeze-up and break-up rates, total distances, and home-range sizes support this pattern of movement.

Evidence that females caring for dependent young use different movement strategies has been found in polar bears (Mauritzen et al. 2003a) and in other mammals (e.g., Beier et al. 1995; Loretto and Vieira 2005). However, females with COYs did not have lower hourly movement rates than

other females in any season, and in fact, moved greater total distances in a year than other females, despite being accompanied by small cubs that might be expected to have more limited mobility. Daily energy expenditure of female mammals with young are about four times their basal metabolic rate because of energy lost through food-sharing and lactation (Ricklefs et al. 1996); therefore, female polar bears with COYs need to eat more than other females in winter and break-up. Emergence from maternity dens may coincide with seal pupping and moulting to maximize the energetic returns from a shorter hunting period (Ramsay and Andriashuk 1986; Amstrup and Gardner 1994). Still, it is likely difficult for females with young to store as much fat as other classes of females, and Atkinson and Ramsay (1995) found that female polar bears with offspring had significantly less body mass, less total body fat, and less fat per unit lean body mass than did solitary females.

Comparisons with other populations

The annual home-range size of Hudson Bay polar bears has not been previously documented, although satellite collars have been used to measure home ranges of bears in the eastern high Arctic (Ferguson et al. 1999), Bering and Chukchi seas (Garner et al. 1991), Beaufort Sea (Amstrup et al. 2000), Barents Sea (Mauritzen et al. 2001), and Northeastern Greenland (Born et al. 1997). The largest annual home ranges were found in the Beaufort Sea (166 694 km²; Amstrup et al. 2000) and in the Canadian archipelago (125 500 km²; Ferguson et al. 1999), and bears in both areas were highly variable, with some ranges up to 600 000 km². Home ranges for bears in the Canadian archipelago were calculated using kernel methods of range estimation, which generally produce smaller areas than the MCP methods (e.g., Barg et al. 2005), so it is likely that the mean MCP range for Canadian archipelago bears is larger than 125 500 km². Unlike bears in the Beaufort Sea or Canadian archipelago, WH bears had a mean home-range size that was more similar to polar bear ranges in the Barents Sea (means from 28 000 to 96 302 km²; Born et al. 1997; Mauritzen et al. 2001).

Polar bear home-range size is largely determined by the availability and predictability of prey (Ferguson et al. 1999; Mauritzen et al. 2003a). Both ringed and bearded seals prefer annual ice and shallow water <200 m deep (Kingsley et al. 1985; Gjertz et al. 2000), and they are rarely found in multiyear ice or hauled out on land (Kingsley et al. 1985; Frost et al. 2004). Therefore, polar bear home ranges are large when they encompass substantial amounts of either multiyear ice or land, as is the case in both the Arctic archipelago and the Beaufort Sea (Stirling and Øritsland 1995; Ferguson et al. 1999). Because Hudson Bay is only 250 m at its deepest (Maxwell 1986) and is covered with annual ice only, productivity is high (Roff and Legendre 1986) and seals have access to the entire Bay. Lunn et al. (1997) found higher seal densities in Hudson Bay than in other areas of the Arctic. Hudson Bay and the Barents Sea are both large open basins without much land, which may explain why polar bear home ranges in these two areas are similar. Furthermore, in other parts of the Canadian Arctic, winter may be less productive for hunting because of lower prey availability and higher proportions of multiyear ice, and bears occa-

sionally go into shelter dens on the ice to wait out inclement weather (Ferguson et al. 2000b). We found no evidence of long-term shelter denning by bears on Hudson Bay sea ice and bears were active throughout the winter.

Movement rates on sea ice and distances traveled have only been measured in a few other polar bear populations (Born et al. 1997; Amstrup et al. 2000; Messier et al. 2001), but movement rates of WH bears were comparable, and bears reached maximum short-term speeds of about 10 km/h, which is similar to rates reported by Amstrup et al. (2000). However, reproductive status did not affect movement rate in Hudson Bay, whereas in the southern Beaufort Sea, solitary females had higher movement rates than females with yearlings (Amstrup et al. 2000). The reason for this difference is unknown but could be associated with more predictable hunting opportunities in Hudson Bay compared with the high Arctic.

Temporal trends in bear movement

Annual home-range size of WH bears declined by 81 255 km² and total annual distance traveled declined by 1 304 km from 1992 to 1998. Lack of change in total distances covered during freeze-up and break-up suggest that home-range size is more dependent on distance covered during winter than in the other two ice seasons. Support for this was evident in the decline in total distance traveled during winter for females with offspring by 42% from 1992 to 1999, and the possible decline in winter short-term movement rates. Changes in sea ice in western Hudson Bay have occurred at a rate of a few days per decade since the 1970s (Stirling et al. 2004), so it is surprising that polar bear movement would have declined so dramatically over a period of only 6 years. One reason for this extreme trend might have been the late break-up in 1992 owing to the 1991 eruption of Mount Pinatubo in the Philippines (Stirling et al. 1999); however, analysis without the 1992 data revealed that the decline still exists.

There are several possible explanations for decreased movement in polar bears. For instance, seal distribution might have become more concentrated or more predictable so that bears do not need to move as much to find food. However, Stirling et al. (1999) showed that polar bears are returning to land in poorer condition than they have in the past, which means their energy intake has declined in relation to their energy output. Since their energy output has not increased, energy intake must be decreasing. Therefore, it is unlikely that seals have become more accessible. Lower energy intake means that bears are eating less over the on-ice hunting period than they have in the past and are accumulating less fat as a result.

Fat storage is critical to polar bear survival, especially in the Hudson Bay region, where there are no hunting opportunities during the summer and pregnant females may not eat for up to 8 months (Stirling and McEwan 1975; Derocher et al. 1993). During the ice-free season, bears lose between 0.70 and 0.85 kg/day (Watts et al. 1987), and loss of body fat accounts for 93% of the change in mass (Atkinson and Ramsay 1995). Maxwell et al. (1988) found that black bears (*Ursus americanus* Pallas, 1780) with insufficient fat stores suffer from dehydration during periods of dormancy because muscle metabolism forces bears to urinate. When bears

metabolize fat instead of muscle, urea is recycled and both protein and water are created metabolically (Nelson et al. 1983), which means that the amount of stored fat on a polar bear will largely determine its fitness. In addition, Atkinson and Ramsay (1995) showed that a direct positive relationship exists between a female polar bear's fat stores and the survival of her cubs; therefore, the decrease in fat accumulation by WH bears has consequences to population-level fitness and may be contributing to observed declines in bear abundance in the area (Regehr et al. 2005).

The reasons for lower energy intake are unclear, but they may be related to recent declines in ringed seal survival and recruitment in Hudson Bay (Ferguson et al. 2005; Stirling 2005). These declines have been attributed to changes in Arctic climate, including increased temperatures and precipitation. Ringed seals require high concentrations of annual ice and enough snowfall to maintain stable birthing lairs on the pack ice and pups in lairs with thinner snow roofs are more vulnerable to predation (Furgal et al. 1996). There is also evidence that fish community composition has changed, with a decrease in a primary prey species for seals, the Arctic cod (*Boreogadus saida* (Lepechin, 1774); Gaston et al. 2003). Another factor that may affect polar bear prey intake is a decrease in the predictability of finding seals. When ice concentration is high, most breathing holes are actively maintained by seals, so a polar bear waiting at a hole has a high chance of actually catching a seal (Stirling and McEwan 1975), whereas when ice is more fragmented, there are more naturally occurring holes at which seals can emerge, and still-hunting by polar bears will be less productive (Derocher et al. 2004). Finally, an important factor contributing to lower polar bear energy intake is shorter ice season duration. In Hudson Bay, freeze-up is occurring later and break-up is occurring progressively earlier than it has in the past (Stirling et al. 1999; Gagnon and Gough 2005). This means that bears in Hudson Bay have less time to hunt on the ice and accumulate fat and a longer ice-free period during which they must rely on their fat stores. Positive correlations between ice break-up date and home-range size and total distance traveled support this hypothesis.

The dramatic decline in bear movement that we found in this study should be regarded with caution because the time period is relatively short (6 years) and sample sizes in 1994 and 1995 were very low. However, despite these limitations, it is clear that the distance travelled by bears has decreased. When a longer time period can be examined, we will have a better understanding of the nature of this decline. The ultimate cause for both decreased movement and poorer bear condition may be related to changes in ice cover, ice extent, and the duration of the ice season in Hudson Bay, all of which have affected seal recruitment and distribution in the Bay. Future research should include building energetic models for polar bears that incorporate both long-term metabolic needs and short-term foraging strategies to identify the determinants of body mass and energy intake (e.g., Moen et al. 1997). To do this, we need a better understanding of polar bear movement and searching strategies and a better understanding of seal abundance and distribution in Hudson Bay. Current data on seal population dynamics are building (Lunn et al. 1997; Ferguson et al. 2005), and the more detailed information available from GPS collars will also pro-

vide valuable insights into what drives bear movement on Hudson Bay.

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References

- Amstrup, S.C., and Gardner, C. 1994. Polar bear maternity denning in the Beaufort Sea. *J. Wildl. Manag.* **58**: 1–10.
- Amstrup, S.C., Durner, G.M., Stirling, I., Lunn, N.J., and Messier, F. 2000. Movements and distribution of polar bears in the Beaufort Sea. *Can. J. Zool.* **78**: 948–966. doi:10.1139/cjz-78-6-948.
- Atkinson, S.N., and Ramsay, M.A. 1995. The effects of prolonged fasting of the body composition and reproductive success of female polar bears (*Ursus maritimus*). *Funct. Ecol.* **9**: 559–567. doi:10.2307/2390145.
- Barg, J.J., Jones, J., and Robertson, R.J. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. *J. Anim. Ecol.* **74**: 139–149. doi:10.1111/j.1365-2656.2004.00906.x.
- Beier, P., Choate, D., and Barrett, R.H. 1995. Movement patterns of mountain lions during different behaviours. *J. Mammal.* **76**: 1056–1070. doi:10.2307/1382599.
- Bethke, R., Taylor, M., Amstrup, S., and Messier, F. 1996. Population delineation of polar bears using satellite collar data. *Ecol. Appl.* **6**: 311–317.
- Beyer, H.L. 2004. Hawth's analysis tools for ArcGIS®. Version 3.21 [computer program]. Available from <http://www.spatial ecology.com/htools> [accessed 15 October 2004].
- Born, E.W., Wiig, Ø., and Thomassen, J. 1997. Seasonal and annual movements of radio-collared polar bears (*Ursus maritimus*) in northeast Greenland. *J. Mar. Syst.* **10**: 67–77. doi:10.1016/S0924-7963(96)00072-3.
- Comiso, J.C. 2002. A rapidly declining perennial sea ice cover in the Arctic. *Geophys. Res. Lett.* **29**(20): 1956. doi:10.1029/2002GL015650.
- Comiso, J.C., and Parkinson, C.L. 2004. Satellite-observed changes in the Arctic. *Phys. Today* [online], **57**: 38–44. Available from <http://www.physicstoday.org/vol-57/iss-8/p38.html> [accessed 30 January 2005].
- Derocher, A.E., and Stirling, I. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. *Can. J. Zool.* **68**: 1395–1403.
- Derocher, A.E., and Stirling, I. 1995. Estimation of polar bear population size and survival in western Hudson Bay. *J. Wildl. Manag.* **59**: 215–221.
- Derocher, A.E., and Stirling, I. 1996. Aspects of survival in juvenile polar bears. *Can. J. Zool.* **74**: 1246–1252.
- Derocher, A.E., Stirling, I., and Andriashek, D. 1992. Pregnancy

- rates and serum progesterone levels of polar bears in western Hudson Bay. *Can. J. Zool.* **70**: 561–566.
- Derocher, A.E., Andriashek, D., and Stirling, I. 1993. Terrestrial foraging by polar bears during the ice-free period in western Hudson Bay. *Arctic*, **46**: 251–254.
- Derocher, A.E., Lunn, N.J., and Stirling, I. 2004. Polar bears in a changing climate. *Integr. Comp. Biol.* **44**: 163–176. doi:10.1093/icb/44.2.163.
- Durner, G.M., Amstrup, S.C., Neilson, R., and McDonald, T. 2004. The use of sea ice habitat by female polar bears in the Beaufort Sea. OCS study No. MMS 2004-014. US Geological Survey, Alaska Science Center, Anchorage, Alaska.
- Environmental Systems Research Institute, Inc. 2005. ArcGIS®. Verison 9.2 [computer program]. Environmental Systems Research Institute, Inc., Redlands, Calif.
- Etkin, D.A. 1991. Break-up in Hudson Bay: its sensitivity to air temperatures and implications for climate warming. *Climatol. Bull.* **25**: 21–35.
- Ferguson, S.H., Taylor, M.K., Born, E.W., Rosing-Asvid, A., and Messier, F. 1999. Determinants of home range size for polar bears (*Ursus maritimus*). *Ecol. Lett.* **2**: 311–318. doi:10.1046/j.1461-0248.1999.00090.x.
- Ferguson, S.H., Taylor, M.K., and Messier, F. 2000a. Influence of sea ice dynamics on habitat selection by polar bears. *Ecology*, **81**: 761–772. doi:10.2307/177375.
- Ferguson, S.H., Taylor, M.K., Rosing-Asvid, A., Born, E.W., and Messier, F. 2000b. Relationships between denning of polar bears and conditions of sea ice. *J. Mammal.* **81**: 1118–1127. doi:10.1644/1545-1542(2000)081<1118:RBDOPB>2.0.CO;2.
- Ferguson, S.H., Stirling, I., and McLoughlin, P. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Mar. Mamm. Sci.* **21**: 121–135.
- Fortin, D., Fryxell, J.M., O’Brodivich, L., and Frandsen, D. 2003. Foraging ecology of bison at the landscape and plant community levels; the applicability of energy maximization principles. *Oecologia (Berl.)*, **134**: 219–227. PMID:12647163.
- Fritz, H., Said, S., and Weimerskirch, H. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proc. R. Soc. Lond. B Biol. Sci.* **270**: 1143–1148.
- Frost, K.J., Lowry, L.F., Pendelton, G., and Nute, H.R. 2004. Factors affecting the observed densities of ringed seals, *Phoca hispida*, in the Alaskan Beaufort Sea, 1996–99. *Arctic*, **57**: 115–128.
- Furgal, C.M.S., Innes, M.S., and Kovacs, K.M. 1996. Characteristics of ringed seal, *Phoca hispida*, subnival structures and breeding habitat and their effects on predation. *Can. J. Zool.* **74**: 858–874.
- Gagnon, A.S., and Gough, W.A. 2005. Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. *Arctic*, **58**: 370–382.
- Garner, G.W., Knick, S.T., and Douglas, D.C. 1991. Seasonal movement of adult female polar bears in the Bering and Chukchi Seas. In *Bears — Their biology and management: Proceedings of the Eighth International Conference on Bear Research and Management*, Victoria, B.C., 20–25 February 1989. Edited by L.M. Darling and W.R. Archibald. International Association for Bear Research and Management, Washington, D.C. pp. 219–226. [Available from Michael R. Pelton, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, P.O. Box 1071, Knoxville, TN 37901-1071, USA.]
- Gaston, A.J., Woo, K., and Hipfner, J.M. 2003. Trends in forage fish populations in northern Hudson Bay since 1981, as determined from the diet of nestling thick-billed murre *Uria lomvia*. *Arctic*, **56**: 227–233.
- Gjertz, I., Kovacs, K.M., Lydersen, C., and Wiig, Ø. 2000. Movements and diving of bearded seal (*Erignathus barbatus*) mothers and pups during lactation and post-weaning. *Polar Biol.* **23**: 559–566. doi:10.1007/s003000000121.
- Gough, W.A., and Wolfe, E. 2001. Climate change scenarios for Hudson Bay, Canada, from general circulation models. *Arctic*, **54**: 142–150.
- Gough, W.A., Cornwell, A.R., and Tsuji, L.J.S. 2004. Trends in seasonal sea ice duration in southwestern Hudson Bay. *Arctic*, **57**: 298–304.
- Hansell, R.I.C., Malcolm, J.R., Welch, H., Jefferies, R.L., and Scott, P.A. 1998. Atmospheric change and biodiversity in the Arctic. *Environ. Monit. Assess.* **49**: 303–325. doi:10.1023/A:1005807212017.
- Hayne, D.W. 1949. Calculation of size of home range. *J. Mammal.* **30**: 1–17. doi:10.2307/1375189.
- Hill, V., and Cota, G. 2005. Spatial patterns of primary productions on the shelf, slope and basin of the western Arctic in 2002. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* **52**: 3344–3354.
- Johnson, C.J., Parker, K.L., Heard, D.C., and Gillingham, M.P. 2002. Movement parameters of ungulates and scale-specific responses to the environment. *J. Anim. Ecol.* **71**: 225–235. doi:10.1046/j.1365-2656.2002.00595.x.
- Jones, E.P., and Anderson, L.G. 1994. Northern Hudson Bay and Foxe Basin: water masses, circulation and productivity. *Atmosphere-Ocean*, **32**: 361–374.
- Jones, R.E. 1977. Movement patterns and egg distribution in cabbage butterflies. *J. Anim. Ecol.* **46**: 195–212.
- Jouventin, P., and Weimerskirch, H. 1990. Satellite tracking of wandering albatrosses. *Nature (London)*, **343**: 746–748. doi:10.1038/343746a0.
- Kareiva, P. 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecol. Monogr.* **52**: 261–282. doi:10.2307/2937331.
- Kareiva, P.M., and Shigesada, N. 1983. Analyzing insect movement as a correlated random walk. *Oecologia (Berl.)*, **56**: 234–238. doi:10.1007/BF00379695.
- Kingsley, M.C.S., and Stirling, I. 1991. Haul out behaviour of ringed and bearded seals in relation to defence against surface predators. *Can. J. Zool.* **69**: 1858–1861.
- Kingsley, M.C.S., Stirling, I., and Calvert, W. 1985. The distribution and abundance of seals in the Canadian high Arctic, 1980–82. *Can. J. Fish. Aquat. Sci.* **42**: 1189–1210.
- Knudsen, B. 1978. Time budgets of polar bears (*Ursus maritimus*) on North Twin Island, James Bay, during summer. *Can. J. Zool.* **56**: 1627–1628.
- Latour, P.B. 1981. Spatial relationships and behaviour of polar bears (*Ursus maritimus* Phipps) concentrated on land during the ice-free season of Hudson Bay. *Can. J. Zool.* **59**: 1763–1774.
- Lee, S.H., and Whitley, T.E. 2005. Primary and new production in the deep Canada Basin during summer 2002. *Polar Biol.* **28**: 190–197. doi:10.1007/s00300-004-0676-3.
- Lentfer, J.W. 1983. Alaskan polar bear movements from mark and recovery. *Arctic*, **36**: 282–288.
- Loretto, D., and Vieira, M.V. 2005. The effects of reproductive and climatic seasons on movements in the black-eared opossum (*Didelphis aurita* Wied-Neuwied, 1826). *J. Mammal.* **86**: 287–293. doi:10.1644/BEH-117.1.
- Lunn, N.J., and Stirling, I. 1985. The significance of supplemental food to polar bears during the ice-free period of Hudson Bay. *Can. J. Zool.* **63**: 2291–2297.
- Lunn, N.J., Stirling, I., and Nowicki, S.N. 1997. Distribution and abundance of ringed (*Phoca hispida*) and bearded seals (*Erig-*

- nathus barbatus*) in western Hudson Bay. *Can. J. Fish. Aquat. Sci.* **54**: 914–921. doi:10.1139/cjfas-54-4-914.
- Lunn, N.J., Stirling, I., Andriashek, D., and Richardson, E. 2004. Selection of maternity dens by female polar bears in western Hudson Bay, Canada and the effects of human disturbance. *Polar Biol.* **27**: 350–356. doi:10.1007/s00300-004-0604-6.
- MacInnes, C.D., Dunn, E.H., Rusch, D.H., Cooke, F., and Cooch, F.G. 1990. Advancement of goose nesting dates in the Hudson Bay region, 1951–1986. *Can. Field-Nat.* **104**: 295–297.
- Maslowski, W., Marble, D.C., Walczowski, W., and Semtner, A.J. 2001. On large-scale shifts in the Arctic Ocean and sea-ice conditions during 1979–98. *Ann. Glaciol.* **33**: 545–550.
- Mauritzen, M., Derocher, A.E., and Wiig, Ø. 2001. Space use strategies of female polar bears in a dynamic sea ice habitat. *Can. J. Zool.* **79**: 1704–1713. doi:10.1139/cjz-79-9-1704.
- Mauritzen, M., Belikov, S.E., Boltunov, A.N., Derocher, A.E., Hansen, E., Ims, R.A., Wiig, Ø., and Yoccoz, N. 2003a. Functional responses in polar bear habitat selection. *Oikos*, **100**: 112–124. doi:10.1034/j.1600-0706.2003.12056.x.
- Mauritzen, M., Derocher, A.E., Pavlova, O., and Wiig, Ø. 2003b. Female polar bears, *Ursus maritimus*, on the Barents Sea drift ice: walking the treadmill. *Anim. Behav.* **66**: 107–113. doi:10.1006/anbe.2003.2171.
- Maxwell, J.B. 1986. A climate overview of the Canadian inland seas. *In Canadian inland seas. Edited by I.P. Martini.* Elsevier Science Publishers, Amsterdam. pp. 79–98.
- Maxwell, R.K., Thorkelson, J., Rogers, L.L., and Brander, R.B. 1988. The field energetics of winter-dormant black bear (*Ursus americanus*) in northeastern Minnesota. *Can. J. Zool.* **66**: 2095–2103.
- McIntyre, N.E., and Wiens, J.A. 1999. Interactions between landscape structure and animal behaviour: the roles of heterogeneously distributed resources and food deprivation on movement patterns. *Landsc. Ecol.* **14**: 437–447. doi:10.1023/A:1008074407036.
- Messier, F., Ferguson, S.H., Taylor, M.K., Rosing-Asvid, A., and Born, E. 2001. Activity and movement patterns of polar bears inhabiting consolidated versus active pack ice. *Arctic*, **54**: 49–57.
- Moen, R., Pastor, J., and Cohen, Y. 1997. A spatially explicit model of moose foraging and energetics. *Ecology*, **78**: 505–521. doi:10.2307/2266026.
- Nelson, R.A., Folk, G.E., Jr., Pfeiffer, E.W., Craighead, J.J., Jonkel, C.J., and Steiger, D.L. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *In Bears — Their Biology and Management: Proceedings of the Fifth International Conference on Bear Research and Management*, Madison, Wis., 10–13 February 1980. *Edited by E.C. Meslow.* International Association for Bear Research and Management, Madison, Wis. pp. 284–290. [Available from Michael R. Pelton, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, P.O. Box 1071, Knoxville, TN 37901-1071, USA.]
- Parkinson, C.L., Cavalieri, D.J., Gloersen, P., Zwally, H.J., and Comiso, J.C. 1999. Arctic sea ice extents, areas, and trends: 1978–1996. *J. Geophys. Res.* **104**: 20837–20856.
- Portner, H.O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A., Johansen, T., Fischer, T., Knust, R., Lannig, G., Naevdal, G., Nedenes, A., Nyhammer, G., Sartoris, F.J., Serendero, I., Sirabella, P., Thorkildsen, S., and Zakhartsev, M. 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Cont. Shelf Res.* **21**: 1975–1997. doi:10.1016/S0278-4343(01)00038-3.
- Prinsenberg, S.J. 1986. The circulation pattern and current structure of Hudson Bay. *In Canadian inland seas. Edited by I.P. Martini.* Elsevier Science Publishers, Amsterdam. pp. 187–204.
- Ramsay, M.A., and Andriashek, D.S. 1986. Long distance route orientation of female polar bears (*Ursus maritimus*) in spring. *J. Zool. Ser. A*, **208**: 63–72.
- Ramsay, M.A., and Stirling, I. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *J. Zool. (Lond.)*, **214**: 601–634.
- Ramsay, M.A., and Stirling, I. 1990. Fidelity of female polar bears to winter-den sites. *J. Mammal.* **71**: 233–236. doi:10.2307/1382172.
- R Development Core Team. 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org>.
- Regehr, E., Lunn, N.J., Amstrup, S.C., and Stirling, I. 2005. Population decline of polar bears in Western Hudson Bay in relation to climatic warming. *In Abstracts of the 16th Biennial Conference on the Biology of Marine Mammals*, San Diego, California, 12–16 December 2005. Society for Marine Mammalogy, Orlando, Fla. No. 233.
- Ricklefs, R.E., Konarzewski, M., and Daan, S. 1996. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. *Am. Nat.* **147**: 1047–1071. doi:10.1086/285892.
- Roff, J.C., and Legendre, L. 1986. Physico-chemical and biological oceanography of Hudson Bay. *In Canadian inland seas. Edited by I.P. Martini.* Elsevier Science Publishers, Amsterdam. pp. 265–291.
- Saucier, F.J., Senneville, S., Prinsenberg, S., Roy, F., Smith, G., Gachon, P., Caya, D., and Laprise, R. 2004. Modelling the sea ice-ocean seasonal cycle in Hudson Bay, Foxe Basin and Hudson Strait, Canada. *Clim. Dyn.* **23**: 303–326.
- Scott, P.A., and Stirling, I. 2002. Chronology of terrestrial den use by polar bears in western Hudson Bay as indicated by tree growth anomalies. *Arctic*, **55**: 151–166.
- Smith, T.G. 1980. Polar bear predation of ringed and bearded seals in the land fast sea ice habitat. *Can. J. Zool.* **58**: 2201–2209.
- Sokal, R.R., and Rohlf, F.J. 2001. *Biometry: The principles and practice of statistics in biological research.* 3rd ed. W.H. Freeman and Company, New York.
- SPSS Inc. 2004. SPSS® for Windows. Version 13.0 [computer program]. SPSS Inc., Chicago.
- Stirling, I. 2005. Reproductive rates of ringed seals and survival of pups in northwestern Hudson Bay, Canada, 1991–2000. *Polar Biol.* **28**: 381–387. doi:10.1007/s00300-004-0700-7.
- Stirling, I., and Archibald, W.R. 1977. Aspects of predation of seals by polar bears. *J. Fish. Res. Board Can.* **34**: 1126–1129.
- Stirling, I., and Derocher, A.E. 1993. Possible impacts of climatic warming on polar bears. *Arctic*, **46**: 240–245.
- Stirling, I., and McEwan, E.H. 1975. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behaviour. *Can. J. Zool.* **53**: 1021–1027. PMID:1167176.
- Stirling, I., and Øritsland, N.A. 1995. Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. *Can. J. Fish. Aquat. Sci.* **52**: 2594–2612.
- Stirling, I., Jonkel, C., Smith, P., Robertson, R., and Cross, D. 1977. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. *Can. Wildl. Serv. Occas. Pap.* No. 33.
- Stirling, I., Calvert, W., and Andriashek, D. 1980. Population ecology studies of the polar bear in the area of southeastern Baffin Island. *Can. Wildl. Serv. Occas. Pap.* No. 44.

- Stirling, I., Spencer, C., and Andriashek, D. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol in the Canadian Arctic. *J. Wildl. Dis.* **25**: 159–168. PMID:2716095.
- Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay. *Arctic*, **52**: 294–306.
- Stirling, I., Lunn, N.J., Iacozza, J., Elliot, C., and Obbard, M. 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.
- Taylor, M.K., Akeagok, S., Andriashek, D., Barbour, W., Born, E.W., Calvert, W., Cluff, H.D., Ferguson, S., Laake, J., Rosing-Asvid, A., Stirling, I., and Messier, F. 2001. Delineating Canadian and Greenland polar bear (*Ursus maritimus*) populations by cluster analysis of movements. *Can. J. Zool.* **79**: 690–709. doi:10.1139/cjz-79-4-690.
- Thomas, D.N., and Dieckmann, G.S. 2003. Sea ice: an introduction to its physics, chemistry, biology and geology. Blackwell Science Ltd., Oxford.
- Watts, P.D., Øritsland, N.A., and Hurst, R.J. 1987. Standard metabolic rate of polar bears under simulated denning conditions. *Physiol. Zool.* **60**: 687–691.
- Zar, J. 1999. Biostatistical analysis. 4th ed. Prentice-Hall Inc., Upper Saddle River, N.J.