

ARCTIC

VOL. 70, NO. 3 (SEPTEMBER 2017) P. 319–327

<https://doi.org/10.14430/arctic4668>Polar bear (*Ursus maritimus*) Migration from Maternal Dens in Western Hudson BayMeredith Yee,¹ Jody Reimer,² Nicholas J. Lunn,³ Ron R. Togunov,¹ Nicholas W. Pilfold,^{1,4}
Alysa G. McCall^{1,5} and Andrew E. Derocher^{1,6}

(Received 30 January 2017; accepted in revised form 30 May 2017)

ABSTRACT. Migration is a common life history strategy among Arctic vertebrates, yet some of its aspects remain poorly described for some species. In February–March, post-parturient polar bears (*Ursus maritimus*) in western Hudson Bay, Canada, migrate from maternity den sites on land to the sea ice with three- to four-month-old cubs. We investigated this migration using data from 10 adult females fitted with satellite-linked global positioning system collars tracked in 2011–16. Directed movement towards the coast began on average on 1 March (range: 31 January to 23 March) and took a mean of 7.8 days to reach the coast. Bears traveled 18 to 100 km from their dens to the coast (mean = 63 km) at a mean rate of 6.7 km/d. Movements were highly directed, with an approximate northeast orientation, but did not follow the shortest path to the coast. Observed migration patterns were broadly similar to those previously documented, although mean departure date from dens was about four days earlier and mean movement rate was only 40% of that from the late 1990s. Given the sensitivity of polar bears to climate change, the phenology of denning may be a meaningful parameter for long-term monitoring.

Key words: denning; Hudson Bay; migration; orientation; polar bear; reproduction; *Ursus maritimus*

RÉSUMÉ. Parmi les vertébrés de l'Arctique, la migration constitue une stratégie de cycle biologique courante et pourtant, pour certaines espèces, certains des aspects de la migration sont toujours mal décrits. En février et en mars, les ours polaires (*Ursus maritimus*) de post-parturition de l'ouest de la baie d'Hudson, au Canada, migrent depuis leurs aires terrestres de mise bas vers la glace de mer avec leurs oursons de trois à quatre mois. Nous avons étudié cette migration en nous servant des données relatives à dix femelles adultes dotées de colliers satellitaires avec système de localisation GPS, données recueillies de 2011 à 2016. En moyenne, les déplacements dirigés vers la côte commençaient le 1^{er} mars (étendue : du 31 janvier au 23 mars) et pour se rendre jusqu'à la côte, il fallait en moyenne 7,8 jours. De leur aire de mise bas jusqu'à la côte, les ours parcouraient de 18 à 100 km (moyenne = 63 km) au taux moyen de 6,7 km/j. Les déplacements étaient fortement dirigés, avec une orientation approximative du nord-est, sans toutefois emprunter le chemin le plus court menant à la côte. Les modèles de migration observés ressemblaient beaucoup aux modèles déjà documentés, quoique la date de départ moyenne des aires de mise bas s'établissait à environ quatre jours plus tôt et que le taux de déplacement moyen ne correspondait qu'à 40 % du taux de la fin des années 1990. Compte tenu de la sensibilité des ours polaires au changement climatique, la phénologie de l'aire de mise bas pourrait constituer un paramètre significatif pour la surveillance à long terme.

Mots clés : aire de mise bas; baie d'Hudson; migration; orientation; ours polaire; reproduction; *Ursus maritimus*

Traduit pour la revue *Arctic* par Nicole Giguère.

INTRODUCTION

Migration is a strategy employed by diverse taxa as a response to predictable seasonal changes in resource availability and environmental conditions (Dingle and Drake, 2007; Ramenofsky and Wingfield, 2007; Cagnacci et al., 2016). Often driven by reproductive cycles, migration can be described as the periodic movement of an organism between feeding and reproducing grounds (Ramenofsky

and Wingfield, 2007; Anderson et al., 2013). Movement between habitats allows species to exploit favourable conditions at distinct breeding and non-breeding regions, increasing reproductive success (Dingle and Drake, 2007; Ramenofsky and Wingfield, 2007; Anderson et al., 2013). Migration distances vary across species (Jenni and Kéry, 2003), but the key defining aspect of migration is the instinctive, goal-oriented behaviour of migrants (Dingle, 2014). Because of the importance of migration to the

¹ Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

² Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta T6G 2G1, Canada

³ Wildlife Research Division, Science and Technology Branch, Environment and Climate Change Canada, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

⁴ Applied Animal Ecology, Institute for Conservation Research, San Diego Zoo Global, San Diego, California 92112, USA

⁵ Polar Bears International, Winnipeg, Manitoba R2W 5K8, Canada

⁶ Corresponding author: derocher@ualberta.ca

persistence of many species and ecosystems, understanding migration can aid conservation planning (Berger, 2004; Anderson et al., 2013).

Polar bears (*Ursus maritimus*) are migratory marine mammals with a circumpolar distribution (DeMaster and Stirling, 1981). Seasonal migration by polar bears follows an annual cycle of sea ice advance, retreat, and in some areas, ice disappearance (Mauritzen et al., 2001; Durner et al., 2009; Cherry et al., 2013). Throughout most of their range, pregnant females migrate from their primary sea ice habitat to terrestrial denning sites, where they give birth to cubs (Harington, 1968; Kolenosky and Preveit, 1983; Richardson et al., 2005). In Hudson Bay, Canada, pregnant females leave the ice in summer and subsequently give birth, nurse cubs, and overwinter in dens, subsisting on fat reserves for up to eight months (Ramsay and Dunbrack, 1986; Watts and Hansen, 1987; Ramsay and Stirling, 1988). This fasting period triggers a state of dormancy, which is associated with a marked reduction in metabolic demands (Ramsay and Dunbrack, 1986; Watts and Hansen, 1987). Females give birth to one to three cubs in November–January, after a brief active gestational period of about 60 days (Ramsay and Stirling, 1988; Derocher et al., 1992). Newborn cubs are altricial, weigh only 0.6 kg, are blind, lack significant fur (Blix and Lentfer, 1979), and must undergo substantial development before they emerge from the den and travel to the sea ice (Ramsay and Dunbrack, 1986).

Mothers and cubs-of-the-year (COYs) emerge from dens in early spring, when cubs are approximately three to four months old (Harington, 1968; Ramsay and Dunbrack, 1986). After emergence, mothers and COYs remain near the den for one to 30 days, presumably to strengthen the cubs, before returning to the ice (Hansson and Thomassen, 1983). Observed post-emergence behaviours of mothers and cubs include play, exploratory locomotion, digging, grazing, nursing, and grooming (Hansson and Thomassen, 1983; Smith et al., 2013). Mothers must budget energy according to the energetic demands of their offspring, and thus they remain in dens or restrict movements for the majority of this period (Hansson and Thomassen, 1983; Ovsvanikov, 1998; Smith et al., 2007, 2013). Adult females invest heavily in this post-emergence period because they have no access to food, and they may cease lactating after emergence if nutritional resources become depleted (Derocher and Stirling, 1996). Nursing females are therefore highly motivated to return to the sea ice to resume hunting, as starvation is among the leading causes of mortality for polar bear cubs (Derocher and Stirling, 1996).

A high-density denning area in western Hudson Bay, Canada, has been active for more than 200 years, with descriptions of denning dating back to at least 1772 (Hearne and Tyrrell, 1911; Ramsay and Stirling, 1990; Scott and Stirling, 2002). The denning ecology of the Western Hudson Bay (WH) subpopulation differs from most other subpopulations in several aspects, one of which is den distribution. In most regions across the polar bear's range, pregnant females den near the coast, with few dens more

than 16 km inland (Harington, 1968; Larsen, 1985; Stirling and Andriashek, 1992; Andersen et al., 2012). In contrast, for reasons that remain unknown, WH females den 20 to 100 km inland (Ramsay and Andriashek, 1986; Stirling and Ramsay, 1986). The substrate in which WH bears den is also unique. The females occupy earthen dens dug into the permafrost of peat banks rather than snow dens (Jonkel et al., 1972; Clark et al., 1997; Richardson et al., 2005) because snow cover in WH is insufficient at the time of parturition in mid-November to mid-December (Jonkel et al., 1972; Derocher et al., 1992; Scott and Stirling, 2002). Because of these unique behaviours, the denning ecology of adult female polar bears in WH, including den site fidelity, denning chronology, and site selection, has been well studied (Ramsay and Stirling, 1990; Scott and Stirling, 2002; Richardson et al., 2005). However, research on the migration of adult WH females as they move between dens and the sea ice is limited. Past studies examined direction of travel (Ramsay and Andriashek, 1986) and the rate and duration of travel (Lunn et al., 2004). WH has undergone significant declines in survival rates and abundance in response to changing sea ice conditions (Lunn et al., 2016) since earlier denning studies were conducted, and we hypothesized that post-denning migration might also have changed.

In this study, we used satellite telemetry to examine and describe the paths of adult female polar bears as they migrated from terrestrial dens to the Hudson Bay coast. Our objectives were to (1) determine when behaviour switches from non-directed to directed movement; (2) examine changes in tortuosity, step length, and turning angles over time as females migrate; (3) describe the mean rate of movement and total distance traveled during migration for each female; (4) compare the mean angle and distance of migration paths taken by WH females to the orientation of the geometrically shortest route to the coast; and (5) examine the degree of directionality females display during migration.

METHODS

Study Area

Most WH bears spend the ice-free period in Hudson Bay on land in northeastern Manitoba, Canada, to the south and southeast of the town of Churchill near or within Wapusk National Park (Fig. 1). The region consists of a transitional zone between boreal forest and tundra and is characterized by spruce (*Picea glauca* and *P. mariana*) and larch (*Larix laricina*), broad bog and fen peatlands, and permafrost (Ritchie, 1960).

Capture and Handling of Polar Bears

Adult female polar bears with COYs or yearlings were collared in September 2009–15 within the management

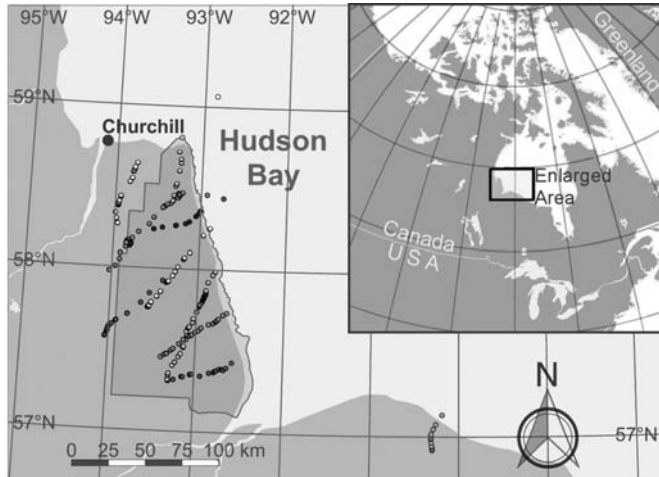


FIG. 1. Migration paths taken by 10 adult female polar bears from maternal dens to the Hudson Bay coast in Manitoba, Canada, 2011–16. Wapusk National Park is outlined and shaded.

boundaries of the WH subpopulation (Fig. 1) (IUCN/SSC Polar Bear Specialist Group, 2010). After location by helicopter, bears were tranquilized via injection of Zoletil® (Laboratories Virbac, Carros, France; Stirling et al., 1989). Bears were fitted with satellite-linked (CS Argos, Lanham, MD) global positioning system (GPS) collars (Telonics Inc., Mesa, AZ) that were programmed to record a location every 4 h and transmit these by satellite once daily. Collars did not have temperature sensors thus precluding accurate estimation of den emergence. All handling procedures were reviewed and approved annually 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).

Data Selection

Data were available from 10 adult females that denned in 2011–16 and provided 6427 telemetry locations (Fig. 1). Three were observed with COY. The family status of the other seven females was not observed; therefore, it is unknown whether these individuals reproduced successfully in the year studied. Only bear locations occurring on land during the denning and post-denning period and the first location of contact with sea ice were used. We mapped locations using QGIS version 2.16 ‘Nødebo’ (QGIS Development Team, 2016), and with the selection criteria above, retained 1477 locations. We removed an additional nine locations because they were biologically impossible (e.g., a movement rate > 120 km/d), leaving 1468 locations. R (R Core Team, 2016) was used to project the remaining coordinates (North American Datum 1983) into UTM (NAD83 Teranet Ontario Lambert, EPSG: 5321) format using the *sp* package (Bivand et al., 2013) and *rgdal* package (Bivand et al., 2015).

Movement Metrics

We used R to calculate three movement metrics: step length, straightness index, and turning angle. Step length was calculated as the straight-line distance (in m) between consecutive locations. Speed was calculated as the movement rate (km/d) between consecutive locations. As a measure of path tortuosity, we chose the straightness index, which was calculated as $\text{straightness index} = D/L$, where D = straight line distance from point A to B, and L = length of path (i.e., sum of the distances between locations 4 h apart) taken to reach B from A along the trajectory composed of recorded GPS locations (Batschelet, 1981). Possible straightness index values range from near 0 (convoluted) to 1 (straight line). We used a moving 24-hour window to determine point B for each point A. Calculated in this way, the straightness index is a reliable estimate of path efficiency for finite goal-oriented behaviour (Benhamou, 2004). Finally, we calculated the turning angle (θ) between consecutive steps, ranging from -180° to 180° . Changes in straightness index, step length, and turning angle were visualized by plotting each metric over time.

Behavioural State Switching and Cluster Analysis

To determine when females first assumed migratory movement, we used a behavioural state model that divided movement into either directional or non-directional behaviour. Using a priori knowledge on the denning ecology of polar bears, we assumed that females remained fairly inactive during the post-den emergence period before beginning migration (Hansson and Thomassen, 1983; Ovsyanikov, 1998; Smith et al., 2007, 2013). Thus, we sought the most parsimonious split in our data, hypothesizing that this would be indicative of both a shift in behavioural states and the start of migration. We used a K-means clustering analysis (Hartigan and Wong, 1979) that divided locations into two clusters on the basis of four dimensions: straightness index, step length, turning angle, and time (i.e., date and time of a location). Examination of additional splits did not yield as substantial a decrease in the sum of squares within groups for any of the bears, demonstrating that the two-cluster split was the most parsimonious. Turning angles were converted to absolute values for use in the cluster analysis, as positive and negative values were assumed to be equally representative of changes in directionality. We scaled these four dimensions using R and then used the clustering algorithm to assign each location to cluster 1 (non-directed behaviour) or cluster 2 (directed behaviour). The K-means clustering algorithm is sensitive to the random initial cluster centers. To ensure robustness, we ran the K-means clustering analysis 10 000 times (Hartigan and Wong, 1979). We defined the migration start date as the mid-point between the mean last date a bear was in cluster 1 and the mean first date it was assigned to cluster 2 from the 10 000 runs.

Mean Movement Rate and Migration Distance

The mean movement rate during migration was determined by taking the mean of the speed values occurring during this period. Migration distance was defined as the Euclidian distance between the first location of cluster 2 (i.e., start of migration) and the first point of contact with sea ice, which was measured using ArcGIS (Environmental Systems Research Institute Inc., Redlands, CA). If the first location on ice was more than 10 km from the coast for any bear, then the time and location at which the bear first reached the coast were interpolated between the last location on land and the first location on ice, and this time and location were used as the migratory endpoint.

Orientation of Migration Paths

The average direction of the path taken by each female was determined by first calculating the direction vectors of each step relative to north, then finding the mean angle formed by the vector means. Mean angles were reported from -180° to 180° , where negative and positive angles are counter-clockwise and clockwise from north (0°), respectively. The overall degree of orientation of migration was determined using angular dispersion (r), a dimensionless measure of the concentration of angles on a circular distribution. r is equal to the vector length of the mean angle (Zar, 2009). The value of r ranges from 0 to 1 and varies inversely with dispersion, so that increasingly unidirectional movement has a larger r value. A circular distribution of angles was plotted for each bear. Ideal path angles were defined as the angle relative to north formed by the shortest path to the coast from the starting location of cluster 2 behaviour, as determined using the analysis toolset in ArcGIS.

We used a one-way ANOVA to compare migration speed, straightness index, and turning angle between females. We used t-tests to examine differences between the ideal and mean angles taken during migration (one-sample t-test) and paths taken compared to the shortest distance (two-sample t-test). Straightness index, speed, and turning angles relative to the distance from the coast were examined with a Pearson correlation. Results are presented as means \pm SE. Significant differences were considered $\alpha_{\text{critical}} \leq 0.05$.

RESULTS

Clustering using our four variables indicated that on average, females displayed a directed movement on March 1 ± 4.5 days (range 31 January–23 March; Table 1). The two clusters are presented for straightness index, step length, and turning angles, with time on the x-axis (online Appendix 1: Figs. S1–S3). On average, females reached the ice on March 9 ± 4.8 days after a migration of 7.8 ± 1.3 days. The mean movement rate during migration was

6.7 ± 1.2 km/d (range 2.6–15.4 km/d; Table 1). The distance of migratory paths ranged from 18 km to 100 km; the mean migration distance was 63 ± 6.8 km ($n = 10$).

The mean angle of individual migration routes ranged from 13° to 83° , and were all oriented towards the northeast (Fig. 2). The overall mean heading for all females pooled was $44^\circ \pm 7.5^\circ$ ($n = 10$). Angular dispersion of paths varied from 0.15 to 0.95, with a mean angular dispersion of 0.55 ± 0.07 (mean of individuals). The mean difference between the angle taken and the angle of the shortest distance to the coast was -29° (95% confidence interval $\pm 19^\circ$), which was significantly different from zero ($t = 3.59$, $df = 9$, $p = 0.006$). The path that bears followed to the coast was not the shortest distance possible ($t = 3.22$, $df = 9$, $p = 0.01$).

Straightness was negatively correlated with distance to the coast ($r = -0.19$, $p < 0.01$). There was no significant correlation between step length ($r = -0.065$, $p = 0.28$) or turning angle and distance to the coast ($r = 0.060$, $p = 0.31$). Although there was no significant difference between females in mean step length ($F_{9,277} = 1.67$, $p = 0.096$), both mean straightness ($F_{9,277} = 4.61$, $p < 0.001$) and turning angle during migration ($F_{9,277} = 3.52$, $p < 0.001$) varied from individual to individual.

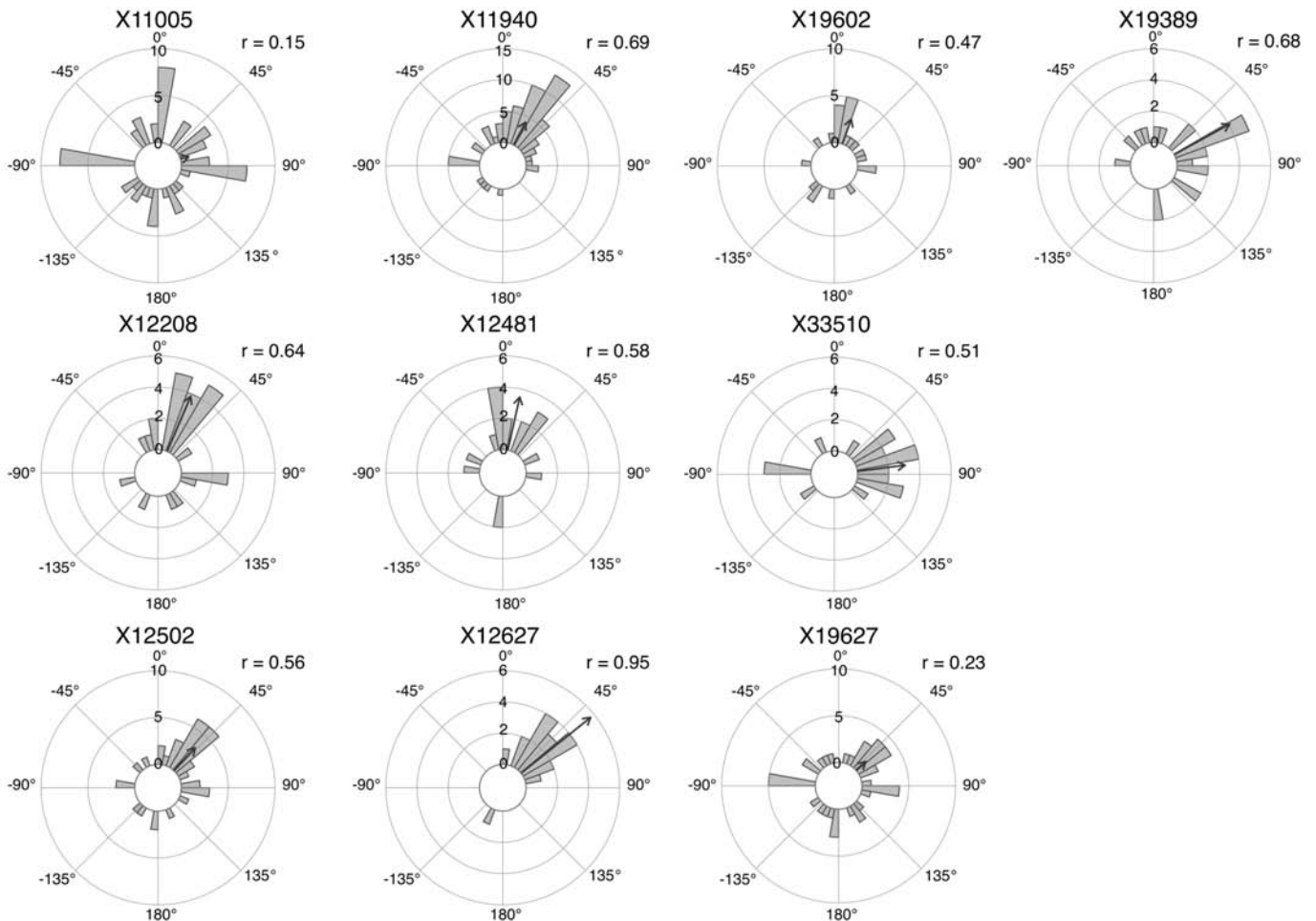
DISCUSSION

Although migration ecology is an integral part of the life history of Arctic marine mammals, it remains poorly described, which has made it difficult to detect temporal changes in migration patterns (Laidre et al., 2008). Although polar bear migration to and from land and sea ice has been studied in western Hudson Bay (Ramsay and Andriashek, 1986; Lunn et al., 2004), descriptions of movement beyond basic parameters were lacking for the post-den migration. Analyses revealed that an eight-day directed migration began in early March, and that movements became more linear closer to the coast. Females did not differ in their movement rates, but migration measured by straightness and turning angles varied among individuals. Migration routes in western Hudson Bay were oriented towards the northeast, but did not correspond with the shortest path from dens to the sea ice. Females exhibited directed behaviour during migration, although the degree of dispersion ranged from highly directed to dispersed.

Lunn et al. (2004) found that female polar bears with COYs in western Hudson Bay in the late 1990s emerged from their dens during the last week of February, and left for the sea ice on average nine days later. The timing of emergence and peri-den period would place the mean migration start date around March 5 (Lunn et al., 2004), compared to our mean of March 1. The mean travel duration (8 days) reported by Lunn et al. (2004) was the same as our finding. However, their reported migration rate of 16.8 km/d was faster than our movement rates (6.7 km/d). Differences in sampling frequency between

TABLE 1. Summary data for migration routes of WH adult female polar bears tracked by satellite telemetry from maternity dens to the Hudson Bay coast.

Bear ID	Migration start date	First day on ice	Total path distance (km)	Migration duration (days)	Mean rate of travel (km/d)
X11005	26 February 2011	14 March 2011	52	16	2.6
X11940	06 March 2012	17 March 2012	81	11	4.6
X12208	04 March 2011	15 March 2011	63	11	3.4
X12481	31 January 2016	03 February 2016	18	3	4.8
X12502	20 February 2011	28 February 2011	64	8	5.3
X12627	01 March 2016	06 March 2016	100	5	15.4
X19389	23 March 2016	29 March 2016	61	6	7.7
X19602	19 March 2012	23 March 2012	63	4	10.6
X19627	25 February 2016	05 March 2016	77	9	6.2
X33510	28 February 2014	05 March 2014	53	5	7.2

FIG. 2. Frequency of orientation of steps taken by 10 adult female polar bears from maternity dens to the coast of Hudson Bay, Manitoba, Canada, in spring 2011–16. The arrow represents the mean orientation of all steps. r is angular dispersion.

the studies may have influenced some results, but would have underestimated movement rates in Lunn et al. (2004) because of lower relocation frequency. The mean date at which females reached the coast was approximately the same as that reported by Lunn et al. (2004). Differences in the distance of dens from the coast may have been a factor, but this relationship could not be assessed.

The directional migration demonstrated by nine of the females is similar to that of family groups observed by Ramsay and Andriashek (1986), which suggests that

these females were accompanied by cubs. The non-linear migratory movement and convoluted path of the remaining female were possibly due to failed reproduction or litter loss because subsequent tracking revealed that she reproduced the following spring. Females without young may not be as nutritionally stressed as those nursing cubs, and therefore do not have the same urgency to return to the sea ice to hunt as do family units (Ramsay and Andriashek, 1986). These females have convoluted paths, with frequent pit-digging, and may display behaviour associated with recent cub

mortality (Ramsay and Andriashek, 1986). The tendency to travel northeast may correspond with the shortest path leading to sea ice with drifts suitable for ringed seal (*Pusa hispida*) birth lairs (Stirling et al., 1993). Females with COY prefer this type of habitat and may travel toward this area to reduce the need to swim, and the associated risk of hypothermia in cubs, or to avoid adult male polar bears that may prey on cubs (Blix and Lentfer, 1979; Stirling et al., 1993; Freitas et al., 2012; Pilfold et al., 2014). The hypothesis of a common migration goal in northeastern Hudson Bay was further supported by the observation that mothers with cubs in the southern Hudson Bay region, southeast of WH, tend to follow migration paths oriented towards the north (Jonkel et al., 1972; Kolenosky and Prevet, 1983). This shared, goal-oriented behaviour could be learned by females, as WH cubs will make at least one trip back to land with their mothers during the ice-free period before weaning (Ramsay and Andriashek, 1986; Ramsay and Stirling, 1988; Derocher and Stirling, 1990). If this behaviour is learned, then the cues prompting the similar orientations of migration paths remain unknown. However, polar bears have a highly refined sense of smell and hunt seals in a crosswind manner (Togunov et al., 2017). Winds in Hudson Bay are predominantly from the northwest (Togunov et al., 2017) so a crosswind movement would orient the bears to the northeast as observed by Ramsay and Andriashek (1986) and in our study. Thus, bears could be using scents carried from Hudson Bay to aid orientation.

At present, no long-term studies of female polar bear migration have been performed. Our findings, however, suggest that WH females may be beginning migration a few days earlier than they did in 1997–98. This change in timing is consistent with hypothesized consequences of increased nutritional stress for denning female bears associated with climate change (Molnár et al., 2011). Predicted changes for Hudson Bay suggest that conditions will continue to worsen for polar bears (Castro de la Guardia et al., 2013). Climatic warming is causing the sea ice in Hudson Bay to break up earlier, and in the first decade of this century, the mean date of breakup was three weeks earlier than it had been 30 years before (Stirling et al., 2004; Gagnon and Gough, 2005; Stirling and Parkinson, 2006; Parkinson, 2014; Stern and Laidre, 2016). Earlier ice breakup forces WH bears to migrate to on-land refugia sooner (Stirling and Derocher, 1993, 2012; Cherry et al., 2013). Earlier ice breakup has been associated with declines in the body condition of polar bears (Sciullo et al., 2016), as well as lower weights in pregnant females, and reduced survival for subadults and senescent adults (Stirling et al., 1999; Stirling and Parkinson, 2006; Regehr et al., 2007; Stirling and Derocher, 2012). Poorer condition among females arriving on land during the ice-free period was associated with reduced natality, and this trend is expected to continue as the date of ice breakup advances (Stirling et al., 1999; Molnár et al., 2011). For pregnant females, the continued reduction in ice access may result in earlier

implantation, gestation, and den entry, to reduce prolonged fasting and expenditure of stored energy (Molnár et al., 2011), although it is unknown whether such plasticity exists. Earlier maternity denning, however, could result in earlier emergence, increasing the probability of a phenological mismatch between the emergence of families and peak prey abundance (Molnár et al., 2011).

Denning is a sensitive component of polar bear life history, and shifts in denning and distribution related to climate change have been observed in northern Alaska (Fischbach et al., 2007) and Svalbard, Norway (Derocher et al., 2011). As climate change has influenced the distribution of maternity dens, associated changes in female polar bear migration have occurred. Climate change is a threat to migratory species because of changes in phenology and the possibility of temporal mismatch in resources (Walther et al., 2002; Durant et al., 2007; Cagnacci et al., 2016). Disruption of environmental cues from climate change can disrupt migration timing and increase the risk of phenological mismatches between migration and resource availability (e.g., Clausen and Clausen, 2013). Long-term predictions for population growth of the WH polar bear population are negative, and the core of the subpopulation, including the main denning area, experienced a decline in abundance from 1185 bears in 1987 to 806 in 2011 (Lunn et al., 2016). Given the vulnerability of polar bears to climate change (Derocher et al., 2004; Stirling and Derocher, 2012; Regehr et al., 2016), monitoring of their migration phenology may provide additional insights into population responses or lack thereof.

ACKNOWLEDGEMENTS

Funding and logistical support was provided by ArcticNet, the Canadian Association of Zoos and Aquariums, the Canadian Circumpolar Institute, the Canadian Wildlife Federation, Care for the Wild International, Environment and Climate Change Canada, EnviroNorth, Hauser Bears, the Isdell Family Foundation, Manitoba Sustainable Development, the Natural Sciences and Engineering Research Council of Canada, the Northern Science Training Program, Parks Canada Agency, Polar Bears International, Quark Expeditions, the University of Alberta, Wildlife Media Inc., and the World Wildlife Fund (Canada). We thank the Churchill Northern Studies Centre for accommodation and field support. We are thankful for the input provided by Tom S. Smith and two anonymous reviewers.

APPENDIX 1

The following figures are available in a supplementary file to the online version of this article at:

<http://arcticjournalhosting.ucalgary.ca/arctic/index.php/arctic/rt/suppFiles/4668/0>

FIG. S1. Straightness index values for cluster 1 and cluster 2 behaviour over time for 10 adult female polar bears during migration from dens to the Hudson Bay coast.

FIG. S2. Step lengths for cluster 1 and cluster 2 behaviour over time for 10 adult female polar bears during migration from dens to the Hudson Bay coast.

FIG. S3. Turning angles for cluster 1 and cluster 2 behaviour over time for 10 adult female polar bears during migration from dens to the Hudson Bay coast.

REFERENCES

- Andersen, M., Derocher, A.E., Wiig, Ø., and Aars, J. 2012. Polar bear (*Ursus maritimus*) maternity den distribution in Svalbard, Norway. *Polar Biology* 35(4):499–508.
<https://doi.org/10.1007/s00300-011-1094-y>
- Anderson, J.J., Gurarie, E., Bracis, C., Burke, B.J., and Laidre, K.L. 2013. Modeling climate change impacts on phenology and population dynamics of migratory marine species. *Ecological Modelling* 264:83–97.
<https://doi.org/10.1016/j.ecolmodel.2013.03.009>
- Batschelet, E. 1981. *Circular statistics in biology*. London: Academic Press.
- Benhamou, S. 2004. How to reliably estimate the tortuosity of an animal's path: Straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology* 229(2):209–220.
<https://doi.org/10.1016/j.jtbi.2004.03.016>
- Berger, J. 2004. The last mile: How to sustain long-distance migration in mammals. *Conservation Biology* 18(2):320–331.
<https://doi.org/10.1111/j.1523-1739.2004.00548.x>
- Bivand, R.S., Pebesma, E., and Gómez-Rubio, V. 2013. *Applied spatial data analysis with R*, 2nd ed. New York: Springer.
- Bivand, R.S., Keitt, T., and Rowlingson, B. 2015. *rgdal: Bindings for the Geospatial Data Abstraction Library*. R package version 1.1.3.
<https://cran.r-project.org/package=rgdal>
- Blix, A.S., and Lentfer, J.W. 1979. Modes of thermal protection in polar bear cubs—at birth and on emergence from the den. *American Journal of Physiology* 236(1):R67–R74.
- Cagnacci, F., Focardi, S., Ghisla, A., van Moorter, B., Merrill, E.H., Gurarie, E., Heurich, M., et al. 2016. How many routes lead to migration? Comparison of methods to assess and characterize migratory movements. *Journal of Animal Ecology* 85(1):54–68.
<https://doi.org/10.1111/1365-2656.12449>
- Castro de la Guardia, L., Derocher, A.E., Myers, P.G., Terwisscha van Scheltinga, A.D., and Lunn, N.J. 2013. Future sea ice conditions in western Hudson Bay and consequences for polar bears in the 21st century. *Global Change Biology* 19(9):2675–2687.
<https://doi.org/10.1111/gcb.12272>
- Cherry, S.G., Derocher, A.E., Thiemann, G.W., and Lunn, N.J. 2013. Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. *Journal of Animal Ecology* 82(4):912–921.
<https://doi.org/10.1111/1365-2656.12050>
- Clark, D.A., Stirling, I., and Calvert, W. 1997. Distribution, characteristics, and use of earth dens and related excavations by polar bears on the western Hudson Bay lowlands. *Arctic* 50(2):158–166.
<https://doi.org/10.14430/arctic1098>
- Clausen, K.K., and Clausen, P. 2013. Earlier Arctic springs cause phenological mismatch in long-distance migrants. *Oecologia* 173(3):1101–1112.
<https://doi.org/10.1007/s00442-013-2681-0>
- DeMaster, D.P., and Stirling, I. 1981. *Ursus maritimus*. *Mammalian Species* 145:1–7.
<https://doi.org/10.2307/3503828>
- Derocher, A.E., and Stirling, I. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. *Canadian Journal of Zoology* 68(7):1395–1403.
<https://doi.org/10.1139/z90-208>
- . 1996. Aspects of survival in juvenile polar bears. *Canadian Journal of Zoology* 74(7):1246–1252.
<https://doi.org/10.1139/z96-138>
- Derocher, A.E., Stirling, I., and Andriashek, D. 1992. Pregnancy rates and serum progesterone levels of polar bears in western Hudson Bay. *Canadian Journal of Zoology* 70(3):561–566.
<https://doi.org/10.1139/z92-084>
- Derocher, A.E., Lunn, N.J., and Stirling, I. 2004. Polar bears in a warming climate. *Integrative & Comparative Biology* 44(2):163–176.
<https://doi.org/10.1093/icb/44.2.163>
- Derocher, A.E., Andersen, M., Wiig, Ø., Aars, J., Hansen, E., and Biuw, M. 2011. Sea ice and polar bear den ecology at Hopen Island, Svalbard. *Marine Ecology Progress Series* 441:273–279.
<https://doi.org/10.3354/meps09406>
- Dingle, H. 2014. *Migration: The biology of life on the move*. Oxford and New York: Oxford University Press.
<https://doi.org/10.1093/acprof:oso/9780199640386.001.0001>
- Dingle, H., and Drake, V.A. 2007. What is migration? *BioScience* 57(2):113–121.
<https://doi.org/10.1641/B570206>
- Durant, J.M., Hjernmann, D.Ø., Ottersen, G., and Stenseth, N.C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33(3):271–283.
<https://doi.org/10.3354/cr033271>
- Durner, G.M., Douglas, D.C., Nielson, R.M., Amstrup, S.C., McDonald, T.L., Stirling, I., Mauritzen, M., et al. 2009. Predicting 21st-century polar bear habitat distribution from global climate models. *Ecological Monographs* 79(1):25–58.
<https://doi.org/10.1890/07-2089.1>
- Fischbach, A.S., Amstrup, S.C., and Douglas, D.C. 2007. Landward and eastward shift of Alaskan polar bear denning associated with recent sea ice changes. *Polar Biology* 30(11):1395–1405.
<https://doi.org/10.1007/s00300-007-0300-4>
- Freitas, C., Kovacs, K.M., Andersen, M., Aars, J., Sandven, S., Skern-Mauritzen, M., Pavlova, O., and Lydersen, C. 2012. Importance of fast ice and glacier fronts for female polar bears and their cubs during spring in Svalbard, Norway. *Marine Ecology Progress Series* 447:289–304.
<https://doi.org/10.3354/meps09516>

- Gagnon, A.S., and Gough, W.A. 2005. Trends in the dates of ice freeze-up and breakup over Hudson Bay and James Bay. *Arctic* 58(4):370–382.
<https://doi.org/10.14430/arctic451>
- Hansson, R., and Thomassen, J. 1983. Behavior of polar bears with cubs in the denning area. *Bears: Their Biology and Management* 5:246–254.
<https://doi.org/10.2307/3872544>
- Harington, C.R. 1968. Denning habits of the polar bear *Ursus maritimus*. *Canadian Wildlife Service Report Series* 5:2–30.
- Hartigan, J.A., and Wong, M.A. 1979. Algorithm AS 136: A K-means clustering algorithm. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 28(1):100–108.
<https://doi.org/10.2307/2346830>
- Hearne, S., and Tyrrell, J.B. 1911. A journey from Prince of Wales's fort in Hudson's Bay to the northern ocean, in the years 1769, 1770, 1771, 1772. Toronto: Champlain Society.
- IUCN/SSC Polar Bear Specialist Group. 2010. Polar bears: Proceedings of the 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 29 June–3 July 2009, Copenhagen, Denmark. Compiled and edited by M.E. Obbard, G.W. Thiemann, E. Peacock, and T.D. DeBruyn. Occasional Paper of the IUCN Species Survival Commission No. 43. Gland, Switzerland: International Union for Conservation of Nature.
- Jenni, L., and Kéry, M. 2003. Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society B* 270(1523):1467–1471.
<https://doi.org/10.1098/rspb.2003.2394>
- Jonkel, C.J., Kolenosky, G.B., Robertson, R.J., and Russell, R.H. 1972. Further notes on polar bear denning habits. *Bears: Their Biology and Management* 2:142–158.
<https://doi.org/10.2307/3872578>
- Kolenosky, G.B., and Prevett, J.P. 1983. Productivity and maternity denning of polar bears in Ontario. *Bears: Their Biology and Management* 5:238–245.
<https://doi.org/10.2307/3872543>
- Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, Ø., Heide-Jørgensen, M.P., and Ferguson, S.H. 2008. Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications* 18(sp2):S97–S125.
<https://doi.org/10.1890/06-0546.1>
- Larsen, T. 1985. Polar bear denning and cub production in Svalbard, Norway. *Journal of Wildlife Management* 49(2):320–326.
<https://doi.org/10.2307/3801524>
- 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 Biology* 27(6):350–356.
<https://doi.org/10.1007/s00300-004-0604-6>
- Lunn, N.J., Servanty, S., Regehr, E.V., Converse, S.J., Richardson, E., and Stirling, I. 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(5):1302–1320.
<https://doi.org/10.1890/15-1256>
- Mauritzen, M., Derocher, A.E., and Wiig, Ø. 2001. Space-use strategies of female polar bears in a dynamic sea ice habitat. *Canadian Journal of Zoology* 79(9):1704–1713.
<https://doi.org/10.1139/cjz-79-9-1704>
- Molnár, P.K., Derocher, A.E., Klanjscek, T., and Lewis, M.A. 2011. Predicting climate change impacts on polar bear litter size. *Nature Communications* 2: 186.
<https://doi.org/10.1038/ncomms1183>
- Ovsyanikov, N. 1998. Den use and social interactions of polar bears during spring in a dense denning area on Herald Island, Russia. *Ursus* 10:251–258.
- Parkinson, C.L. 2014. Spatially mapped reductions in the length of the Arctic sea ice season. *Geophysical Research Letters* 41(12):4316–4322.
<https://doi.org/10.1002/2014GL060434>
- Pilfold, N.W., Derocher, A.E., and Richardson, E. 2014. Influence of intraspecific competition on the distribution of a wide-ranging, non-territorial carnivore. *Global Ecology and Biogeography* 43(4):425–435.
<https://doi.org/10.1111/geb.12112>
- QGIS Development Team. 2016. Open source geographical information system. Open Sources Geospatial Foundation Project.
<http://www.qgis.org/>
- Ramenofsky, M., and Wingfield, J.C. 2007. Regulation of migration. *BioScience* 57(2):135–143.
<https://doi.org/10.1641/B570208>
- Ramsay, M.A., and Andriashek, D.S. 1986. Long distance route orientation of female polar bears (*Ursus maritimus*) in spring. *Journal of Zoology (London)* 208(1):63–72.
<https://doi.org/10.1111/j.1469-7998.1986.tb04709.x>
- Ramsay, M.A., and Dunbrack, R.L. 1986. Physiological constraints on life-history phenomena: The example of small bear cubs at birth. *The American Naturalist* 127(6):735–743.
<https://doi.org/10.1086/284522>
- Ramsay, M.A., and Stirling, I. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of Zoology (London)* 214(4):601–633.
<https://doi.org/10.1111/j.1469-7998.1988.tb03762.x>
- . 1990. Fidelity of female polar bears to winter-den sites. *Journal of Mammalogy* 71(2):233–236.
<https://doi.org/10.2307/1382172>
- R Core Team. 2016. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
<http://www.R-project.org>
- Regehr, E.V., Lunn, N.J., Amstrup, S.C., and Stirling, L. 2007. Effects of earlier sea ice breakup on survival and population size of polar bears in western Hudson Bay. *Journal of Wildlife Management* 71(8):2673–2683.
<https://doi.org/10.2193/2006-180>
- Regehr, E.V., Laidre, K.L., Akçakaya, H.R., Amstrup, S.C., Atwood, T.C., Lunn, N.J., Obbard, M., Stern, H., Thiemann, G.W., and Wiig, Ø. 2016. Conservation status of polar bears (*Ursus maritimus*) in relation to projected sea-ice declines. *Biology Letters* 12(12): 20160556.
<https://doi.org/10.1098/rsbl.2016.0556>

- Richardson, E., Stirling, I., and Hik, D.S. 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(6):860–870.
<https://doi.org/10.1139/z05-075>
- Ritchie, J.C. 1960. The vegetation of northern Manitoba V. Establishing the major zonation. *Arctic* 13(4):210–229.
<https://doi.org/10.14430/arctic3703>
- Sciullo, L., Thiemann, G.W., and Lunn, N.J. 2016. Comparative assessment of metrics for monitoring the body condition of polar bears in western Hudson Bay. *Journal of Zoology (London)* 300(1):45–58.
<https://doi.org/10.1111/jzo.12354>
- 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(2):151–166.
<https://doi.org/10.14430/arctic700>
- Smith, T.S., Partridge, S.T., Amstrup, S.C., and Schliebe, S. 2007. Post-den emergence behavior of polar bears (*Ursus maritimus*) in northern Alaska. *Arctic* 60(2):187–194.
<https://doi.org/10.14430/arctic243>
- Smith, T.S., Miller, J.A., and Layton, C. 2013. An improved method of documenting activity patterns of post-emergence polar bears (*Ursus maritimus*) in northern Alaska. *Arctic* 66(2):139–146.
<https://doi.org/10.14430/arctic4285>
- Stern, H.L., and Laidre, K.L. 2016. Sea-ice indicators of polar bear habitat. *The Cryosphere* 10:2027–2041.
<https://doi.org/10.5194/tc-10-2027-2016>
- Stirling, I., and Andriashek, D. 1992. Terrestrial maternity denning of polar bears in the eastern Beaufort Sea area. *Arctic* 45(4):363–366.
<https://doi.org/10.14430/arctic1415>
- Stirling, I., and Derocher, A.E. 1993. Possible impacts of climatic warming on polar bears. *Arctic* 46(3):240–245.
<https://doi.org/10.14430/arctic1348>
- . 2012. Effects of climate warming on polar bears: A review of the evidence. *Global Change Biology* 18(9):2694–2706.
<https://doi.org/10.1111/j.1365-2486.2012.02753.x>
- Stirling, I., and Parkinson, C.L. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 59(3):261–275.
<https://doi.org/10.14430/arctic312>
- Stirling, I., and Ramsay, M.A. 1986. Polar bears in Hudson Bay and Foxe Basin: Present knowledge and research opportunities. In: Martini, I.P., ed. *Canadian inland seas*, Chapter 17. Amsterdam: Elsevier Science Publishers. 341–354.
[https://doi.org/10.1016/S0422-9894\(08\)70910-3](https://doi.org/10.1016/S0422-9894(08)70910-3)
- Stirling, I., Spencer, C., and Andriashek, D. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arctic. *Journal of Wildlife Diseases* 25(2):159–168.
<https://doi.org/10.7589/0090-3558-25.2.159>
- Stirling, I., Andriashek, D., and Calvert, W. 1993. Habitat preferences of polar bears in the western Canadian Arctic in late winter and spring. *Polar Record* 29(168):13–24.
<https://doi.org/10.1017/S0032247400023172>
- Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52(3):294–306.
<https://doi.org/10.14430/arctic935>
- Stirling, I., Lunn, N.J., Iacozza, J., Elliott, 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(1):15–26.
<https://doi.org/10.14430/arctic479>
- Togunov, R.R., Derocher, A.E., and Lunn, N.J. 2017. Windscares and olfactory foraging in a large carnivore. *Scientific Reports* 7: 46332.
<https://doi.org/10.1038/srep46332>
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
<https://doi.org/10.1038/416389a>
- Watts, P.D., and Hansen, S.E. 1987. Cyclic starvation as a reproductive strategy in the polar bear. *Symposia of the Zoological Society of London* 57:305–318.
- Zar, J.H. 2009. *Biostatistical analysis*, 5th ed. Upper Saddle River, New Jersey: Prentice Hall.