

Collar temperature sensor data reveal long-term patterns in southern Beaufort Sea polar bear den distribution on pack ice and land

J. W. Olson^{1,*}, K. D. Rode², D. Eggett³, T. S. Smith¹, R. R. Wilson⁴, G. M. Durner²,
A. Fischbach², T. C. Atwood², D. C. Douglas⁵

¹Plant and Wildlife Sciences, 5049 LSB, Brigham Young University, Provo, UT 84602, USA

²U.S. Geological Survey Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA

³Center for Collaborative Research and Statistical Consulting, Department of Statistics, Brigham Young University, Provo, UT 84602, USA

⁴U.S. Fish and Wildlife Service, 1011 E Tudor Road, Anchorage, AK 99503, USA

⁵U.S. Geological Survey, Alaska Science Center, 250 Egan Drive, Juneau, AK 99801, USA

ABSTRACT: In response to a changing climate, many species alter habitat use. Polar bears *Ursus maritimus* in the southern Beaufort Sea have increasingly used land for maternal denning. To aid in detecting denning behavior, we developed an objective method to identify polar bear denning events using temperature sensor data collected by satellite-linked transmitters deployed on adult females between 1985 and 2013. We then applied this method to determine whether southern Beaufort Sea polar bears have continued to increase land denning with recent sea-ice loss and examined whether sea-ice conditions affect the distribution of dens between pack-ice and coastal substrates. Because land use in summer and autumn has also increased, we examined potential associations between summering substrate and denning substrate. Statistical process control methods applied to temperature-sensor data identified denning events with 94.5% accuracy in comparison to direct observations ($n = 73$) and 95.7% accuracy relative to subjective classifications based on temperature, location, and activity sensor data ($n = 116$). We found an increase in land-based denning during the study period. The frequency of land denning was directly related to the distance that sea ice retreated from the coast. Among females that denned, all 14 that summered on land subsequently denned there, whereas 29% of the 69 bears summering on ice denned on land. These results suggest that denning on land may continue to increase with further loss of sea ice. While the effects that den substrate have on nutrition, energetics, and reproduction are unclear, more polar bears denning onshore will likely increase human–bear interactions.

KEY WORDS: Den · Habitat use · Land use · *Ursus maritimus* · Alaska · Control charts · Sea ice

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INTRODUCTION

Arctic marine mammals are typically resilient to annual variation in their environment (Derocher et al. 2004, Harington 2008, Laidre et al. 2008); however, rapid climate warming may challenge their adaptive capacity (Moore & Huntington 2008). Dramatic changes in the timing, dynamics, composition,

and distribution of sea ice (Cavalieri & Parkinson 2012, Stroeve et al. 2012, 2014) can have demographic consequences for ice-dependent animals (Tynan & DeMaster 1997, Laidre et al. 2008, Wassmann et al. 2011). As a sea-ice dependent species, polar bears *Ursus maritimus* are sensitive to climate-induced habitat changes in the Arctic (Stirling et al. 1999, Laidre et al. 2008, Kovacs et al. 2011, Bromaghin et

al. 2015). Unlike other marine mammals that temporarily haul-out on ice, polar bears rely on sea ice as a platform for hunting, breeding, traveling, and resting (Laidre et al. 2008). Declines in body condition, reproduction, and survival have been linked to reductions in sea ice for some populations (Stirling et al. 1999, Regehr et al. 2007, 2010, Rode et al. 2010a), whereas there have been no apparent population-level effects for others (Stirling et al. 2011, Peacock et al. 2013, Rode et al. 2014). The negative effects of sea-ice loss have generally been attributed to reduced access to prey, but loss of sea ice may also affect polar bear reproduction by altering access to or quality of maternal denning habitat (Derocher et al. 2011, Stirling & Derocher 2012).

Maternal denning is critical to polar bear population dynamics. Unlike other ursids, only pregnant female polar bears den during winter months, giving birth in dens excavated in snowdrifts. Dens provide warmth and protection in which to give birth to altricial neonates (Blix & Lentfer 1979, Lentfer & Hensel 1980, Amstrup 1993). While some polar bears in the Beaufort and Chukchi Seas den on drifting pack ice (Lentfer 1975, Amstrup & Gardner 1994), bears in most of their range den on land or on land-fast ice (Ramsay & Stirling 1990, Durner et al. 2003). Dens on sea ice require a substrate that remains stable throughout the winter (Fischbach et al. 2007), whereas access to terrestrial denning habitat requires that ice freezes or drifts in time for bears to either walk or swim to shore (Derocher et al. 2004). Thus, declines in sea ice, particularly north of Eurasia and Alaska where ice retreats northward away from land during the summer and autumn (Amstrup et al. 2008), may affect the quality of sea ice for denning and the ability of bears to access land in time for denning (Derocher et al. 2004, 2011, Bergen et al. 2007, Stirling & Derocher 2012).

In the southern Beaufort Sea (SB), 67% of maternal denning occurred primarily on the sea ice in the 1980s and 1990s (Lentfer & Hensel 1980, Amstrup & Gardner 1994). Between 1985 and 2005, maternal denning substrates shifted such that by 2005, 67% of maternal denning occurred on land (Fischbach et al. 2007). This change was concurrent with declines in multi-year ice, which could have affected sea-ice stability for denning (Fischbach et al. 2007). Thus, by increasingly relying on land for denning, SB polar bears now face the potential challenge of accessing land to den as sea ice retreats farther, and for a longer period, from the coast (Bergen et al. 2007). Increases in land-based denning have occurred simultaneous to increases in summer and

autumn land use in the SB, which has been linked to reduction in the extent of summer pack ice (Schliebe et al. 2008, Atwood et al. 2016, Pongracz & Derocher 2016). Females that summer onshore (i.e. spend a portion of time onshore during summer or autumn months when ice is reduced) may have a greater propensity to den onshore since den entry has typically occurred in November (Amstrup & Gardner 1994) shortly after the August to October timeframe when bears summer onshore (Atwood et al. 2016). Land-fast ice begins to form in October or November (Mahoney et al. 2012), corresponding with bears' departure from shore, so bears that summer onshore may or may not return to the sea ice before denning. In the adjacent Chukchi Sea sub-population, pregnant females often summered and subsequently denned onshore, increasing their total time on land by 30 d between the periods 1985–1996 and 2008–2013, a response that was related to sea-ice conditions (Rode et al. 2015).

Understanding patterns of terrestrial denning behavior has important implications for managing bear-human interactions, both for human safety and minimization of potential den disturbance, and in further understanding the changing ecology of Arctic regions. Increased denning onshore may increase the risk of human disturbance (Amstrup 1993, Linnell et al. 2000) because oil and gas development, infrastructure, and 3 communities (i.e. Barrow, Nuiqsut, and Kaktovik) occur along the SB coast of Alaska. Further, while there is some evidence to suggest that denning substrate does not affect cub production (Amstrup & Gardner 1994), observed and projected declines in snow depth on sea ice (Warren et al. 1999, Hezel et al. 2012) and changes in sea-ice conditions in recent years could affect denning phenology in these 2 habitats. For example, stable, multi-year ice occurs at more northerly areas than it has in the past such that access and timing of sea-ice denning may have changed. Because conditions differ for denning on land and sea-ice habitats, where a bear dens could affect the dates of den commencement and completion (Amstrup & Gardner 1994). Cub size is known to be related to den phenology (i.e. fewer days in the den results in smaller cubs; Robbins et al. 2012) and is directly related to survival (Derocher & Stirling 1996).

Because polar bears occupy vast and remote habitats and often create maternity dens on the sea ice, which drifts with prevailing wind and ocean currents, identification of maternal denning behavior via direct observation and satellite location data is challenging. Fischbach et al. (2007) successfully identi-

fied maternal denning using satellite-collar temperature and activity sensor data as well as location frequency and quality. However, this method required that denning signatures be identified by qualitative examination of seasonal sensor and location quality plots. As a first objective of our research, we sought to create an algorithm that systematically used temperature sensor data alone, collected in collars deployed on adult females between 1985 and 2013, as an efficient tool for remotely identifying maternal denning distribution and behavior.

To improve our understanding of trends in den substrate choice relative to a period of sea-ice decline, we then applied the results of our algorithm to determine whether the increase in land denning found by Fischbach et al. (2007) continued during 8 additional years (2006–2013). We also addressed the following questions: (1) Is the frequency of maternal denning on land continuing to increase? (2) Is the frequency of land-based maternal denning related to sea-ice conditions? (3) Is increased land use during summer related to increases in terrestrial denning, i.e. do bears that summer on shore also den there?

MATERIALS AND METHODS

Study area

The SB subpopulation of polar bears comprises approximately 900 individuals (90% confidence interval: 606–1212) (Bromaghin et al. 2015) and has a range that extends from Icy Cape, Alaska, USA (159°W), to Tuktoyaktuk, Northwest Territories, Canada (133°W), with a northern boundary of approximately 74° (Fig. 1). This subpopulation experienced a 25 to 50% decline in abundance from 2004 through 2006 due to low survival rates that have subsequently increased from 2007 to 2009 for most sex and age classes (Bromaghin et al. 2015). The Beaufort Sea is nearly 100% ice-covered from November to June. Since 1996, declines in summer sea ice have caused the ice edge to retreat north beyond the narrow (~100 km) continental shelf and into the deep waters of the Canada Basin (Pagano et al. 2012). Most SB bears follow the retreating ice north, while a proportion (17.5% in 2000–2013, Atwood et al. 2016; 27% in 2007–2010, Pongracz & Derocher 2016) of the subpopulation moves to land.

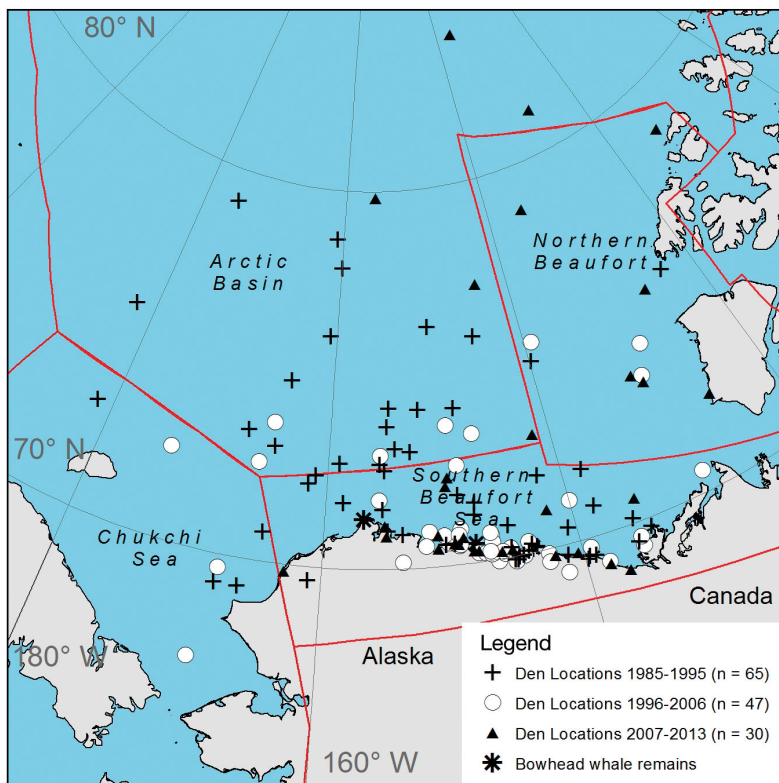


Fig. 1. Denning locations of female polar bears *Ursus maritimus* in the southern Beaufort Sea between 1985 and 2013. Denning was identified based on temperature data collected by satellite radio collars

Polar bear capture and collaring

Polar bears were captured and released on the sea ice during spring (mid-March to mid-May) and occasionally during late summer and autumn (August to November) in the Alaska portion of the SB by the US Geological Survey (USGS) during most years between 1985 and 2013. Polar bears were located from a helicopter and immobilized with a rapid-injection dart (Palmer Cap-Chur Equipment) containing zolazepam-tiletamine (Telazol®) (Stirling et al. 1989) from 1987 to 2013, or Sernylan, M-99, or phencyclidine before 1987. Spring captures overlapped with timing of den emergence, but generally lasted beyond the period when all females would have emerged from dens (i.e. early May, Amstrup & Gardner 1994). Platform-transmittal-terminal satellite radio collars (Telonics), which included a thermistor for measuring temperature, were deployed on a subset of adult females between 1985 and 2013, except during 1993 to

1997 and in 2010. Argos (www.argos-system.org) or global positioning system (GPS) locations were estimated every hour to every 5 d, and temperature data were recorded every 20 min to once per 4 to 7 h duty cycle (mean number of temperature observations per day of data acquisition = 5.5 ± 0.03 SE). Duty cycles (i.e. the period when data were transmitted via satellite) ranged from daily to every 5 d. Some individuals provided data for more than 1 yr. Though warmed by the body temperature of a bear, temperature sensors generally track ambient conditions (Fischbach et al. 2007). When females enter maternity dens, the ambient temperature is higher than ambient temperatures outside of the den (Fischbach et al. 2007). A denning bear's collar typically records temperatures more than 20°C higher than a non-denning bear, which is far greater than the nominal error of the temperature sensor ($\pm 2.5^\circ\text{C}$) reported by the manufacturer (Fischbach et al. 2007).

Our analysis included only individual polar bears whose satellite location data allowed us to assign them to the SB subpopulation (Fig. 1; Obbard et al. 2010). A bear was assigned to the SB if >50% of its locations occurred within the SB subpopulation boundaries or if >50% of a bear's locations occurred in the area identified as the Arctic Basin subpopulation (Fig. 1) and the remainder of its locations occurred within the SB boundaries.

Classifying denning behavior using sensor temperature

We used statistical process control methods (i.e. control charts; Shewart 1931) to identify maternal denning behavior in polar bears based on telemetered temperature data. Commonly used in industrial manufacturing and quality control, control charts quantify the underlying variation in a stochastic process using upper and lower control limits around the expected mean. Observations beyond these limits indicate the potential presence of a special cause of variation (Montgomery 2001). Individual observations of the variable of interest are binned into subgroups and plotted along the y-axis, while the x-axis represents a time scale or sample number (Fig. 2; Morrison 2008).

We quantified the routine variation in the temperatures of non-denning bears ($n = 109$) that were previously identified by Fischbach et al. (2007) in order to identify extended periods of warmth indicative of denning animals. The expected mean and control limits were derived using a subset of temperature

records from individual female polar bears in which denning status (i.e. denning or non-denning) had been assigned qualitatively using a combination of activity, temperature, and location quality data ($n = 113$ bear-winters; Fischbach et al. 2007). Each record (hereafter referred to as a 'bear-winter') spanned from 1 July to 30 June, centering on the fall and winter denning period in order to capture potential maternal denning. We smoothed the daily averages of non-denning bear temperatures using a locally weighted scatterplot smoothing (i.e. LOESS; span = 0.35) (Cleveland 1979) to create an expected seasonal mean for our control charts. Because individual temperature profiles varied substantially from this expected average, we adjusted the starting intercept of the expected seasonal mean for each bear-winter using the mean of the first 5 temperature observations in an individual bear's temperature dataset. This altered the actual temperature but maintained the seasonal variation typical of non-denning bears. If the first recorded temperatures occurred during typical denning months (October–April), the mean of the final 5 observations was used rather than the first 5 observations to adjust the starting intercept for a bear-winter.

While control charts commonly use a 3-sigma (3 standard deviations) distance to define upper and lower control limits, these limits may be adjusted to influence the sensitivity of detection (Morrison 2008). We used an upper control limit of 1.8-sigma, which provided a standard deviation of 9°C for all bear-winters. Setting the control limit to 1.8-sigma provided the temperature limits that most accurately distinguished between denning and non-denning bear-winters ($n = 418$) as previously determined by Fischbach et al. (2007). Temperature observations were plotted as daily means in control charts because they are more useful in indicating a long-term sustained behavior like denning (Fischbach et al. 2007).

The number of mean daily temperature observations in a given bear-winter varied greatly over time due to variable collar programming and signal degradation. As a result, we based den status classifications on the number of days a bear's temperature remained above the upper control limit. Bear temperatures were considered above or below control limits when >1 consecutive mean daily temperature rose above or below the upper control limit, respectively. We used temperatures from previously identified denning bears (Fischbach et al. 2007) to calculate a minimum number of days a bear's temperature remained above the upper control limit to be classified as denning. Bear-winters that met the minimum duration of 34 d

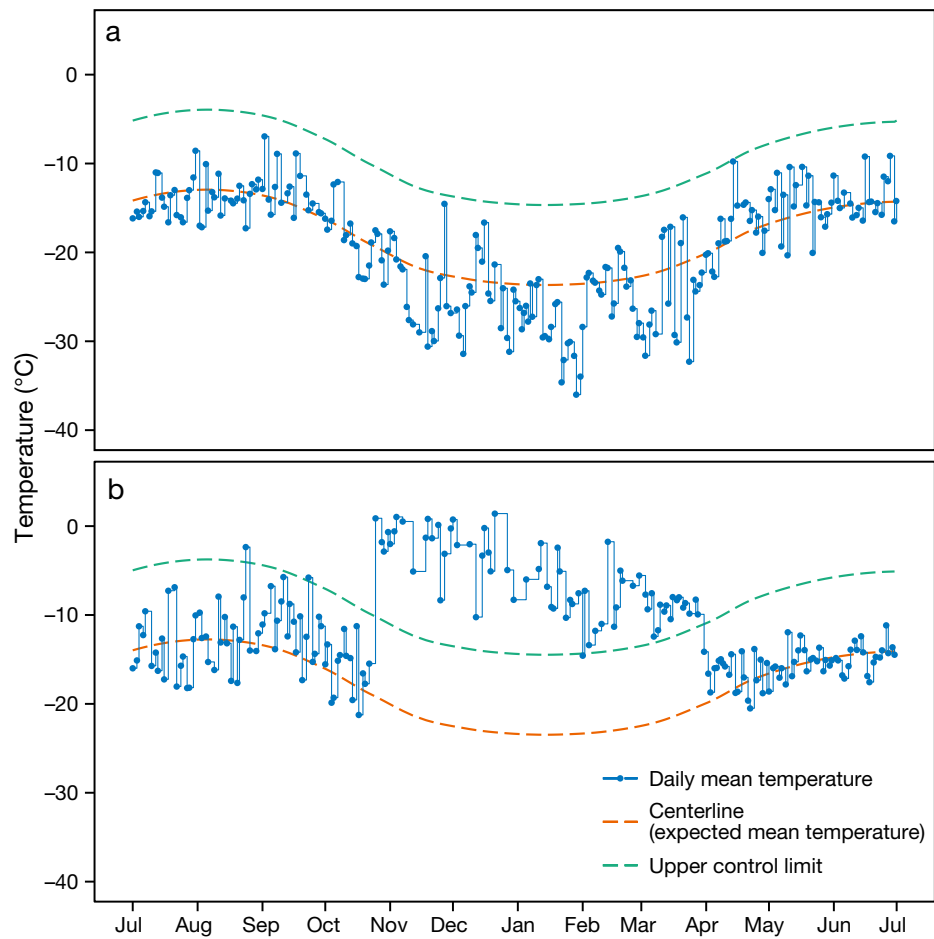


Fig. 2. Example control charts of temperatures from both (a) non-denning and (b) denning female polar bears *Ursus maritimus* in the southern Beaufort Sea. Daily mean temperatures were measured by thermistors on-board satellite collars. Expected mean temperatures and upper control limits were calculated using data from 109 non-denning females. Consecutive observations above the upper control line with a duration of >34 d were considered denning events

but had <6 mean daily temperature observations were considered to have insufficient data for classification. We also excluded bear-winters that had no observations during denning months (October–April), and those in which observations ended before 1 January unless denning status was identified before 1 January. Bear deaths or shucking of collars were determined from location and activity sensor data (Fischbach et al. 2007) and were excluded from the dataset. Of the dataset including 360 bear-winters, 117 and 113 were previously classified by Fischbach et al. (2007) as denning and non-denning, respectively, and the remaining 130 had not been previously classified. Thus, the algorithm was trained using about half of the denning bears in the dataset.

Validation of den classification

We validated our classifications of denning behavior using direct observations of denning made via VHF radio tracking or of females with dependent

cubs during annual spring capture efforts. We further compared our classifications to those made via qualitative classification informed by activity and temperature sensor data and location quality (Fischbach et al. 2007), although this was not an independent comparison since classifications from Fischbach et al. (2007) were used to develop our methodology.

Determining substrate use: sea ice versus land

Denning substrate was determined using telemetered location estimates, estimated by either Argos, an onboard GPS derived, or via aerial VHF telemetry. Argos locations were accompanied with location accuracy codes ranging from <250 to >1500 m (see www.argos-system.org/web/en/78-faq.php#faq-theme-55). These location data were filtered to remove implausible locations using the Douglas Argos-Filter algorithm (Douglas et al. 2012), which retained all standard quality class locations (classes 3, 2, and 1), rejected all class Z locations, and retained auxil-

ary class locations (0, A, and B) if they were corroborated by a consecutive location within 10 km (maxredun = 10), or if movement rates were $<10 \text{ km h}^{-1}$ (minrate = 10) and turning angles were not extremely acute such that bears were immediately returning to a location where they had just been. Accuracy estimates for Argos locations were provided by Collecte Localisation Satellites, the operator of the Argos satellite data collection system (i.e. 3: $<250 \text{ m}$, 2: $250\text{--}500 \text{ m}$, 1: $500\text{--}1500 \text{ m}$, 0: 1500 m ; www.argos-system.org/manual/). Because location accuracies were not provided for auxiliary location classes A or B, we prescribed conservative location accuracies of 5000 and 10000 m, respectively. Some collars deployed between 2004 and 2008 and all collars deployed between 2009 and 2014 transmitted GPS-derived location estimates. We assigned locations obtained from GPS collars an accuracy of 30 m (Frair et al. 2010).

Because the physical properties of polar bear dens often attenuate transmission, location data were frequently unavailable or of low quality during the denning period. If at least 1 observed location at the start of, during, or at the end of the denning period identified via temperature data occurred on land and locations preceding or subsequent to denning demonstrated a trajectory to or from that location, it was assumed that the den occurred on land. We conducted the analysis both excluding and including 8 bear-winters in which dens were identified as occurring on land-fast ice ($n = 8$ of 142 bear-winters). Previous analyses lumped dens on land-fast ice with land-based dens when reporting land and ice denning (Amstrup & Gardner 1994), so we analyzed the data including this lumping of land-fast ice dens with land-based dens and excluding them from the analysis altogether. We report the statistical results excluding dens on land-fast ice followed by a comparison of those results when dens on land-fast ice were included.

Substrate use before denning was determined based on the number of days bears spent onshore during the months of August to October. Bears were classified as having summered on land if they spent ≥ 25 consecutive days onshore anytime between July and October, a timespan intended to identify longer durations rather than shorter visits to shore. Because location data were collected at varying intervals and with varying location accuracies, we modeled daily locations based on a continuous time correlated random walk (crawl) model (Johnson et al. 2008, Johnson 2013) that had been validated for estimating polar bear land use in a previous study (Rode et al.

2015). We then used these modeled daily locations to determine the number of days a bear spent onshore before denning. Locations were projected to a Cartesian coordinate system prior to the crawl modeling to reduce biases inherent to angular coordinates near the pole. See Rode et al. (2015) for parameterization and validation of the crawl modeling of daily locations.

A bear was classified as being on land if its predicted location was within 5 km of land as identified by the Global Self-consistent, Hierarchical, High-resolution, Geographic Database (GSHHG version 2.3.4; www.soest.hawaii.edu/pwessel/gshhg/). Because transmissions cannot be propagated when a bear is in the water because the antenna is submerged (Pagano et al. 2012), it is unlikely that locations received within 5 km on shore occurred in water. The 5 km buffer was used to account for low accuracy of some locations. Our 5 km buffer might have resulted in some bears that were on ice being classified as on land but this was less likely to occur during the August to October timeframe in which we analyzed land use because land-fast ice is largely absent during this period (Mahoney et al. 2012) and the pack ice has generally receded far north of the coast, or if present near shore is too thin to support a bear. Thus, bears within 5 km of the coast during this time were likely to have been on land.

Changes over time and relationships with sea ice

We compared the frequency of denning on land and fast ice versus pack ice in 2 ways: (1) via a binomial regression with year as a continuous variable and (2) across 3 periods: 1985–1995, 1996–2006, and 2007–2013. These periods were chosen due to their use in previous studies of denning and habitat changes (Fischbach et al. 2007, Durner et al. 2009), and to allow for non-linear changes among periods. Additionally, during these time intervals notable declines in multi-year ice (Maslanik et al. 2011) and increases in annual melt season durations (Stroeve et al. 2014) have occurred across the Arctic. Individual bear-winters were assigned to a period by the spring year in which den emergence was presumed to have occurred.

We tested for potential relationships between den substrate and sea-ice conditions during the prior autumn. Although most female polar bears do not enter dens until after the September sea-ice minimum, conditions during the minimum are likely to reflect the timing of ice returning to coastal regions

and the accessibility of coastal regions for denning. We evaluated the effect of 2 measures of the daily mean distance (hereafter referred to as 'distance') from the coast to the edge of the pack ice defined at the 15% and the 50% sea-ice concentration thresholds, averaged across all days during the month of September (the month of the sea-ice minimum) within the SB subpopulation boundaries. Mean daily distance was calculated as the average of distances to the sea ice for each of the 25 km pixels along the coast. The area in which sea-ice conditions were measured is described and illustrated in Rode et al. (2014). Ice concentrations were determined from 25 × 25 km resolution passive microwave satellite imagery (Cavalieri et al. 1996). These concentrations were chosen since polar bears often select for ~50% sea-ice concentration during summer (Durner et al. 2009), and concentrations of 15% are considered edge habitats infrequently used by polar bears (Durner et al. 2006b, Pagano et al. 2012, Cherry et al. 2013, Laidre et al. 2015).

Statistical analysis

We programmed our control chart algorithm using SAS/STAT[®] software (Version 9.4), while all statistical analyses were performed using program R version 3.0.3 (R Development Core Team 2014). We used the `glmer` function in the R 'lme4' (Bates et al. 2015) package to perform mixed effects, binary, logistic models to test hypotheses involving the effects of distance to pack ice on den substrate choice (i.e. land versus sea-ice denning) and to compare den substrate among study periods. Den substrate was included as a binary dependent variable (0 for land den, 1 for ice den), and distance to ice and study period were included as a continuous covariate and categorical fixed effect, respectively, in separate analyses. Pairwise comparisons of den substrate by period were made using least-squares means (R package 'lsmeans;' Lenth 2016). We included individual animals as a random effect in mixed models to account for repeated denning observations from individual bears. We used an analysis of variance *F*-test (ANOVA) with a Tukey post hoc test to examine differences among periods in the distance from the coastline to sea ice at 15 and 50% concentrations during the September before denning. A Cook's distance test was conducted to identify potential outliers and the influence of those outliers on observed relationships. Relationships between summer location and den substrate were analyzed using a chi-squared test.

RESULTS

We applied our denning behavior classification algorithm to 360 bear-winters for which temperature-sensor data were collected from polar bears instrumented with radio collars in the SB from 1985 to 2013 (Fig. 2). These data included 183 unique individuals, of which 99 individuals were telemetered for >1 bear-winter (mean = 2.7 ± 1.1). We culled 69 bear-winters due to insufficient data. Of the remaining 291 bear-winter records, we classified 151 as denning and 140 as non-denning based on our algorithm. Of our denning behavior classifications, 73 had field observations of denning or family groups. Of those, 94.5% of classifications made using the temperature algorithm agreed with independent observations. Additionally, of 116 denning and 102 non-denning classifications, 95.7 and 97.1%, respectively, agreed with the classifications by Fischbach et al. (2007). Only the 151 bear-winters (113 unique individuals) classified as denning using the temperature algorithm were used in analysis of den distribution.

Den substrate trends among study periods

Of 134 bear-winters in which we determined den substrate, 54.5% (73) occurred on pack ice and 45.5% (61) were located within the 5 km buffer of land (Fig. 1). Land denning increased across years; however, this trend was only marginally significant ($\beta = 0.04 \pm 0.02$ SE; $p = 0.055$). Land denning constituted 34.4% (21 of 61) of dens in 1985–1995, 54.6% (24 of 44) in 1996–2006, and 55.2% (16 of 29) in 2007–2013. There was no difference in the probability of denning on land between 1996–2006 and 2007–2013 ($\beta = 0.31 \pm 0.73$, $p = 0.67$). The difference in the probability of denning on land between 1985–1995 and 1996–2006 ($\beta = 1.04 \pm 0.60$) and 1985–1995 and 2007–2013 ($\beta = 1.35 \pm 0.78$) was marginally significant at $p = 0.08$. When 8 dens that occurred on land-fast ice were included in this analysis as land-based dens, there was no difference between any 2 time periods ($p > 0.23$) and no trend with year ($\beta = 0.03 \pm 0.02$ SE; $p = 0.098$).

Den substrate in relation to sea-ice availability

During the 3 periods, the distance to ice from the coast in September increased (15% concentration sea ice: $F_{2,26} = 13.2$, $p < 0.0001$; 50% concentration

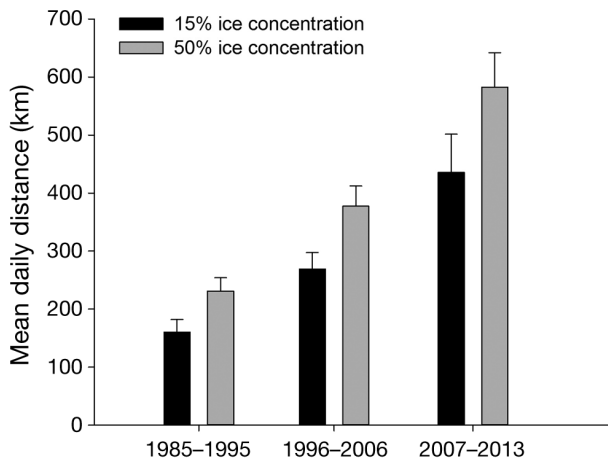


Fig. 3. Mean daily distance between sea ice and the southern Beaufort Sea coast in September during 3 periods. Bars indicate SE

sea ice: $F_{2,26} = 20.4$, $p < 0.0001$; Fig. 3). The mean distance to 50% sea-ice concentration in September increased by 146.4 ± 48.5 km between 1985–1995 and 1996–2006 (Tukey test; $p = 0.02$), and by 205.0 ± 55.0 km between 1996–2006 and 2007–2013 ($p = 0.003$), with a total increase of 351.4 ± 55.0 km between 1985–1995 and 2007–2013 ($p < 0.0001$). The distance to 15% sea-ice concentration did not increase between 1985–1995 and 1996–2006 ($p = 0.07$), but did increase by 166.5 ± 53.7 km between 1996–2006 and 2007–2013 ($p = 0.01$), for a total increase of 275.3 ± 53.7 km between 1985–1995 and 2007–2013 ($p < 0.0001$).

Across all years, 1985–2013, land denning was not more common as the distance between the coast and sea ice increased for 15% concentration ($\beta = 0.002 \pm 0.001$, $p = 0.15$), but was more common for 50% concentration ($\beta = 0.002 \pm 0.001$, $p = 0.05$). However, in 2012 the mean distance to 15 and 50% concentration ice was 773 and 866 km, respectively, which was 209 and 307 km farther offshore, respectively, than any previous year. The only 2 dens in 2012 occurred on the sea ice, and these values had a substantive influence on the results and were identified as outliers (Cook's distance = 0.081; cutoff = $[4/n]$ or 0.027). By excluding 2012, land denning increased with increasing distance between the coast and 15% sea-ice concentration ($\beta = 0.004 \pm 0.002$, $p = 0.02$; Fig. 4a) and increasing distance between the coast and 50% sea-ice concentration ($\beta = 0.003 \pm 0.001$, $p < 0.001$; Fig. 4b). For every 100 km increase in the distance to 50% sea-ice concentration, frequency of denning on land increased on average by 32% (95% CI = 8–56%). For every 100 km increase in the distance to

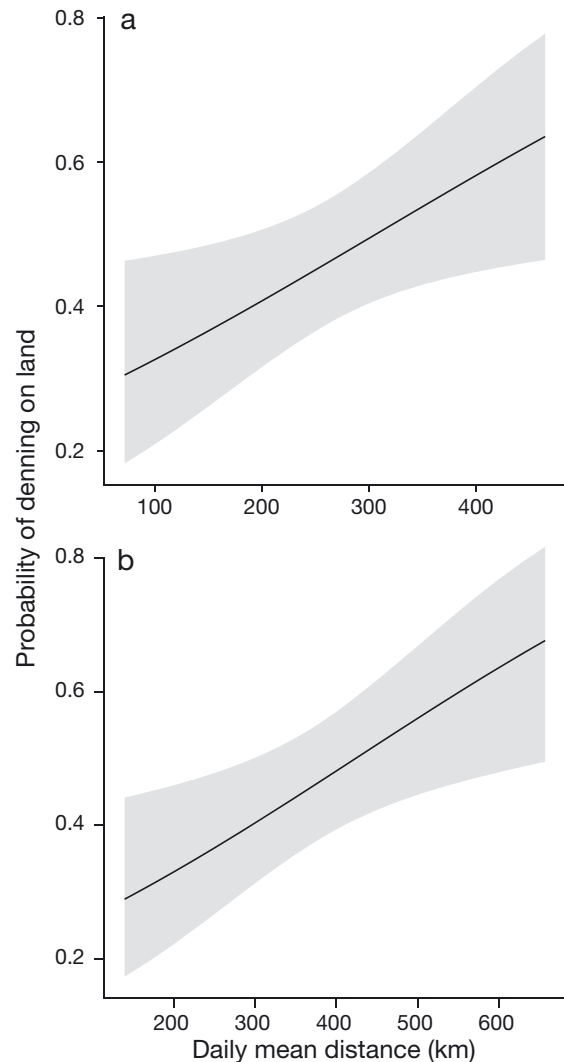


Fig. 4. Relationship between the probability of female polar bears *Ursus maritimus* denning on land and the mean distance between the Beaufort Sea coast and sea ice of (a) 15% and (b) 50% concentrations for 1985–2013 as determined from a binary logistic regression. This figure excludes 8 instances in which bear dens were identified as occurring on land-fast ice, but the statistical results were similar to these plots when those dens were categorized as land-based dens. These plots exclude outlier data from 2012 in which the ice retreated 308 km farther offshore than in any previous year and the 2 denning bears denned on the sea ice, contrary to the pattern of more bears denning onshore as the distance increased. Shaded area represents the 95% confidence interval

15% sea-ice concentration, the probability of denning on land increased by approximately 35% (95% CI = 6–66%). These results were similar when including dens on land-fast ice as land-based dens. However, we were unable to account for repeated measures from individuals due to convergence issues.

Den substrate and summer location

There was a significant relationship between the substrate used by a bear before denning and the den substrate ($\chi^2 = 21.4$, $df = 1$, $p < 0.001$). All bears that entered dens in a year in which they spent ≥ 25 d on land before den entrance denned on land ($n = 14$). Among pregnant bears that did not spend at least 25 d on land before denning, only 29% denned on land while 71% remained on sea ice to den ($n = 69$). We were not able to account for repeated measures from individuals by using generalized linear models due to the lack of variation in the den substrate of bears that summered on land (i.e. all bears that summered on land denned on land).

A total of 29 individuals were tracked to a particular den substrate during more than 1 denning season. Of these, 21 bears were faithful to their original den substrate, while the remaining 8 individuals used a different substrate during at least 1 denning season; 5 bears transitioned from sea ice to land dens, while 3 bears changed from land to sea ice for maternal denning. Of those individuals that remained faithful to their original denning substrate, 11 were faithful to land and 10 maintained denning on pack ice.

DISCUSSION

The distance between retreating pack ice and coastal denning habitat, and summer substrate use appear to be important factors determining maternal den substrate use in the SB. Stirling & Derocher (2012) suggested that increasing distances of sea ice from coastal areas, as indicated by the distance of sea-ice retreat off the SB coastline, could preclude polar bears from reaching land-based denning areas. In our study, we found that bears that spent substantial time (≥ 25 d) on land before denning were also highly likely to den on land, whereas only 29% of those that remained on pack ice during the sea-ice minimum came to land for denning. The much lower proportion of land-based maternal denning by denning females that summered on the sea ice (29%) compared to those that summered onshore (100%) suggests that some polar bears in this region may be precluded from reaching land for denning by the distance between the summer sea ice and land. Our observation that the 2 bears that denned following the summer when the distance to sea ice was over 200 km farther from the coast than any preceding year denned on the sea ice further supports the fact that there may be a threshold at which returning to

land to den may be precluded. However, land-based denning for all other years increased amongst the SB bears as the distance between sea ice and land increased, suggesting that there may now be some benefit to denning on shore versus on sea ice. For example, the proportion of bears summering on shore is much lower (17.5% in 2000–2013; Atwood et al. 2016) than the proportion denning there (45.5%). This suggests that the majority of bears denning onshore come from the sea ice, and that there is some motivation for bears that are on the sea ice to come to den onshore despite increasing distances between summer sea ice and land in the late summer and autumn.

The role of sea-ice availability and characteristics in determining den distribution likely varies by region due to differences in the availability of terrestrial denning habitat and the seasonal distribution of sea ice. The SB subpopulation is unique in that historically, the majority of bears have denned on the sea ice. Stirling & Andriashek (1992) suggested that SB bears may have adopted this behavior due to onshore harvest pressure. However, hunting practices changed following the Inuvialuit-Inupiat Polar Bear Management Agreement of 1988 to exclude hunting of females with cubs at den sites. Thus, within the timeframe of our study, changes in hunting practices may not explain changes in den substrate use. In all other populations, including the adjacent Chukchi Sea subpopulation, bears primarily den on land (Rode et al. 2015). In western Hudson Bay, northward shifts in maternal denning may have been in response to changing sea-ice distributions (Ramsay & Stirling 1990). Similarly, at Hopen Island near the southern portion of the Svalbard Archipelago in the Barents Sea, later arrival of sea ice has resulted in a lower number of dens; and in years with very late freeze-up, bears did not reach the island in time for denning (Derocher et al. 2011). Changes in den distribution have also occurred in Baffin Bay, where bears are denning at higher elevations and on steeper slopes than they have in the past, presumably as a result of changes in snow availability (Escajeda 2016). Thus, while changes in den distribution may be a somewhat common response to sea-ice loss across subpopulations, increased land-based denning may be unique to the SB subpopulation.

The weak significance of the difference in den substrate between time periods (i.e. $p = 0.08$) and the borderline significance ($p = 0.055$) of the relationship between year and den substrate may be a result of annual variation in sea-ice conditions. The relationship between den substrate and ice conditions was

stronger than the relationship across years, suggesting that choice of substrate is tracking the long-term trend as well as the annual variation that occurs under sea-ice conditions. The lack of a difference in the frequency of land-based denning between 1996–2006 and 2007–2013 indicates that the initial increase in land-based denning that occurred sometime between the 1980s and early 2000s (Fischbach et al. 2007) has slowed and may further explain why the relationship between year and denning substrate was weak.

The nutritional implications of pregnant polar bears summering and denning on land in the SB are unclear. Declines in body condition and reproduction have been observed and associated with sea-ice conditions in the SB, but the exact nutritional mechanism causing those declines has not been identified (Cherry et al. 2009, Rode et al. 2010a). In most locations throughout their range, polar bears summering onshore are unable to meet their energetic requirements by foraging on land and lose substantial body mass while onshore (Stirling et al. 2008, Rode et al. 2010b). In the SB, however, an increasing proportion of bears avoid fasting onshore during the open-water period by feeding on remains of subsistence-harvested bowhead whale *Balaena mysticetus* carcasses (Schliebe et al. 2008, Rogers et al. 2015). In contrast, individuals that remain on ice during late summer and autumn months are thought to have limited access to seals (Whiteman et al. 2015), which become more pelagic as open water increases (Harwood & Stirling 1992, Pomeroy 1997, Schliebe et al. 2008). The unique situation of marine foods being predictably available onshore in the SB means that increased land-based denning may not have the negative nutritional consequences for pregnant females that are expected elsewhere where such foods are not predictably available. However, the degree to which pregnant females use this resource is unclear. Fischbach et al. (2007) found that females did not visit whale carcasses before denning during the den entrance seasons of 1985 through 2006, but Miller et al. (2015) reported observing lone females at carcasses in 2005–2007, and 67% of collared females that came onshore visited whale carcasses between 2009 and 2013 (Ware et al. unpubl.).

An increase in bears summering and denning on land in response to sea-ice declines could have implications for human–bear interactions (Stirling & Parkinson 2006, Towns et al. 2009). In northern Alaska, oil and gas developments span approximately one-third of the SB coast and are expected to expand (Amstrup et al. 2004). Industrial activity typi-

cally peaks during winter months, minimizing effects on most wildlife and vegetation; however, these activities coincide with the polar bear maternal denning season (Durner et al. 2006a). Denning females with altricial cubs are particularly susceptible to human disturbance (Linnell et al. 2000). While anecdotal evidence suggests that many bears can be tolerant of human activity near dens (Smith et al. 2007), avoidance of premature abandonment due to disturbance requires proactive management (Amstrup 1993) and may become a growing concern if industrial activities increase or if bears increasingly den in coastal habitats.

In years when the distance from the pack ice to the coast is large, travel to terrestrial denning areas may incur substantial energetic costs. A rise in the number of bears attempting long-distance swims between pack ice and land has been documented in recent years (Durner et al. 2011, Pagano et al. 2012, Pilfold et al. 2016). Although polar bears are considered good swimmers, such attempts may increase risk of drowning due to fatigue or adverse sea conditions (Monnett & Gleason 2006). However, even at the maximum distance of 394 km to 15% sea-ice concentration, which occurred in 2009, 3 individuals in our study were able to reach land to den after having spent the summer on pack ice. Meanwhile, females that remain on sea ice to den may be exposed to more dynamic movements of pack ice (Derocher et al. 2004). The energetic and reproductive tradeoffs between reaching land to den versus remaining on ice in low ice years are not well understood.

Climate change is affecting land and ice habitats differently, and could be a factor affecting den site suitability and the observed increases in land-based denning by SB polar bears as a function of increasing summer melt. For example, while snowfall is projected to decline on sea ice (Hezel et al. 2012), it is expected to increase on land (Martin et al. 2009), potentially making land preferable for polar bear denning. In northern Alaska, denning females typically select habitat features that include coastal or island bluffs and river banks where prevailing winds drift sufficient snow for den construction (Durner et al. 2001). However, recent increases in open water have dramatically increased erosion along shorelines in the SB, including barrier island bluffs where many polar bears den (Jorgenson & Brown 2005, Durner et al. 2006a). This erosion has the potential to result in the loss of important denning habitat (Durner et al. 2006a). An apparent northward shift in the location of dens on sea ice (Fig. 1) corresponds with a reduction in multi-year ice (Comiso 2012) and the increase

in the distance between land and sea ice during the summer just prior to den entrance (Rode et al. 2015). Females may be entering dens at more northerly locations due to reduced summer sea ice and/or because suitable multi-year ice is more available farther north. If reductions in multi-year ice continue and offshore snow deposition decreases while onshore snow deposition increases, terrestrial denning habitat may increase in its suitability relative to offshore denning habitat.

Fidelity to denning areas and den substrate has been documented in SB polar bears (Amstrup & Gardner 1994). However, of bears followed for multiple years in our study, 31% changed denning substrate at least once. Such observations of behavioral plasticity may be significant in a warming Arctic. If preferred denning areas become unsuitable or inaccessible, bears are likely to change den substrates between denning attempts, provided that alternative habitat is spatially and temporally available (Zeyl et al. 2010).

We found that control charts using temperature were reliable in identifying denning behavior in polar bears. These charts provided a consistent and automated method to remotely identify denning bears with relatively high accuracy, although some limitations exist. Of 75 identified dens confirmed visually via VHF radio tracking, 4 were classified as non-denning by our algorithm. Of these, 1 bear-winter had no temperature observations from November to April, but was not filtered out by our algorithm, which only removed positively identified dens based on very few observations and bear-winters with no observations during denning months (October to April). A second bear-winter also met the minimum data requirements, but had observations too sparse to effectively fit an intercept of expected mean temperatures. Such misclassifications could be filtered out in future analyses if the minimum amount of data required for classification is increased. The remaining 2 bear-winters did exhibit consecutive bouts of elevated temperatures, but these elevated temperatures did not persist beyond the threshold duration requirement (>34 d) to be considered maternal dens in our algorithm despite satellite location data suggesting they remained at a potential den site for 44 and 34 d. These bears may have attempted to establish a den site, but did not meet our requirement for time in a den. One of the benefits of using temperature to identify denning is that the duration of time in a den, which is accompanied by the physiological changes associated with hibernation (Lohuis et al. 2005, Stenvinkel et al. 2013) and is likely to

affect reproductive success (Robbins et al. 2012), can be identified, rather than the time spent near a den pre- and post-denning.

Declining summer sea-ice cover in the Arctic is projected to continue, and may ultimately lead to a seasonally ice-free Arctic Ocean (Holland et al. 2006, Serreze et al. 2007). As open water between land and the remaining ice increases, more denning bears in the SB are likely to move towards the coast in search of suitable habitat. Moreover, these bears may arrive earlier and remain on land longer than has been observed historically as more females summer on land rather than on pack ice (Atwood et al. 2016). Increased potential for human–bear interactions is likely to accompany increased denning on land. Policies and measures to guard against the disturbance of polar bears will likely become more important as a greater proportion of females rely on terrestrial habitat for denning.

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*Editorial responsibility: Kyle Elliott,
Sainte-Anne-de-Bellevue, Québec, Canada*

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