Original Article

Migration dynamics of polar bears (*Ursus maritimus*) in western Hudson Bay

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Migration is predicted to change both spatially and temporally as climate change alters seasonal resource availability. Species in extreme environments are especially susceptible to climate change; hence, it is important to determine environmental and biological variables that influence their migration. Polar bears (*Ursus maritimus*) are an Arctic apex carnivore whose migration phenology has been affected by climate change and is vulnerable to future changes. Here, we used satellite-linked telemetry collar data from adult female polar bears in western Hudson Bay from 2004 to 2016 and multivariate response regression models to demonstrate that 1) spatial and temporal migration metrics are correlated, 2) ice concentration and wind are important environmental variables that influence polar bear migration in seasonal ice areas, and 3) migration did not vary across the years of our study, highlighting the importance of continued monitoring. Specifically, we found that ice concentration, wind speed, and wind direction affected polar bear migration onto ice during freeze-up and ice concentration and wind direction affected migration onto land during breakup. Bears departed from land earlier with increased wind speed and the effect of wind direction on migration may be linked to prey searching and ice drift. Low ice concentration was associated with higher movement during freeze-up and breakup. Our findings suggest that migration movement may increase in response to climate change as ice concentration and access to prey declines, potentially increasing nutritional stress on bears.

Key words: **Arctic, climate change, migration, movement ecology, multivariate analysis**

INTRODUCTION

Migration is a behavioral movement in response to predictable phenological pulses in resources (Dingle and Drake 2007; Dingle 2014), which increase migrant fitness (Avgar et al. 2014). Seasonal movement between habitats provides migrant species with access to food and mates (Dingle and Drake 2007; Avgar et al. 2014) and refugia from predators (Gliwicz 1986; Hebblewhite and Merrill 2007) and parasites (Folstad et al. 1991; Altizer et al. 2000). The ecological importance of migration varies between species, and a thorough investigation of migration and mechanistic drivers contributes to a comprehensive understanding of ecology.

Although migration often follows a predictable pattern, climate change is altering weather and resource fluctuations (Grebmeier 2012; Serreze and Stroeve 2015; Wolfe et al. 2017). In particular, temporal shifts in resource availability may cause earlier or delayed migration (Lehikoinen and Jaatinen 2012; Hauser et al.

2017). How these changes in migration timing may affect species survival remains unclear. One potential impact of shifting migration phenology may include increased energetic deficits. Migration is energetically costly (McNamara and Houston 2008) and is only considered adaptive when the energetic costs are balanced by energetic gain (Avgar et al. 2014). Climate change is predicted to decrease resource availability (Stirling and Parkinson 2006; Both et al. 2010), increase competition (Ahola et al. 2007; Stirnemann et al. 2012), and increase predation risk (Sharma et al. 2009; Prop et al. 2015), resulting in greater energy costs for migration. Specialists inhabiting extreme habitats are particularly vulnerable to climate change (Laidre et al. 2008; Iknayan and Beissinger 2018) and can serve as a model for how other migratory species may respond to future changes. By determining the drivers for migration in specialists, we may gain insight into how climate change may affect species' energetic budgets, adaptation, and survival.

Migration can be influenced by environmental and biological drivers. Migrants may use environmental cues, including weather and resource fluctuations (Sabine et al. 2002; Hauser et al. 2017; Le

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Corre et al. 2017). Some species are more likely to migrate in years following harsh winters (Eggeman et al. 2016) and some are more likely to travel further in resource-poor environments to increase their potential of obtaining higher quality forage (Teitelbaum et al. 2015). Migration can also be influenced by biological variables, such as age (Eggeman et al. 2016), body condition (Zduniak and Yosef 2012), and reproductive status (Singh and Ericsson 2014). In extreme environments, such as the Arctic, both environmental and biological variables should be investigated concurrently as they may influence migration and be altered by climate change.

Polar bears (*Ursus maritimus*) are the only nonaquatic apex carnivores that exhibit migration, whereas other carnivores follow migratory prey, exhibiting nomadism (Parker 1973; Hofer and East 1993; Avgar et al. 2014). Even among polar bear movement ecology studies, few have examined migration (Flyger and Townsend 1968; Cherry et al. 2013; Yee et al. 2017). Migration is integral to polar bear ecology, where the more southerly populations migrate annually onto sea ice during freeze-up and are forced ashore when sea ice melts (Stirling et al. 1999; Stirling and Parkinson 2006). Bears rely on sea ice to access their main prey, ringed seals (*Pusa hispida*), and bearded seals (*Erignathus barbatus*; Stirling et al. 1977; Sciullo et al. 2017). The spring feeding period is critical for polar bears to obtain sufficient fat stores that allow them to survive on land when their primary prey is inaccessible (Lunn and Stirling 1985; Ramsay and Stirling 1988; Stirling and Derocher 1993). The feeding period is also critical for female reproductive success (Atkinson and Ramsay 1995; Derocher and Stirling 1996). Polar bears in the seasonal ice ecoregion (Amstrup et al. 2007) are one of the Arctic species most affected by climate-induced habitat change due to their migration phenology being linked to sea ice formation and melt, affecting their body condition and reproduction (Stirling et al. 1999; Stirling and Parkinson 2006; Laidre et al. 2008). Several bear populations have altered their migration in response to climate change, where departure and arrival on land have become later and earlier, respectively (Cherry et al. 2013; Prop et al. 2015).

Migration is a complex behavior and is often examined using few metrics. With migration encompassing both spatial and temporal patterns, there are several avenues of investigation. Phenology (Cherry et al. 2013; Prop et al. 2015), distance, and home range (Parks et al. 2006) have been studied, whereas tortuosity has been largely ignored in polar bear migration literature. Additionally, few studies examine both spatial and temporal migration metrics or consider the relationships between metrics when quantifying migration. We used multiple spatial and temporal migration metrics to 1) determine how migration metrics are related, 2) investigate the effects of environmental and biological variables on polar bear migration, and 3) investigate interannual migration changes. The known environmental and biological variables that affect polar bear movement include sea ice and reproductive status: local-level ice habitat influences the timing of bear migration (Cherry et al. 2016) and females will spatially separate on the ice due to differences in offspring mobility. While onshore, females with offspring avoid males due to the risk of infanticide (Pilfold et al. 2014) and will inhabit the interior of Hudson Bay, whereas males and lone females inhabit areas closer to the coast (Derocher and Stirling 1990). Migration may be influenced by additional environmental and biological variables that have not been investigated previously: wind direction, wind speed, body condition, and bear age. We hypothesized that migration would be influenced by both environmental and biological variables, with sea ice characteristics and reproductive status

having the strongest influence on migration. Additionally, we investigated how migration metrics changed over our study period, providing insight into the effects of climate change. This approach highlights the need to examine the complexity of migration using a variety of metrics to provide stronger biological interpretations. We sought to gain insight into the mechanistic link between polar bear migration and driving variables to increase our understanding of the response of polar bears to climate change.

METHODS

Study area

Our study area was Hudson Bay, Canada, which is a shallow inland sea with a 125-m mean depth (Jones and Anderson 1994) that experiences an annual sea ice freeze-up (October–December) and breakup (May–August; Saucier et al. 2004; Gagnon and Gough 2005; Joly et al. 2011). Ice forms initially in the northwest in Nunavut due to the colder water in northern Hudson Bay (Saucier et al. 2004) and freeze-up progresses southward toward Manitoba and Ontario due to the counter-clockwise gyre (Prinsenberg 1988). The duration of ice cover varies within the Bay and between years (Wang et al. 1994; Parkinson 2014). The Western Hudson Bay (WH) polar bear population occurs in one of the more southern regions of the species circumpolar range and includes Manitoba and parts of Nunavut and Ontario (Figure 1).

Female bears with offspring were captured onshore in and around Wapusk National Park, Manitoba, during August– September 2004–2015, via helicopter and remotely immobilized using tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®, Virbac Laboratoires, Carros, France; Stirling et al. 1989) as part of ongoing, long-term research on the ecology of the WH population (e.g., Ramsay and Stirling 1988; Derocher and Stirling 1995; Stirling et al. 1999; Regehr et al. 2007; Lunn et al. 2016). Satellite-linked Argos (CLS America Inc., Largo, MD; www. argos-system.org) or Iridium (Iridium Satellite Communications, McLean, VA; www.iridium.com) telemetry collars with on-board GPS receivers (Telonics, Mesa, AZ) were deployed on adult female bears (≥5 years old). Collars could not be secured on male bears as their necks are wider than their heads, precluding them from tracking. Each collar had a release mechanism (CR-2a, Telonics, Mesa, AZ) that was programmed with a predetermined date to release after 1–2 years following deployment; otherwise, collars were removed upon recapture. Body length (straight-line distance between the tip of the nose and the end of the last caudal vertebra [centimeters]), axillary girth (circumference of the chest directly behind the forelimbs at exhalation), number of cubs, and cub age were recorded at capture. Cubs ≤10 months old were classified as cubs-of-the-year (COYs) and cubs 21–22 months old were classified as yearlings (YRLGs). Age of adult bears was known if originally captured as a COY or YRLG, determined by counting cementum layers in an extracted vestigial premolar (Calvert and Ramsay 1998) or by derivation from a previous cementum count. Animal handling procedures were reviewed and approved by the University of Alberta BioSciences Animal Policy and Welfare Committee and the Environment and Climate Change Canada Western and Northern Animal Care Committee and were consistent with the guidelines of the Canadian Council on Animal Care (www.ccac.ca).

Bears were tracked between September 2004 and August 2016. The number of bears tracked per year ranged from 9 to

Figure 1

Map of Hudson Bay and Wapusk National Park. The Western Hudson Bay population boundary includes the portion of the Hudson Bay coast used to calculate maximum distance to coast.

15. GPS location (30 m accuracy; Tomkiewicz et al. 2010) intervals varied but were standardized to one every 4 h. Incidents of collar failure were variable, resulting in gaps in GPS locations from 4 h to >2 weeks. Using the "sp" (Pebesma and Bivand 2018) and "rgdal" package (Bivand et al. 2018) in R version 3.4.3 (R Core Team 2016), longitude and latitude coordinates (North American datum 1983) were projected into Universal Trans Mercator coordinate system (NAD83 Teranet Ontario Lambert, EPSG: 5321). Biologically impossible data (rate of movement >30 km/h) and data from dropped collars (i.e., GPS locations matched ice drift) were removed (Togunov et al. 2020). We filtered GPS data to only include locations on sea ice.

Time on ice was defined for each bear by finding the land departure and arrival dates using ArcGIS version 10.6 (Environmental Systems Research Institute, Redlands, CA). Land departure dates were determined as the first location on sea ice in Hudson Bay within November–December with no subsequent locations on land until the following summer–autumn breakup season (Cherry et al. 2013). Land arrival dates were determined as the first location on land during July–September, not followed by three consecutive

locations on sea ice in Hudson Bay until November–December. Bears initially remain near the coastline when they migrate on land and, due to the lack of fine-scale accuracy of collars and ice imagery, some locations appear on water. We observed that using three consecutive sea ice locations as a cutoff was a natural break for determining when bears arrived on land.

Data were divided into a freeze-up and breakup migration ice season, specific for each bear, to control for variation in ice (Figure 2) and movement phenology (Figure 3). Several bears had movement data from multiple years; we retained only one year of data to avoid pseudoreplication (Supplementary Table S1). Additional information on how we divided ice seasons and on the data selection process is in the Supplementary Material.

Migration response variables

As bear movement is partially involuntary due to ice drift (Mauritzen et al. 2003; Auger-Méthé et al. 2016), we subtracted ice drift from GPS location data to account for bear displacement due to drift. We used Polar Pathfinder Daily 25 km Ease-Grid Sea Ice
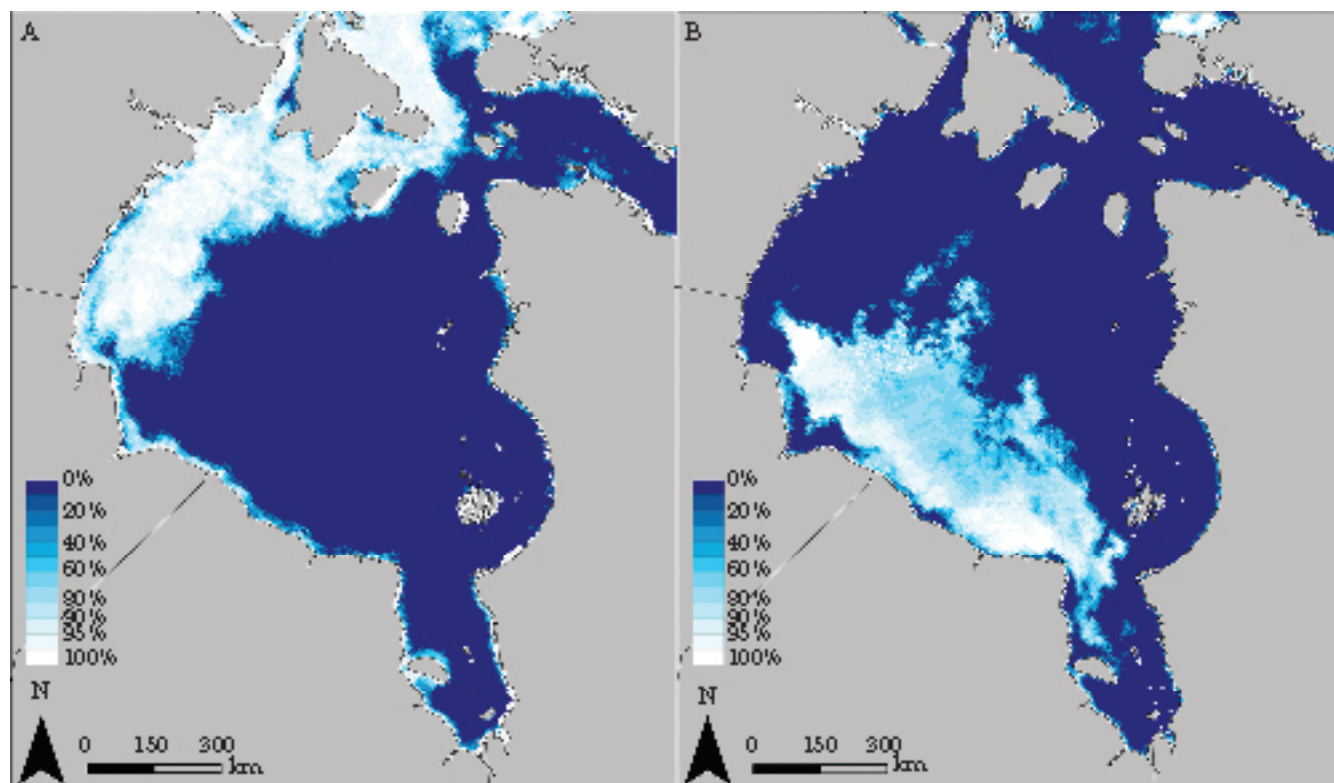
Figure 2
Examples of seasonal sea ice concentration (%) in Hudson Bay. (A) Freeze-up, December 1, 2008, and (B) breakup, July 15, 2009. The ice season of 2008–2009 was typical for 2004–2016. The dates shown are median dates within the time frame of each ice season.
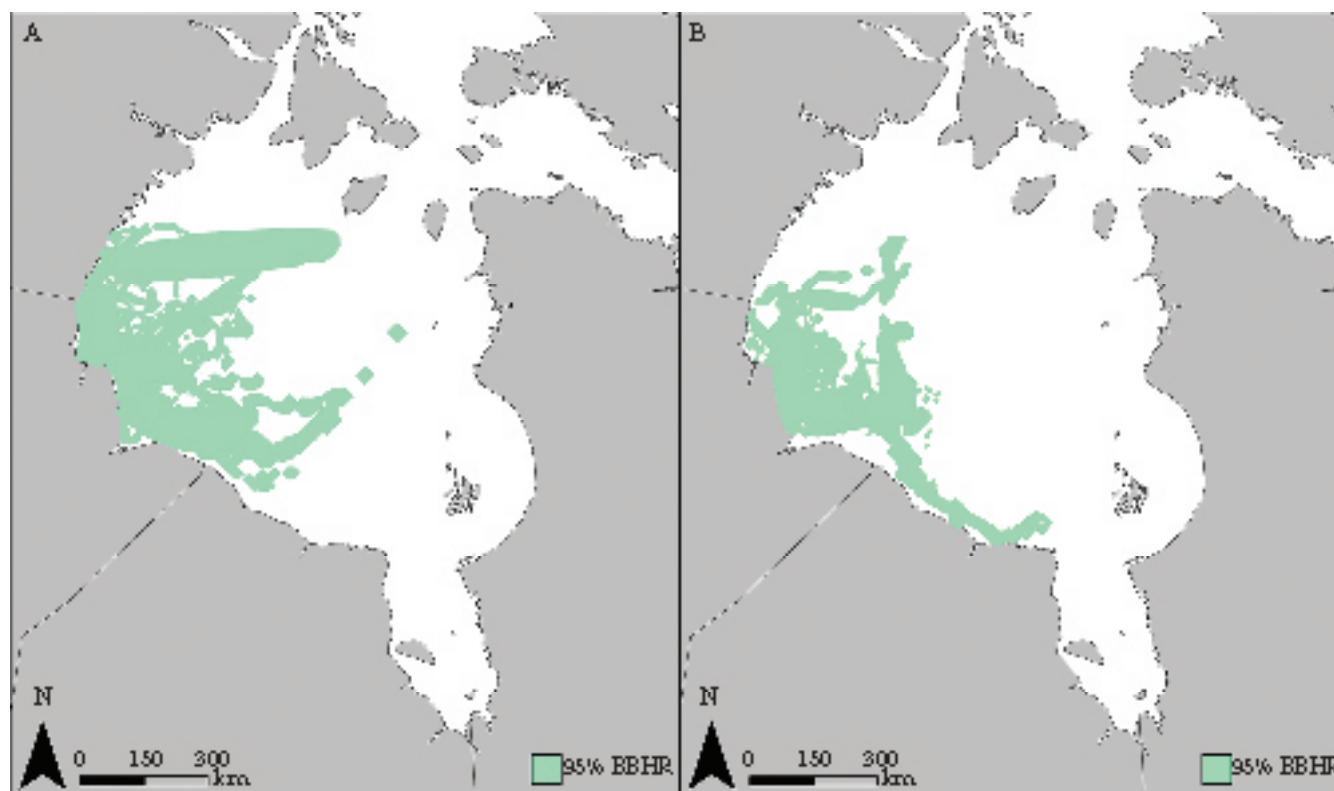
Figure 3
Seasonal Brownian bridge home ranges (95%) of female polar bears in western Hudson Bay (2004–2016). (A) Freeze-up season ($n = 61$) and (B) breakup season ($n = 38$).

Motion Vectors ice drift data from the National Snow and Ice Data Center (Tschudi et al. 2016). Inverse distance weighting was used to spatially interpolate ice drift for GPS locations (Li and Heap 2011; Togunov et al. 2017, 2018).

We estimated daily movement metrics using a 24-h moving window. Within a 24-h window, our data contained zero to six locations depending on gaps between GPS locations. For our daily movement metrics, we only used data where five or six locations per 24-h moving window were present to ensure statistically precise movement metrics (i.e., straightness index). We measured migration using movement variables corrected for ice drift: speed (kilometers per hour) between consecutive locations and daily straightness index (Supplementary Table S4). Speed was measured as the displacement (kilometers) between consecutive GPS locations over time (hours). We calculated the daily straightness index using a moving 24-h window and straightness index = D/L, where D was the Euclidean distance between the start and end location and L was the sum of 4-h interval step lengths between the start and end location within the 24-h time window (Batschelet 1981). Straightness index values range from 1.0 (straight movement) with an increasingly tortuous movement toward 0.0. Other migration variables included land departure and arrival dates (Supplementary Table S4). To measure differences in space use, we used GPS locations to estimate the 95% Brownian bridge home range (square kilometers; Supplementary Table S4) for each individual using the "adehabitatHR" R package (Horne et al. 2007; Calenge 2015; Walter et al. 2015). We used the R package "rgeos" (Bivand et al. 2019) and GPS locations to calculate the maximum straight-line distance (kilometers) of the furthest location from the WH coastline (Figure 1; Supplementary Table S4).

Environmental and biological covariates

We investigated the effect of both environmental and biological covariates on migration. Environmental covariates consisted of ice concentration, wind speed, and wind direction. Ice concentration was calculated for each bear location using collar locations not corrected for ice drift as described in "Data collection." We determined wind speed (meters per second) and wind direction for each location using surface wind direction and speed data from the National Center for Environmental Prediction (NCEP; ftp.cdc. noaa.gov/Datasets/NARR/Dailies/monolevel). NCEP provides 3-h interval gridded wind estimates with 0.3° resolution; therefore, we spatially and temporally interpolated wind data to match bear locations using inverse distance weighting (Li and Heap 2011). Wind was initially spatially interpolated before and after the time of bear locations using the four closest grid values, then linearly interpolated to align with the location fix times (Togunov et al. 2017, 2018). Wind direction ranged from −180° to 180° and was categorized into four groups: north (≥−45° and ≤45° from wind bearings), east (>45° and ≤135°), south (>135° and ≤−135°), and west (>−135° and <−45°).

Biological covariates consisted of bear age, body condition, cub age, and number of cubs (Supplementary Tables S2 and S3). Body condition index at capture was calculated using estimated body mass (kilograms; Thiemann et al. 2011) and body condition index (Cattet and Obbard 2005). Reproductive status was inferred from the time of collaring unless resighted and confirmed the following collaring season based on a 3-year polar bear interbirth interval (Derocher and Stirling 1995). COYs captured in autumn have between 35% and 83% survival and YRLGs have a minimum of

51% survival (Derocher and Stirling 1996). Reproductive status is less likely to change for females with YRLGs than females with COYs in the freeze-up season. Females with September YRLGs were likely alone during the following breakup season, as offspring typically stay with their mothers until their second year (Ramsay and Stirling 1986, 1988). Bears were removed if their on-land locations reflected no movement from September to March, indicating denning (Stirling and Jonkel 1972; Ramsay and Stirling 1982).

Statistical analysis

We examined the relationship of migration movement metrics with environmental and biological covariates, with year as a covariate, and with how migration metrics correlated with one another. We fit separate multivariate response regression models using the "mcglm" R package (Bonat 2016) for freeze-up and breakup. Multivariate response models allow multiple response variables to be included within one model (while holding them constant), instead of using several models separately, and estimate the correlation between each response variable (Bonat 2016). Since our response variables reflected median individual values per year (or maximum), the estimated correlations can be interpreted as among-individual correlations. Our models included all spatial and temporal migration metrics (e.g., maximum distance to coast, Brownian bridge home range size, median speed, median straightness index, departure ordinal date [1–365], and arrival ordinal date) as response variables within the same model. We included median ice concentration, median wind speed, and median wind direction as environmental predictor covariates in our models, and bear age, cub age, and number of cubs as biological predictor covariates. Both wind direction and cub age were categorical variables. Cub age and number of cubs were coded based on age and number at the time of capture. Cub age was coded as "0" for COYs and "1" for YRLGs. Bear body condition index was included as a biological covariate only within our freeze-up models due to fluctuations and unpredictability of body condition and predation success throughout other ice seasons (Pilfold et al. 2015). We included year as a continuous predictor covariate to assess interannual trends of migration metrics following Cherry et al. (2013). We tested correlations of predictor covariates using Pearson's correlation to determine collinearity (>|0.6|; Fox 2002). No covariates exhibited collinearity; therefore, we included all predictor covariates in our models.

We ran separate models for freeze-up and breakup seasons, as well as separate models where we excluded and included reproductive status. When we included reproductive status in our models, bears that were resighted the following year after capture and had lost cubs were excluded because we cannot infer when cubs were lost. When we excluded reproductive status in our models, we used all bears, including bears who lost cubs, therefore, increasing our sample size. Reproductive status included cub age and number of cubs as an interaction in our models. A combination of Gaussian or gamma-log error distributions were included depending on residual normality of each response variable. Diagnostics for appropriate error distributions were determined using Q-Q plots included within the "mcglm" R package (Bonat 2016). We used pseudo Akaike's Information Criterion (pAIC) values calculated in "mcglm" to determine model selection as no information criterion corrected for small sample size was available for this method (Bonat 2016). The pAIC is similar to Akaike's Information Criterion (AIC) used in model selection (Burnham et al. 2011) but contains penalty terms to account for multiple response variables in the model (Bonat 2016). When there were

multiple top models (ΔpAIC<2), we chose the model with the fewest covariates as the top model because the addition of a covariate will mathematically be within 2ΔpAIC units of the least covariate model yet does not improve model fit (Burnham and Anderson 2002), making it uninformative (Arnold 2010). We examined multivariate response variable model parsimony for our top models by comparing pAICs between multivariate models and single-response variable models we fit using the covariates in our top models (Bonat 2016).

RESULTS

Environmental and biological effects excluding reproductive status

We found that polar bear migration was most influenced by environmental covariates as our multivariate response models contained only environmental covariates in all selected top models. Neither biological covariate, age or body condition, were present in our selected top models. Ice concentration (Supplementary Figure S3) and wind direction were the common environmental covariates that were present in both migration top models (Table 1). The top model for freeze-up contained ice concentration, wind speed, wind direction, and year, whereas breakup contained ice concentration and wind direction (Table 1).

Not all covariates had significant relationships with response variables in our top models. Here, we report significant relationships. In freeze-up, we found that maximum distance to coast was negatively influenced by northerly and easterly winds (Figure 4A). Home range size was negatively affected by ice concentration. Median speed and straightness had a negative relationship with northerly winds. Departure date was positively influenced by ice concentration and negatively influenced by wind speed and year (Figure 4A). During breakup, home range size had a positive relationship with northerly winds (Figure 4B). Speed had a positive relationship with northerly winds and a negative relationship with ice concentration. Arrival date had a positive relationship with northerly and southerly winds.

All top multivariate response models were compared to single-response models for goodness-of-fit by comparing pAIC values. We found that the multivariate response models were more parsimonious than the single-response models (Supplementary Table S5).

Environmental and biological effects including reproductive status

Migration models contained only environmental covariates in the most parsimonious models. Reproductive status was not present in top selected models. Our top freeze-up migration model contained wind direction and the top breakup model contained ice concentration and wind direction as predictor variables (Table 2), with significant relationships to our response variables (Figure 4C,D).

We tested the appropriateness of multivariate response models compared to individual single-response models using our reproductive status top models. We found that multivariate response models were more parsimonious than single-response models (Supplementary Table S6).

Interannual migration trends

We found that only land departure date had a significant relationship with year out of our six migration metrics (Figure 4) and year was only present in our top selected model for freeze-up migration, excluding reproductive status (Table 1). We did not detect any other changes in migration over time as no significant relationships between other migration metrics and year were present (Supplementary Figures S4 and S5).

Correlations between migration metrics

All multivariate response models calculated the correlations between the response variables, but we only report the correlations for our top models not including reproductive status due to the increased sample size. There were strong positive correlations between maximum distance to coast and home range size in migration movement (freeze-up and breakup seasons; Figure 5). Freeze-up migration showed strong negative correlations between departure date and maximum distance to coast, as well as departure date and

Table 1

Comparison (using pAIC) of top 5 female polar bear migration (freeze-up and breakup season) nonreproductive status multivariate response models in western Hudson Bay

Season	Model	ΔpAIC	w
Freeze-up	**MD, BB, SP, ST, DD ~ Iceconc + windspeed + winddirection + year**	**0.00**	**0.84**
	MD, BB, SP, ST, DD ~ Iceconc + windspeed + winddirection	3.74	0.13
	MD, BB, SP, ST, DD ~ Iceconc + winddirection + year	8.04	0.02
	MD, BB, SP, ST, DD ~ Age + iceconc + windspeed + winddirection	9.12	0.01
	MD, BB, SP, ST, DD ~ Iceconc + windspeed + year	10.56	0.00
Breakup	**MD, BB, SP, ST, AD ~ Iceconc + winddirection**	**0.00**	**0.83**
	MD, BB, SP, ST, AD ~ Age + iceconc + windspeed + winddirection	4.44	0.09
	MD, BB, SP, ST, AD ~ Iceconc + windspeed + winddirection	5.48	0.05
	MD, BB, SP, ST, AD ~ Age + iceconc + windspeed + winddirection + year	7.84	0.02
	MD, BB, SP, ST, AD ~ Iceconc + windspeed + winddirection + year	8.16	0.01

Data were collected from adult females in western Hudson Bay from 2004 to 2016. Response variables: maximum distance from coast (MD), Brownian bridge home range area (BB), median speed (SP), median straightness (ST), land departure dates (DD), and land arrival dates (AD). The ΔpAIC is the difference between the top model pAIC value (modified AIC score to account for multiple response variables) and the respective models and w is the weight of the pAIC score given the available data and candidate models. Covariate definitions: iceconc is the median ice concentration in the local habitat of an individual bear, windspeed is the median wind speed (m/s) in the local habitat of a bear, winddirection is the median direction of the wind in the local habitat of a bear, year is the year of the data, and age is the age of the bear. Top models are shown in bold.

A

	Intercept	Ice Conc	Wind sp	Wind N	Wind S	Wind W	Year
MD	+				−	−	
BB	+	−					
SP	+				−		
ST	−				−		
DD	+	+	−				−

B

	Intercept	Ice Conc	Wind N	Wind S	Wind W
MD	+				
BB	+			+	
SP	+	−		+	
ST	−				
AD	+		+	+	

C

	Intercept	Wind N	Wind S	Wind W
MD	+		−	
BB	+		−	
SP	+		−	−
ST	−		−	
DD	+			

D

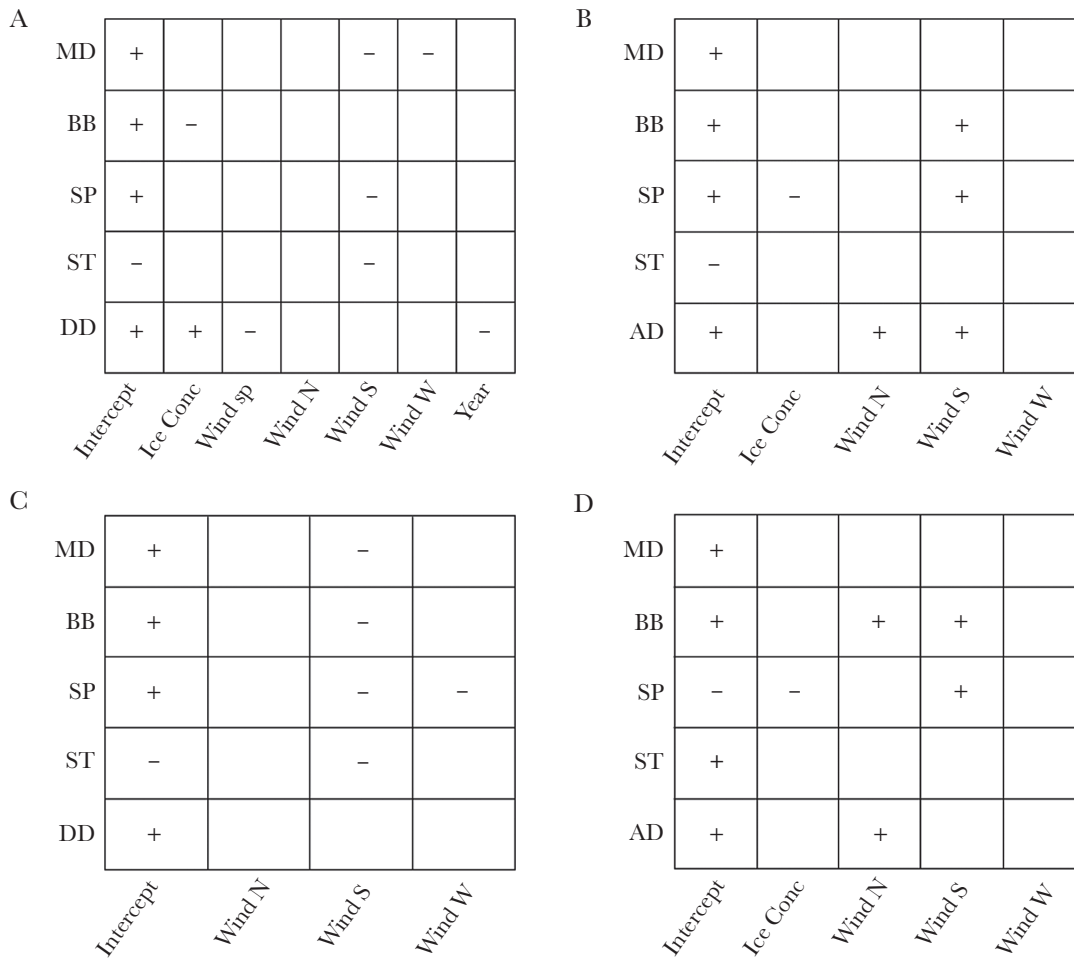|	Intercept	Ice Conc	Wind N	Wind S	Wind W
MD	+				
BB	+		+	+	
SP	−	−		+	
ST	+				
AD	+		+		

Figure 4

Coefficient tables of female polar bear movement multivariate response regression top models by season. All continuous variables were scaled to 0 for coefficient interpretation. (A) Freeze-up, excluding reproductive status bears. (B) Breakup, excluding reproductive status bears. (C) Freeze-up, including reproductive status bears. (D) Breakup, including reproductive status bears. MD is the maximum distance to coast, BB is the Brownian bridge home range size, SP is the median speed between consecutive locations, ST is the median daily straightness index value, DD is the departure date bears departed land and began their migration on sea ice, and AD is the arrival date bears arrived on land from sea ice. Intercept coefficients include the east wind categorical variable. Iceconc is the median ice concentration, wind sp is the median wind speed, wind n, wind s, and wind w, are north, south, and west winds, respectively. Movement data was collected via GPS locations from 2004 to 2016 in western Hudson Bay. All significant covariate relationships are denoted by a positive or negative (+/−; α = 0.05).

home range size (Figure 5A). Additionally, there was a strong positive correlation between speed and straightness. There were strong positive correlations in breakup migration: maximum distance to coast and straightness, arrival date and maximum distance to coast, arrival date and home range size, arrival date and straightness, and home range size and straightness (Figure 5B).

DISCUSSION

Migration complexity

The complexity of migration is often oversimplified by quantifying a single aspect (Visser et al. 2009; Lehikoinen and Jaatinen 2012; Eggeman et al. 2016). By measuring the relationship between several migration metrics (temporal and spatial) and using multivariate response models to consider multiple metrics simultaneously, we encapsulated the complexity of migration. Our results show that temporal and spatial migration metrics were correlated. As such, future migration studies should consider both temporal and

spatial metrics to ensure a thorough understanding of migration. Investigating similar metrics in other polar bear populations in habitats with different sea ice regimes may provide insight into how populations differ and how they may respond to climate change.

There were several notable correlations between migration metrics for WH polar bears. During freeze-up, female bears exhibited fast and straight movement, demonstrating the importance of accessing prey via sea ice (Smith 1980). The highest median speed (2.3 km/h) and median straightness (1.0) were measured in freeze-up. Our findings were consistent with Yee et al. (2017), where denning polar bears had higher straightness when migrating from dens to sea ice. During breakup, bears that arrived onshore earlier exhibited lower straightness. Onshore arrival dates were influenced by ice concentration as bears only return to land once sea ice has melted (Cherry et al. 2013; Pilfold et al. 2017). Bears who return to land later may demonstrate straighter movement by accessing sea ice, swimming between patches of sea ice, or directly swimming to land (Pilfold et al. 2017). Additionally, we note that our

breakup results contained a smaller sample size (38% lower than freeze-up) due to collar failure or swimming behavior, which reduces successful transmission of location fixes, potentially reflected by straighter movement. The difference in movement between freeze-up and breakup may be due to energetic needs and prey accessibility. During freeze-up migration, ice forms initially along the northwest part of Hudson Bay and continues south, whereas the majority of ice during the breakup season persists along the south part of Hudson Bay (Saucier et al. 2004). Bears are nutritionally stressed in the freeze-up season due to having fasted while on land (Russell 1975; Stirling et al. 1977; Lunn and Stirling 1985), whereas

bears reach maximum body fat in the breakup season (Galicia et al. 2020) due to peak feeding and prey availability in spring (McLaren 1958; Stirling and Archibald 1977; Hammill and Smith 1991).

Environmental and biological variables of migration

Our findings did not support our hypothesis that both environmental and biological variables influence migration. Of the environmental and biological variables used in our study, we found that polar bear migration was predominantly influenced by

Table 2

Comparison (using pAIC) of top 5 female polar bear migration (freeze-up and breakup season) reproductive status multivariate response models in western Hudson Bay

Season	Model	ΔpAIC	w
Freeze-up	MD, BB, SP, ST, DD ~ Iceconc + winddirection + year	0.00	0.29
	MD, BB, SP, ST, DD ~ Iceconc + windspeed + winddirection + year	0.04	0.28
	MD, BB, SP, ST, DD ~ Winddirection	**0.68**	**0.21**
	MD, BB, SP, ST, DD ~ Iceconc + winddirection	1.40	0.14
	MD, BB, SP, ST, DD ~ Iceconc + windspeed + winddirection	2.92	0.07
Breakup	**MD, BB, SP, ST, AD ~ Iceconc + winddirection**	**0.00**	**0.80**
	MD, BB, SP, ST, AD ~ Winddirection	2.94	0.18
	MD, BB, SP, ST, AD ~ Cubnum	9.84	0.01
	MD, BB, SP, ST, AD ~ Cubage × cubnum, age, iceconc, windspeed, winddirection	10.22	0.00
	MD, BB, SP, ST, AD ~ Iceconc, windspeed, winddirection	11.68	0.00

Data were collected from adult females in western Hudson Bay from 2004 to 2016. Response variables: maximum distance from coast (MD), Brownian bridge home range area (BB), median speed (SP), median straightness (ST), land departure dates (DD), and land arrival dates (AD). The ΔpAIC is the difference between the top model pAIC value (modified AIC score to account for multiple response variables) and the respective models, and w is the weight of the pAIC score given the available data and candidate models. Covariate definitions: iceconc is the median ice concentration in the local habitat of an individual bear, winddirection is the median direction of the wind in the local habitat of a bear, year is the year of the data, windspeed is the median wind speed (m/s) in the local habitat of a bear, cubnum is the number of cubs, cubage is the age of the cub(s), and age is the age of the bear. Top models are shown in bold.
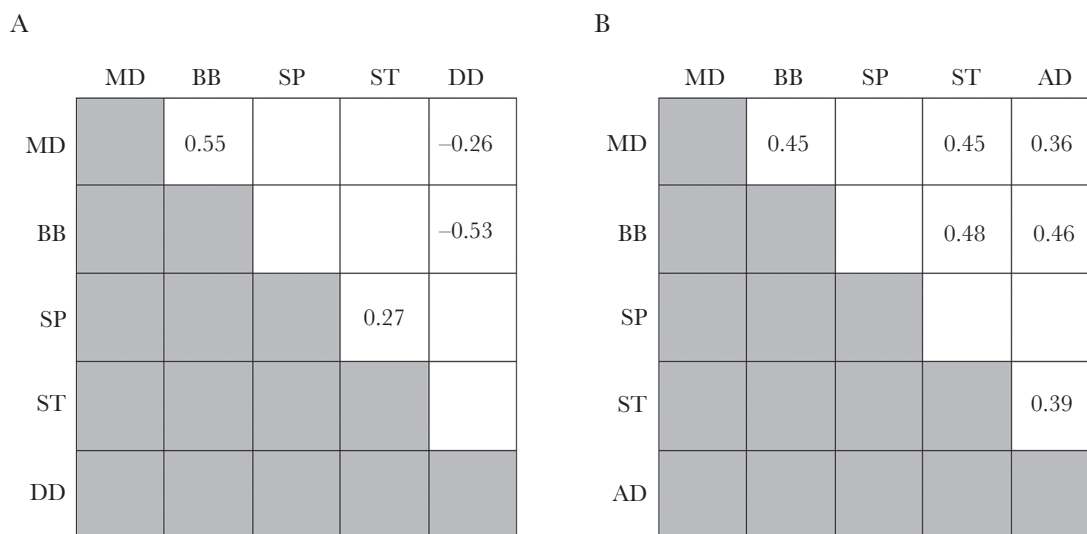

Figure 5
Seasonal migration patterns of female polar bears in western Hudson Bay based on GPS location data collected from 2004 to 2016. Pearson's correlations of response variables used in multivariate response regression models in (A) freeze-up and (B) breakup. MD is the maximum distance to coast, BB is the Brownian bridge home range size, SP is the median speed between consecutive locations, ST is the median daily straightness index value, DD is the departure date bears departed land and began their migration on sea ice, and AD is the arrival date bears arrived on land from sea ice. Only significant correlations ($P < 0.05$) are depicted.

environmental variables. This was similar to Cherry et al. (2016), who found that ice was the main variable influencing the timing of polar bear migration in WH. However, other studies have found that both environmental and biological variables play a role in elk (*Cervus elaphus*; Eggeman et al. 2016) and salamander (*Ichthyosaura alpestris* and *Lissotriton vulgaris*) migration (Mettouris et al. 2018). Failure to include both types of variables may be an oversight, as noted by Jahn et al. (2010), who found that biological variables only partially explained migration patterns and suggested that environmental hypotheses should also be examined.

We found that ice concentration was one of the most influential environmental variables on polar bear migration. Polar bears spend the majority of the year on sea ice to access prey and potential mates (Stirling et al. 1999; Laidre et al. 2008). Our results further support the importance of ice influencing migration in the freeze-up and breakup seasons. During freeze-up, we found that lower ice concentrations were associated with bears that had larger home ranges. This may be a result of bears traveling more in search of prey, resulting in larger home ranges, when ice concentration is low. Furthermore, during breakup, we found that bears present in low ice concentration areas had higher rates of movement. Bears may move faster to find higher ice concentration areas and/or areas with seals before being forced ashore. In spring, ringed seals occur in abundance on ice near the WH coast, whereas bearded seals are more abundant on pack ice further from the coast (Chambellant et al. 2012). Higher movement may incur higher energetic costs in spring (Pagano et al. 2018), when bears have the final opportunity to buildup fat stores (Galicia et al. 2020). Additionally, the length of the sea ice season in Hudson Bay has decreased and is projected to continue declining, with ice freeze-up being delayed and ice breakup occurring earlier (Parkinson 2014; Stern and Laidre 2016). Ice fragmentation has increased and the quality of ice habitat for polar bears has declined in WH (Sahanatien and Derocher 2012). This decline may cause lower ice concentrations, resulting in bears spending more energy traveling to different areas in search of prey. Understanding the importance of ice concentration in polar bear migration and how it influences their migration may provide insight into how this and other populations may respond to a changing environment altered by climate change.

The importance of wind on bear movement when hunting is apparent (Togunov et al. 2017, 2018). We found further support that wind also influences polar bear movement, where migration was influenced by wind speed and direction. Wind speed influenced the timing of migration onto sea ice, where bears exhibited earlier departures from land as wind speeds increased. Earlier departures may be facilitated by high wind speeds moving northern ice southward along the WH coast. Climate change is predicted to cause increases in wind speeds (McInnes et al. 2011) and to delay ice formation as water temperatures increase (Joly et al. 2011). Increased wind speeds may facilitate earlier bear migration onto ice, but it may be counteracted by delayed ice formation. We found that wind direction influenced migration both onto sea ice and onto land. Migration onto sea ice is suggested to be influenced by wind, where bears primarily travel downwind and east (Togunov et al. 2017, 2018). The influence of wind direction on breakup migration could be due to both prey searching and ice drift (Togunov et al. 2017, 2018) as bears actively forage and accumulate peak fat during breakup (Galicia et al. 2020). WH bear movement follows ice drift similarly during ice breakup (Klappstein et al. 2020) and ice drift is due to both wind (Saucier et al. 2004) and a counter-clockwise gyre (Prinsenberg 1988).

Our findings support other evidence that suggests that polar bear migration is more strongly influenced by environmental variables than biological variables. Consistent with previous studies (Cherry et al. 2016; Pilfold et al. 2017), we did not find any support that body condition, bear age, or reproductive status influenced migration movement. Our results suggest that adult females of all reproductive states could be equally vulnerable to changes in ice conditions during freeze-up and melt.

Although we did not find any influence of biological variables on migration when compared to environmental variables, uninvestigated biological variables may influence bear migration, such as prey and bear distribution. Although earlier studies provide abundance estimates of seals in WH (Lunn et al. 1997; Chambellant et al. 2012), they do not span our study period. Seal distribution would likely influence bear migration as seals are the main prey of polar bears (Stirling et al. 1977; Sciullo et al. 2017). As we only tracked adult females, expansion of analyses to include other biological variables (e.g., subadults, males, competition, infanticide risk, mating, and prey) may add to a better understanding of migration ecology for the entire population.

Although some polar bear populations have access to ice year-round, studies in WH may serve as a model for these populations as climate change is causing ice declines across the Arctic (Serreze and Stroeve 2015; Stern and Laidre 2016). As ice declines, some populations are shifting behavior to become more like bears in WH (e.g., terrestrial denning; Fischbach et al. 2007; greater land use; Rode et al. 2015; Atwood et al. 2016). Migration behaviors may change in other bear populations and reflect the annual migrations in WH, as sea ice declines and access to seals is restricted.

Interannual migration trends

Climate change is predicted to alter migration phenology, with phenological shifts already evident in several species (Jenni and Kéry 2003; Lehikoinen and Jaatinen 2012; Hauser et al. 2017). Our results suggest that migration patterns have remained broadly similar over our 12-year study; however, longer monitoring may detect pattern changes. Migration stability may be due to the temporary sea ice stability, where there were no directional trends in sea ice (ice concentration, freeze-up date, and breakup date) in Hudson Bay over our study (Lunn et al. 2016). Another finding suggested that land departure dates became earlier over our study, although the contrary is expected. Mean temperatures have increased in northern Canada over the past few decades (Ding et al. 2014), but 2013 and 2014 were anomalous years due to lower temperatures, possibly resulting in earlier departure dates within those years (Supplementary Figure S5). Consistent with this interpretation, analyses excluding these 2 years provided no evidence for an effect of year on departure dates (results not shown). Over a longer period, land departure dates were later and land arrival dates earlier when comparing polar bear migration from 1991–1997 to 2004–2009 in WH (Cherry et al. 2013). Due to the location frequency of the collars deployed in 1991–1997 (locations 2–10 days apart), we were unable to include this data in our analyses, but we expect that changes in migration may have been detected with a longer study.

When examining any long-term trend in response to climate change, the detection of an effect is dependent on the period examined. However, the time extent for detecting changes may vary depending on species. For example, phenological changes in caribou (*Rangifer tarandus*) migration near Hudson Bay were detected over 11 years (Le Corre et al. 2017). Although we did not detect

changes in migration, such change could have been evident with a longer time series. Long-term data is critical for all migrating species as it enables researchers to measure the effects of climate change on migration patterns.

CONCLUSION

Migration is a complex behavior that should be investigated thoroughly to increase ecological understanding. Using both temporal and spatial migration metrics, we identified variables that influenced polar bear migration by investigating both environmental and biological variables. We determined that migration in WH polar bears was most influenced by environmental variables regardless of reproductive status. We provide a novel framework for analyzing migration by examining multiple migration metrics and their relationships with each other, which could be used in migration studies. We found that polar bear migration patterns remained relatively unchanged over our 12-year study, although continued monitoring may detect future changes. Our framework may be used to aid conservation efforts on polar bears and other migratory species responding to climate change.

SUPPLEMENTARY MATERIAL

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REFERENCES

Ahola MP, Laaksonen T, Eeva T, Lehikoinen E. 2007. Climate change can alter competitive relationships between resident and migratory birds. J Anim Ecol. 76:1045–1052.

Altizer SM, Oberhauser KS, Brower LP. 2000. Associations between host migration and the prevalence of a protozoan parasite in natural populations of adult monarch butterflies. Ecol Entomol. 25(2):125–139.

Amstrup SC, Marcot BG, Douglas DC. 2007. Forecasting the range-wide status of polar bears at selected times in the 21st century. Administrative Report. Anchorage (AK): US Geological Survey, Alaska Science Center. 126 p.

Arnold TW. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. J Wildl Manage. 74(6):1175–1178.

Atkinson SN, Ramsay MA. 1995. The effects of prolonged fasting of the body-composition and reproductive success of female polar bears (*Ursus maritimus*). Funct Ecol.. 9(4):559–567.

Atwood TC, Peacock E, McKinney MA, Lillie K, Wilson R, Douglas DC, Miller S, Terletzky P. 2016. Rapid environmental change drives increased land use by an arctic marine predator. PLoS One. 11:e0155932.

Auger-Méthé M, Lewis MA, Derocher AE. 2016. Home ranges in moving habitats: polar bears and sea ice. Ecography. 39(1):26–35.

Avgar T, Street G, Fryxell JM. 2014. On the adaptive benefits of mammal migration. Can J Zool. 92(6):481–490.

Batschelet E. 1981. Circular statistics in biology. London: Academic Press.

Bivand R, Keitt T, Rowlingson B. 2018. Rgdal: bindings for the geospatial data abstraction library. R package version 1.3– 6. https://CRAN.R-project.org/package=rgdal.

Bivand R, Rundel C, Pebesma E, Stuetz R, Hufthammer KO, Giraudoux P, Davis M, Santilli S. 2019. Rgeos: interface to geometry engine - open source ('GEOS'). R package version 0.5–2. https://CRAN.R-project.org/package=rgeos.

Bohart AM, Lunn NJ, Derocher AE, McGeachy D. 2021. Data from: migration dynamics of polar bears (*Ursus maritimus*) in western Hudson Bay. Behav Ecol. doi: 10.5061/dryad.cnp5hqc3m.

Bonat W. 2016. Mcglm: multivariate covariance generalized linear models. R package version 0.5.0. https://CRAN.R-project.org/package=mcglm.

Both C, Van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc Biol Sci. 277(1685):1259–1266.

Burnham K, Anderson D. 2002. Model selection and multi-model inference. 2nd ed. New York: Springer.

Burnham KP, Anderson DR, Huyvaert KP. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol. 65(1):23–35.

Calenge C. 2015. Home range estimation in r: the adehabitathr package. https://CRAN.R-project.org/package=adehabitat.

Calvert W, Ramsay MA. 1998. Evaluation of age determination of polar bears by counts of cementum growth layer groups. Ursus. 10:449–453.

Cattet MRL, Obbard ME. 2005. To weigh or not to weigh: conditions for the estimation of body mass by morphometry. Ursus. 16(1):102–107.

Chambellant M, Lunn NJ, Ferguson SH. 2012. Temporal variation in distribution and density of ice-obligated seals in western Hudson Bay, Canada. Polar Biol. 35(7):1105–1117.

Cherry SG, Derocher AE, Lunn NJ. 2016. Habitat-mediated timing of migration in polar bears: an individual perspective. Ecol Evol. 6:5032–5042.

Cherry SG, Derocher AE, Thiemann GW, Lunn NJ. 2013. Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. J Anim Ecol. 82:912–921.

Derocher AE, Stirling I. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. Can J Zool. 68(7):1395–1403.

Derocher AE, Stirling I. 1995. Temporal variation in reproduction and body mass of polar bears in western Hudson Bay. Can J Zool. 73(9):1657–1665.

Derocher AE, Stirling I. 1996. Aspects of survival in juvenile polar bears. Can J Zool. 74(7):1246–1252.

Ding QH, Wallace JM, Battisti DS, Steig EJ, Gallant AJE, Kim HJ, Geng L. 2014. Tropical forcing of the recent rapid Arctic warming in northeastern Canada and Greenland. Nature. 509(7499):209.

Dingle H. 2014. Migration: the biology of life on the move. 2nd ed. New York: Oxford Univ Press.

Dingle H, Drake VA. 2007. What is migration? Bioscience. 57(2):113–121.

Eggeman SL, Hebblewhite M, Bohm H, Whittington J, Merrill EH. 2016. Behavioural flexibility in migratory behaviour in a long-lived large herbivore. J Anim Ecol. 85:785–797.

Fischbach AS, Amstrup SC, Douglas DC. 2007. Landward and eastward shift of Alaskan polar bear denning associated with recent sea ice changes. Polar Biol. 30(11):1395–1405.

Flyger V, Townsend MR. 1968. The migration of polar bears. Sci Am. 218(2):108–117.

Folstad I, Nilssen AC, Halvorsen O, Andersen J. 1991. Parasite avoidance: the cause of post-calving migrations in *Rangifer*? Can J Zool. 69(9):2423–2429.

Fox J. 2002. An r and s-plus companion to applied regression. Thousand Oaks (CA): Sage Publications.

Gagnon AS, Gough WA. 2005. Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. Arctic. 58(4):370–382.

Galicia MP, Thiemann GW, Dyck MG. 2020. Correlates of seasonal change in the body condition of an Arctic top predator. Glob Chang Biol. 26:840–850.

Gliwicz MZ. 1986. Predation and the evolution of vertical migration in zooplankton. Nature. 320(6064):746–748.

Grebmeier JM. 2012. Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Ann Rev Mar Sci. 4:63–78.

Hammill M, Smith T. 1991. The role of predation in the ecology of the ringed seal in Barrow Strait, Northwest Territories, Canada. Mar Mamm Sci. 7(2):123–135.

Hauser DDW, Laidre KL, Stafford KM, Stern HL, Suydam RS, Richard PR. 2017. Decadal shifts in autumn migration timing by Pacific Arctic beluga whales are related to delayed annual sea ice formation. Glob Chang Biol. 23:2206–2217.

Hebblewhite M, Merrill EH. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia. 152:377–387.

Hofer H, East ML. 1993. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. I. Social organization. Anim Behav. 46(3):547–557.

Horne JS, Garton EO, Krone SM, Lewis JS. 2007. Analyzing animal movements using Brownian bridges. Ecology. 88:2354–2363.

Iknayan KJ, Beissinger SR. 2018. Collapse of a desert bird community over the past century driven by climate change. PNAS. 115(34):8597–8602.

Jahn AE, Levey DJ, Hostetler JA, Mamani AM. 2010. Determinants of partial bird migration in the Amazon Basin. J Anim Ecol. 79:983–992.

Jenni L, Kéry M. 2003. Timing of autumn bird migration under climate change: advances in long–distance migrants, delays in short–distance migrants. Proc Biol Sci. 270(1523):1467–1471.

Joly S, Senneville S, Caya D, Saucier FJ. 2011. Sensitivity of Hudson Bay sea ice and ocean climate to atmospheric temperature forcing. Clim Dyn. 36(9–10):1835–1849.

Jones EP, Anderson LG. 1994. Northern Hudson Bay and Foxe Basin: water masses, circulation and productivity. Atmos-Ocean. 32(2):361–374.

Klappstein NJ, Togunov RR, Reimer JR, Lunn NJ, Derocher AE. 2020. Patterns of sea ice drift and polar bear (*Ursus maritimus*) movement in Hudson Bay. Mar Ecol Prog Ser.. 641:227–240.

Laidre KL, Stirling I, Lowry LF, Wiig O, Heide-Jørgensen MP, Ferguson SH. 2008. Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. Ecol Appl. 18:S97–125.

Le Corre M, Dussault C, Côté SD. 2017. Weather conditions and variation in timing of spring and fall migrations of migratory caribou. J Mammal. 98(1):260–271.

Lehikoinen A, Jaatinen K. 2012. Delayed autumn migration in northern European waterfowl. J Ornithol. 153(2):563–570.

Li J, Heap AD. 2011. A review of comparative studies of spatial interpolation methods in environmental sciences: performance and impact factors. Ecol Inform. 6(3–4):228–241.

Lunn NJ, Servanty S, Regehr EV, Converse SJ, Richardson E, 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. Ecol Appl. 26:1302–1320.

Lunn NJ, Stirling I. 1985. The significance of supplemental food to polar bears during the ice-free period of Hudson Bay. Can J Zool. 63(10):2291–2297.

Lunn NJ, Stirling I, Nowicki SN. 1997. Distribution and abundance of ringed and bearded seals in western Hudson Bay. Can J Fish Aquat Sci. 54(4):914–921.

Mauritzen M, Derocher AE, Pavlova O, Wiig Ø. 2003. Female polar bears, *Ursus maritimus*, on the Barents Sea drift ice: walking the treadmill. Anim Behav. 66(1):107–113.

McInnes KL, Erwin TA, Bathols JM. 2011. Global climate model projected changes in 10 m wind speed and direction due to anthropogenic climate change. Atmos Sci Lett. 12(4):325–333.

McLaren IA. 1958. The biology of the ringed seal (*Phoca hispida schreber*) in the eastern Canadian Arctic. Ottawa (Canada): Fisheries Research Board of Canada.

McNamara JM, Houston AI. 2008. Optimal annual routines: behaviour in the context of physiology and ecology. Phil Trans R Soc Lond B Biol Sci. 363(1490):301–319.

Mettouris O, Pitta E, Giokas S. 2018. Breeding-migration patterns and reproductive dynamics of two syntopic newt species (amphibia, salamandridae) at a temporary pond in southern Greece. Hydrobiologia. 819(1):1–15.

Pagano AM, Durner GM, Rode KD, Atwood TC, Atkinson SN, Peacock E, Costa DP, Owen MA, Williams TM. 2018. High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. Science. 359:568–572.

Parker GR. 1973. Distribution and densities of wolves within barren-ground caribou range in northern mainland Canada. J Mammal. 54(2):341–348.

Parkinson CL. 2014. Spatially mapped reductions in the length of the Arctic sea ice season. Geophys Res Lett. 41:4316–4322.

Parks E, Derocher A, Lunn N. 2006. Seasonal and annual movement patterns of polar bears on the sea ice of Hudson Bay. Can J Zool. 84(9):1281–1294.

Pebesma E, Bivand R. 2018. Package 'sp'. R package version 1.0–13. https://CRAN.R-project.org/package=sp.

Pilfold NW, Derocher AE, Richardson E. 2014. Influence of intraspecific competition on the distribution of a wide-ranging, non-territorial carnivore. Glob Ecol Biogeogr. 23(4):425–435.

Pilfold NW, Derocher AE, Stirling I, Richardson E. 2015. Multi-temporal factors influence predation for polar bears in a changing climate. Oikos. 124(8):1098–1107.

Pilfold NW, McCall A, Derocher AE, Lunn NJ, Richardson E. 2017. Migratory response of polar bears to sea ice loss: to swim or not to swim. Ecography. 40(1):189–199.

Prinsenberg S. 1988. Ice-cover and ice-ridge contributions to the freshwater contents of Hudson Bay and Foxe Basin. Arctic. 41(1):6–11.

Prop J, Aars J, Bårdsen BJ, Hanssen SA, Bech C, Bourgeon S, de Fouw J, Gabrielsen GW, Lang J, Noreen E. 2015. Climate change and the increasing impact of polar bears on bird populations. Front Ecol Evol. 3:33.

R Core Team. 2016. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Ramsay MA, Stirling I. 1982. Reproductive biology and ecology of female polar bears in western Hudson Bay. Nat Can. 109(4):941–946.

Ramsay MA, Stirling I. 1986. On the mating system of polar bears. Can J Zool. 64(10):2142–2151.

Ramsay MA, Stirling I. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). J Zool. 214(4):601–633.

Regehr EV, Lunn NJ, Amstrup SC, Stirling I. 2007. Effects of earlier sea ice breakup on survival and population size of polar bears in western Hudson Bay. J Wildl Manage. 71(8):2673–2683.

Rode KD, Wilson RR, Regehr EV, St Martin M, Douglas DC, Olson J. 2015. Increased land use by chukchi sea polar bears in relation to changing sea ice conditions. PLoS One. 10:e0142213.

Russell RH. 1975. The food habits of polar bears of James Bay and southwest Hudson Bay in summer and autumn. Arctic. 28(2):117–129.

Sabine DL, Morrison SF, Whitlaw HA, Ballard WB, Forbes GJ, Bowman J. 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. J Wildl Manage. 66(3):718–728.

Sahanatien V, Derocher A. 2012. Monitoring sea ice habitat fragmentation for polar bear conservation. Anim Conserv. 15(4):397–406.

Saucier FJ, Senneville S, Prinsenberg S, Roy F, Smith G, Gachon P, Caya D, Laprise R. 2004. Modelling the sea ice-ocean seasonal cycle in Hudson Bay, Foxe Basin and Hudson Strait, Canada. Clim Dyn. 23(3–4):303–326.

Sciullo L, Thiemann GW, Lunn NJ, Ferguson SH. 2017. Intraspecific and temporal variability in the diet composition of female polar bears in a seasonal sea ice regime. Arct Sci. 3(4):672–688.

Serreze MC, Stroeve J. 2015. Arctic sea ice trends, variability and implications for seasonal ice forecasting. Philos Trans A Math Phys Eng Sci. 373(2045):20140159.

Sharma S, Couturier S, Cote SD. 2009. Impacts of climate change on the seasonal distribution of migratory caribou. Global Change Biol. 15(10):2549–2562.

Singh NJ, Ericsson G. 2014. Changing motivations during migration: linking movement speed to reproductive status in a migratory large mammal. Biol Lett. 10(6):20140379.

Smith TG. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Can J Zool. 58(12):2201–2209.

Stern HL, Laidre KL. 2016. Sea-ice indicators of polar bear habitat. Cryosphere. 10(5):2027–2041.

Stirling I, Archibald WR. 1977. Aspects of predation of seals by polar bears. J Fish Board Can. 34(8):1126–1129.

Stirling I, Derocher AE. 1993. Possible impacts of climatic warming on polar bears. Arctic. 46(3):240–245.

Stirling I, Jonkel C. 1972. The great white bears. Nature Canada (Ottawa). 1(3):15–18.

Stirling I, Jonkel C, Smith P, Robertson R, Cross D. 1977. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. Canadian Wildlife Service Occasional Paper 33. Ottawa (Canada): Canadian Wildlife Service.

Stirling I, Lunn NJ, 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.

Stirling I, Parkinson CL. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. Arctic. 59(3):261–275.

Stirling I, Spencer C, Andriashek D. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol in the Canadian Arctic. J Wildl Dis. 25:159–168.

Stirnemann RL, O'Halloran J, Ridgway M, Donnelly A. 2012. Temperature-related increases in grass growth and greater competition for food drive earlier migrational departure of wintering whooper swans. Ibis. 154(3):542–553.

Teitelbaum CS, Fagan WF, Fleming CH, Dressler G, Calabrese JM, Leimgruber P, Mueller T. 2015. How far to go? Determinants of migration distance in land mammals. Ecol Lett. 18:545–552.

Thiemann GW, Lunn NJ, Richardson ES, Andriashek DS. 2011. Temporal change in the morphometry-body mass relationship of polar bears. J Wildl Manage. 75(3):580–587.

Togunov RR, Derocher AE, Lunn NJ. 2017. Windscapes and olfactory foraging in a large carnivore. Sci Rep. 7:46332.

Togunov RR, Derocher AE, Lunn NJ. 2018. Corrigendum: windscapes and olfactory foraging in a large carnivore. Sci Rep. 8:46968.

Togunov RR, Klappstein NJ, Lunn NJ, Derocher AE, Auger-Methe M. 2020. Opportunistic evaluation of modelled sea ice drift using passively drifting telemetry collars in Hudson Bay, Canada. Cryosphere. 14(6):1937–1950.

Tomkiewicz SM, Fuller MR, Kie JG, Bates KK. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philos Trans R Soc B Biol Sci. 365(1550):2163–2176.

Tschudi M, Fowler C, Maslanik J, Stewart JS, Meier W. 2016. Polar pathfinder daily 25 km ease-grid sea ice motion vectors. Version 3. [November 2004 - July 2016]. Boulder (CO). NASA National Snow and Ice Data Center. Distributed in netcdf format by the Integrated Climate Data Center (http://icdc.Zmaw; University of Hamburg, 2013).

Visser ME, Perdeck AC, van Balen JH, Both C. 2009. Climate change leads to decreasing bird migration distances. Global Change Biol. 15(8):1859–1865.

Walter WD, Onorato DP, Fischer JW. 2015. Is there a single best estimator? Selection of home range estimators using area-under-the-curve. Mov Ecol. 3:10.

Wang J, Mysak LA, Ingram RG. 1994. A numerical simulation of sea ice cover in Hudson Bay. J Phys Oceanogr. 24(12):2515–2533.

Wolfe JD, Ralph CJ, Wiegardt A. 2017. Bottom-up processes influence the demography and life-cycle phenology of Hawaiian bird communities. Ecology. 98:2885–2894.

Yee M, Reimer J, Lunn NJ, Togunov RR, Pilfold NW, McCall AG, Derocher AE. 2017. Polar bear (*Ursus maritimus*) migration from maternal dens in western Hudson Bay. Arctic. 70(3):319–327.

Zduniak P, Yosef R. 2012. Crossing the desert barrier: migration ecology of the lesser whitethroat (S*ylvia curruca*) at Eilat, Israel. J Arid Environ. 77:32–38.