

Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics

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Summary

1. Understanding how seasonal environmental conditions affect the timing and distribution of synchronized animal movement patterns is a central issue in animal ecology.
2. Migration, a behavioural adaptation to seasonal environmental fluctuations, is a fundamental part of the life history of numerous species. However, global climate change can alter the spatiotemporal distribution of resources and thus affect the seasonal movement patterns of migratory animals.
3. We examined sea ice dynamics relative to migration patterns and seasonal geographical fidelity of an Arctic marine predator, the polar bear (*Ursus maritimus*). Polar bear movement patterns were quantified using satellite-linked telemetry data collected from collars deployed between 1991–1997 and 2004–2009.
4. We showed that specific sea ice characteristics can predict the timing of seasonal polar bear migration on and off terrestrial refugia. In addition, fidelity to specific onshore regions during the ice-free period was predicted by the spatial pattern of sea ice break-up but not by the timing of break-up. The timing of migration showed a trend towards earlier arrival of polar bears on shore and later departure from land, which has been driven by climate-induced declines in the availability of sea ice.
5. Changes to the timing of migration have resulted in polar bears spending progressively longer periods of time on land without access to sea ice and their marine mammal prey. The links between increased atmospheric temperatures, sea ice dynamics, and the migratory behaviour of an ice-dependent species emphasizes the importance of quantifying and monitoring relationships between migratory wildlife and environmental cues that may be altered by climate change.

Key-words: Arctic marine ecosystems, migratory behaviour, satellite-linked telemetry, sea ice break-up and freeze-up, seasonal habitat use, site fidelity, spatiotemporal mismatch

Introduction

Migration is a behavioural adaptation to seasonal environmental fluctuations and an integral component of the life history of many species (Fryxell & Sinclair 1988; Laidre *et al.* 2004; Dingle & Drake 2007). The predictable and recurrent nature of many seasonally dependent ecological processes allows migratory species to maximize energy gains by altering seasonal habitat use to overlap with abundant or accessible nutritional resources (Tynan & DeMaster 1997; Rojas-Martínez *et al.* 1999; Alerstam, Hedenström & Åkesson 2003; Rasmussen *et al.* 2007).

Migration is also often associated with seasonal fidelity to familiar areas, which can increase foraging efficiency and the likelihood of reproductive success (Greenwood & Harvey 1982; Switzer 1993; Brown, Brown & Brazeal 2008; Peron, Lebreton & Crochet 2010). Specific seasonal environmental changes are commonly thought to act as migration triggers for species that show predictable and cyclical fidelity to different habitat ranges. For example, onset of migration for migratory birds has been shown to correlate with photoperiod (Berthold 1991; Gwinner 1996; Dawson 2008) and some bird species appear to alter rates of migration in response to environmental conditions such as weather or plant phenology (Marra *et al.* 2005). In addition, seasonal movement in migratory white-tailed

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deer populations seems to be triggered by snow depth and possibly other seasonal stimuli such as temperature, photoperiod and presence of snow (Sabine *et al.* 2002). Increasing global temperatures have the potential to alter the timing of numerous seasonally dependent ecological processes and consequently disrupt the migratory behaviour and seasonal habitat use of several species (Walther *et al.* 2002; Stefanescu, Peñuelas & Filella 2003; Rosenzweig *et al.* 2008; Saino *et al.* 2009; Singh & Milner-Gulland 2011). Such disruptions can result in a spatiotemporal mismatch between important life history events, such as breeding and seasonal food abundance (Both *et al.* 2006) and cause negative energetic and reproductive consequences for migratory wildlife (Post & Forchhammer 2008; Bronson 2009; Milligan, Holt & Lloyd 2009). Quantifying ecological connections between environmental factors and the seasonal distribution of populations is therefore important for examining potential effects of climate change (Post & Forchhammer 2002).

The Western Hudson Bay population of polar bears (*Ursus maritimus*) displays an annual migration pattern on- and off-ice that is linked to seasonal sea ice dynamics. In early to mid-summer, when sea ice in Hudson Bay completely melts, polar bears migrate to on-land refugia and spend the ice-free months relying on endogenous fat reserves during an extended fast until they return to the sea ice and resume hunting (Lunn & Stirling 1985; Ramsay & Stirling 1988; Stirling & Derocher 1993). Ice-associated seals, the primary prey of polar bears, are inaccessible without a sea ice platform from which to hunt (Stirling & Derocher 1993; Ferguson, Taylor & Messier 2000; Derocher, Lunn & Stirling 2004). When sea ice melts to the stage that highly fractured ice makes mobility and hunting inefficient, polar bears move towards their annual terrestrial habitat. Although terrestrial foraging by polar bears has been reported (Derocher, Andriashek & Arnould 1993; Stempniewicz 2006; Smith *et al.* 2010), terrestrial foods do not contribute substantially to their annual energy budget (Ramsay & Hobson 1991; Hobson, Stirling & Andriashek 2009). Migration between marine and terrestrial environments therefore represents a transition between positive and negative energy states. Early melting of the sea ice will have strongly negative impacts on polar bear energy budgets because it simultaneously shortens the hyperphagic period of late spring and early summer, when hunting conditions are most favourable, and extends the duration of the on-land period through which polar bears must survive on reduced and finite stores of body fat. Progressively earlier break-up over the last three decades has been linked to declines in polar bear body condition, reproduction and population numbers (Stirling, Lunn & Iacozza 1999; Reg-ehr *et al.* 2007). Projected ongoing declines in sea ice duration will further reduce adult survival rates and reproductive success (Molnár *et al.* 2010, 2011) and threaten the persistence of the Western Hudson Bay population. Climate-induced lengthening of the summer

fasting period exemplifies how phenological behaviour, such as seasonal movements or migrations, can be disrupted by rising global temperatures.

In addition to altering the timing of migration, changes to sea ice freeze-thaw cycles can affect the seasonal geographical distribution of polar bears (Mauritzen *et al.* 2003; Schliebe *et al.* 2008; Durner *et al.* 2009). Seasonal site fidelity has been deemed beneficial for many animals due to the energetic efficiency associated with accessing familiar resources such as food or quality breeding sites (Baker *et al.* 1995; Deutsch *et al.* 2003; Mansfield *et al.* 2009). Polar bears show a high degree of fidelity to terrestrial refugia along the Manitoba coast between the Churchill and Nelson Rivers (Fig. 1) (Derocher & Stirling 1990; Lunn, Stirling & Andriashek 2004; Stirling *et al.* 2004). Returning to the same maternity denning area may allow females to imprint offspring with appropriate travel routes and summering habitat (Derocher & Stirling 1990; Stirling *et al.* 2004). Spatial fidelity to terrestrial habitat may be affected by sea ice as southerly currents along the western coast of Hudson Bay carry the last remaining ice during break-up to the coastal regions of Manitoba and Ontario (Wang, Mysak & Ingram 1994; Gough & Allakhverdova 1999; Saucier *et al.* 2004). How changes in the timing of sea ice break-up will affect fidelity of polar bears to onshore denning areas is not known, but Derocher, Lunn & Stirling (2004) predicted that population boundaries could change with altered ice patterns and the resulting disruptions to habitat connectivity. Should polar bears attempt to extend their time on ice in the face of earlier seasonal melt, they may drift further south of traditional areas and be forced to travel back on land at a greater energetic cost or use unfamiliar territory. Southern portions of Hudson Bay are the last regions to re-freeze in the fall (Gough & Allakhverdova 1999) and therefore spending the ice-free period in these areas would also result in a delayed return to the sea ice.

Although polar bear migration is inevitably determined by the availability of sea ice, the specific landscape-scale environmental factors that drive migration phenology are largely not known. Using satellite-linked telemetry, we examined how sea ice characteristics during break-up and freeze-up affect the migration phenology of polar bears. We also examined temporal trends in the dates polar bears from the Western Hudson Bay population moved on and off the sea ice. Trends towards earlier break-up (Gagnon & Gough 2005a; Stirling & Parkinson 2006; Scott & Marshall 2010) and later freeze-up (Gagnon & Gough 2005a; Towns *et al.* 2009; Hochheim & Barber 2010) have been documented within Hudson Bay. We hypothesized these sea ice trends would result in changes in the timing of polar bear movements between terrestrial and marine habitats. Finally, we analysed movement data from collared polar bears to determine if the timing and rate of sea ice break-up as well as geographical distribution of sea ice during break-up affect fidelity to on-land regions.

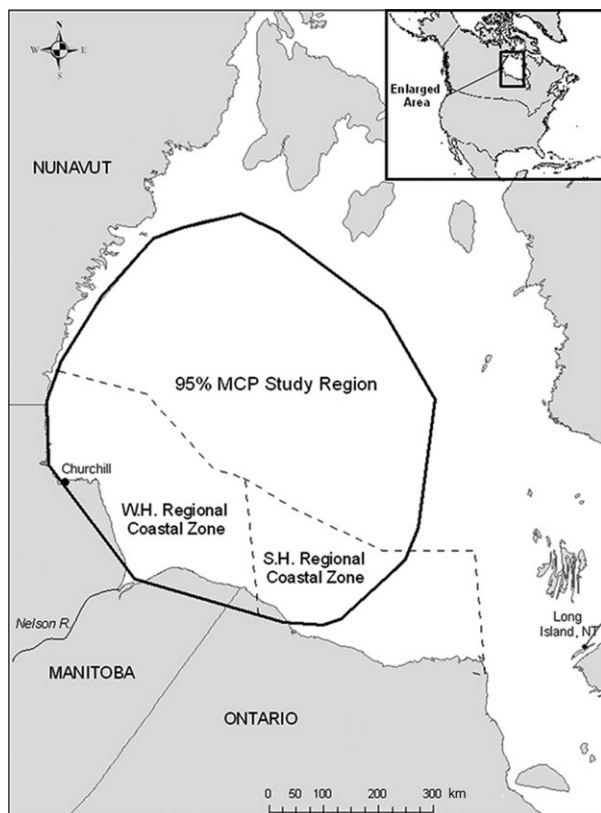


Fig. 1. Map of Hudson Bay showing the 95% minimum convex polygon (solid line) of all marine polar bear locations (1991–97 and 2004–09) and the two coastal zones (dashed lines).

Materials and methods

Polar bears were captured along the western coast of Hudson Bay between Churchill, Manitoba and the Ontario border (Fig. 1). Bears were located from a helicopter and immobilized via remote injection of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil[®], Laboratories Virbac, Carros, France; Stirling, Spencer & Andriashek 1989). All captures occurred on land either in August or September (autumn) when bears were ashore during the ice-free season or in February or March (spring) when females were emerging from maternity dens with cubs-of-the-year. In 1991–97, 46 Doppler shift Argos[®] satellite-linked collars (Telonics, Mesa, Arizona) were deployed on 41 different adult female polar bears with either cubs-of-the-year or 1-year-old cubs. The interval between successive locations varied depending on short-term research objectives and ranged from 2 to 10 days. In 2004–09, 74 global positioning system (GPS) Argos[®] satellite-linked collars (Gen III and IV collars, Telonics, Mesa, AZ) were deployed on 68 adult females. These collars were programmed to obtain one GPS location every 4 h. No collars were deployed between 1998 and 2004.

Due to the longer intervals between locations for the Doppler shift collars, data from the newer GPS collars were subsampled to match the mean location interval of Doppler shift collars. A geographical information system (ArcInfo 9.3, Environmental Systems Research Institute, Redlands, California) was used to extract daily sea ice concentrations approximated from daily Special Sensor Microwave/Imager (SSM/I) passive microwave

data obtained from the National Snow and Ice Data Center (Boulder, Colorado). Sea ice concentrations were analysed at a resolution of 25×25 km cells. Daily sea ice concentrations were determined using the mean concentration value from all pixels within analysis-specific regions of interest.

To determine the relationship between migration phenology and sea ice dynamics, we examined a number of linear regression models to assess both the timing of various sea ice concentrations and the rate of ice disappearance as potential predictors of arrival ashore (Table 1). We defined arrival ashore as the date of a bear's first location on land that was not followed by a location off-shore until freeze-up in the following autumn. The timing of several sea ice concentration values were tested as predictors, starting at 90% and decreasing in 10% increments. The timing of these *a priori* increments represented an evenly distributed range of sea ice conditions from the beginning to end of annual break-up. Ice concentrations for these analyses were derived from an area within a 95% minimum convex polygon (MCP) determined from on-ice polar bear locations collected throughout the entire study (Fig. 1). The date of each 10% sea ice concentration increment was determined using the first day mean ice concentration became \leq the given increment value. Rate of ice disappearance from each increment was the number of days between the given ice concentrations and the date sea ice disappeared (i.e. concentration became $\leq 5\%$). The interaction between rate of ice disappearance and the timing of sea ice increments was also tested (Table 1).

Similar sets of regression models were used to determine which sea ice predictor variables best corresponded to when polar bears departed from shore during freeze-up (Table 1). Departure from shore was defined as the first location off-shore that was not followed by a location on land until break-up the next year. The timing of several sea ice concentrations in the 95% MCP, starting at 10% and increasing in 10% increments, were tested as predictors of departure from shore. The date of each 10% sea ice increment was determined using the day sea ice concentration became \geq the given increment value. Rate of freeze-up was included in these linear regression models using the number of days between the first appearance of sea ice (i.e. concentration became $\geq 5\%$) and date of the given sea ice increment. The inter-

Table 1. Example of candidate linear regression models to predict polar bear date ashore for one of several *a priori* sea ice concentrations (i.e. 90%) occurring during spring break-up within the 95% MCP. Identical models were tested for all sea ice concentration increments between 90 and 10% at 10% increments. Definitions of variables: 90% sea ice is the date of 90% sea ice concentration during break-up, 90% to disappearance is the number of days between date of 90% sea ice concentration and ice disappearance. Similar sets of candidate models were used to predict polar bear departure from shore dates with the exception of using number of days between ice appearance and given ice concentrations

Model I.D.	Model
1	90% sea ice
2	90% to disappearance
3	90% sea ice, 90% to disappearance
4	90% sea ice, 90% to disappearance, 90% sea ice \times 90% to disappearance
37	Null

action between rate of freeze-up and the timing of sea ice increments was also tested (Table 1). Departures from shore during freeze-up are lacking for 1993 because collars were not deployed that autumn and no previously deployed collars were still functioning at that time. To examine inter-annual trends in the timing of migration, we used a linear regression model to analyse the relationship between year and arrival ashore. A separate linear regression tested the relationship between year and departure from shore.

Finally, we tested various sea ice predictor variables hypothesized to affect the fidelity of polar bears to the western Hudson Bay coast. We used the distance between a bear's capture location and where it came ashore during break-up the following year(s) as a measurement of fidelity. Predictor variables in model(s) with substantial evidence to describe arrival ashore were used in linear regressions to test whether factors correlated to the timing of migration also affected fidelity. In addition, we hypothesized that the relative distribution of sea ice during break-up may differ among years and consequently affect where polar bears arrive on land. To examine the distribution of sea ice as it pertains to where polar bears came ashore, we compared daily ice concentrations for two areas along the coast of western and southern Hudson Bay (Fig. 1). These two coastal zones were chosen because they encompassed all locations where collared bears came ashore (except for one that came ashore on Long Island, east of James Bay; Fig. 1) and represented areas known to differ significantly from one another in the timing of break-up (Stirling *et al.* 2004). The line dividing the regional coastal zones runs along the boundary between Western and Southern Hudson Bay populations (PBSG 2006). Each coastal zone extended 150–200 km off-shore because bears travel through these coastal areas immediately before arriving on land and it is also where the last ice typically remains (Stirling *et al.* 2004). The relative amount of ice in the southern zone compared to the western zone was used as a metric to describe sea ice distribution during break-up. This predictor variable was determined by dividing the ice concentration in the southern zone by that in the western zone on the date of sea ice concentration increment(s) (in the 95% MCP) that best corresponded to arrival ashore determined by previously described regression models. In years that GPS collars were used, locations where bears came ashore were identified using the first location on land determined by the highest temporal resolution data available (i.e. not data subsampled to match the Doppler shift collar location frequencies). Linear regression models were used to examine fidelity in relation to all combinations of potential predictor variables and two-way interactions.

Akaike's Information Criterion (AIC) was used to separately test the relative support for various models examining predictor variables related to arrival ashore, departure from shore and

fidelity (Burnham & Anderson 2002). Models with $\Delta\text{AIC} < 2$ relative to the best performing model were considered to have substantial evidence to support our data (Burnham & Anderson 2002). Predictor variables in multiple linear regressions were mean-centred to mitigate multicollinearity in the interaction terms. Multicollinearity was assessed for models by examining variance inflation factors (VIF) for all mean-centred predictor variables and interaction terms. When $\text{VIF} < 10$, multicollinearity was not considered to be a concern (Allison 1999). Unstandardized beta parameter estimates (β) and 95% confidence intervals are provided for each predictor variable.

Results

We recorded 76 arrivals ashore and 105 departures over the course of the study. Collar malfunctions and dropped collars negatively affected sample sizes. Mean annual sample sizes were 5.4 (S.E. = 0.9) for arrivals ashore and 8.8 (S.E. = 1.3) for departures from shore. All mean-centred predictor variables and interaction terms in multiple linear regression models had VIFs < 10 . The best fit regression model for predicting polar bear arrivals ashore used the date of 30% sea ice concentration during break-up, the number of days between 30% sea ice concentration and ice disappearance, and the interaction between these two variables (Model 28, $F_{3, 72} = 10.73$, $P < 0.001$) (Table 2). Examination of the parameter estimates for the best model indicated that the date of 30% ice concentration and the interaction between this date and the number of days until ice disappearance were strong predictors for arrival ashore (Table 4). Relatively earlier dates of 30% ice concentration resulted in earlier arrival ashore for collared bears and these effects were exacerbated when rates of ice disappearance were relatively high (Table 4). Throughout the study, bears arrived ashore a mean of 28.3 days (S.E. = 1.8) after 30% ice cover (Fig. 2). The second best model predicting arrival ashore had a $\Delta\text{AIC} < 2$ and thus also had substantial evidence to support our data (Burnham & Anderson 2002). The second ranked model predicting polar bear arrival ashore had analogous results to the best model, but used parameters related to the 20% sea ice concentration increment (Model 32, $F_{3, 72} = 10.25$, $P < 0.001$) (Tables 2, 4). All other models tested for predicting polar bear arrival ashore had $\Delta\text{AIC} > 2$ (Table 2).

The best fitting regression model predicting when polar bears departed from shore used the date of 10% sea ice

Table 2. AIC results for the best 5 of 36 candidate models to predict polar bear date ashore. AIC is the AIC score for each model, ΔAIC is the difference in AIC scores between different candidate models and the best model, and w is the AIC weight or the weight of evidence that a model is the best approximating model given the data and the set of models considered

Model I.D.	Model parameters	AIC	ΔAIC	W
28	30% Sea ice, 30% to disappearance, 30% sea ice \times 30% to disappearance	634.26	0	0.21
32	20% Sea ice, 20% to disappearance, 20% sea ice \times 20% to disappearance	635.32	1.06	0.12
30	20% Sea ice	636.34	2.08	0.07
17	50% Sea ice	636.60	2.34	0.06
21	40% Sea ice	636.80	2.54	0.06

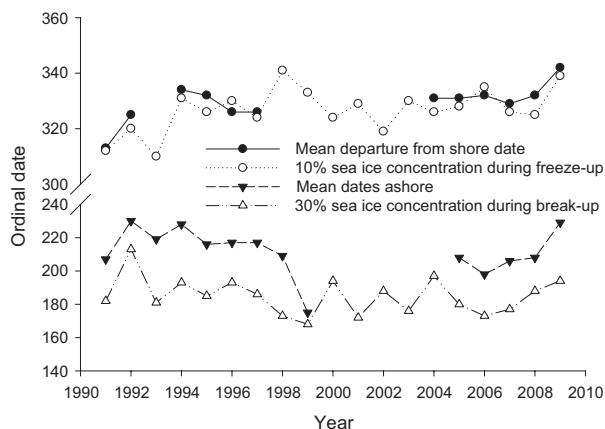


Fig. 2. Dates of sea ice concentrations that best corresponded to dates ashore during break-up and departure from shore dates during freeze-up for collared polar bears in western Hudson Bay. Dates ashore and departure from shore dates are shown as annual means for all collared polar bears.

Table 3. AIC results for the best 5 of 36 candidate models to predict polar bear departure from shore dates. AIC is the AIC score for each model, Δ AIC is the difference in AIC scores between different candidate models and the best model, and w is the AIC weight or the weight of evidence that a model is the best approximating model given the data and the set of models considered

Model I.D.	Model parameters	AIC	Δ AIC	w
3	10% Sea ice, appearance to 10%	696.44	0	0.43
4	10% Sea ice, appearance to 10%, 10% sea ice \times appearance to 10%	697.48	1.04	0.26
1	10% Sea ice	699.82	3.38	0.08
16	40% Sea ice, appearance to 40%, 40% sea ice \times appearance to 40%	700.62	4.18	0.05
20	50% Sea ice, appearance to 50%, 50% sea ice \times appearance to 50%	701.10	4.66	0.04

concentration during freeze-up and the number of days between appearance of ice and 10% ice concentrations (Model 3, $F_{2, 102} = 30.16$, $P < 0.001$) (Table 3). Examination of the parameter estimates for the best model indicated that all parameters included were strong predictors for departure from shore (Table 4). Later dates of 10% sea ice concentration and slower ice formation during freeze-up tended to result in delayed departures. Collared polar bears departed from shore an average of 2.5 days, S.E. = 0.7, after 10% freeze-up (Fig. 2). The second best model predicting arrival ashore had a Δ AIC < 2 and had all of the same parameters as the best model but also included the interaction between 10% sea ice concentration and the number of days between ice appearance and 10% sea ice concentration (Model 4, $F_{3, 101} = 20.40$, $P < 0.001$). Examination of the parameter estimates in the

second best model, however, indicated that the interaction term was not a strong predictor of departure date (Table 4). Arrival ashore for collared bears showed a temporal trend towards occurring earlier ($\beta = -0.88$, CI = -1.50 to -0.26 , $P < 0.01$) and departure from shore showed a trend towards occurring later ($\beta = 0.67$, CI = 0.44 – 0.90 , $P < 0.001$).

The distances between polar bear capture locations and where they came to shore during break-up in subsequent year(s) ranged from 3 to 720 km (mean = 118, S.E. = 17). Throughout the study, 12% of the arrival ashore locations occurred outside the western zone. If bears did not arrive ashore in the western zone, they typically came to shore further south and east. Only one bear came ashore north of Churchill (approximately 20 km north of the town in 2008). The lowest degree of fidelity occurred in 2007, when four of nine females came to shore in the southern zone and three bears came to shore between the Ontario border and Nelson River (Fig. 1).

All the models with substantial evidence to predict polar bear fidelity generated similar conclusions regarding potential sea ice variables (Model 9, $F_{3, 72} = 10.74$, $P < 0.001$; Model 22, $F_{3, 72} = 9.99$, $P < 0.001$; Model 13, $F_{4, 71} = 8.00$, $P < 0.001$; Tables 5, 6). The date of a given sea ice concentration during break-up (i.e. 30 or 20%) and the rate of ice disappearance were either excluded or found to be weak predictors in these models (Table 6). Conversely, polar bear fidelity in these models was predicted by the ice concentration in the southern Hudson Bay zone relative to the western Hudson Bay zone and the interaction between this variable and the rate of ice disappearance (Table 6). Polar bears tended to show less fidelity when there was relatively more ice present in the southern Hudson Bay zone compared to the western Hudson Bay zone, and this pattern was exacerbated when rates of ice disappearance were relatively high (Table 6).

Discussion

Highly mobile marine predators have few barriers to impede their movement so factors determining their geographical distribution and migration patterns are likely linked to fluctuations in environmental conditions, the spatiotemporal distribution of resources and energetic benefits received from site fidelity (Vibe 1967; Cotté *et al.* 2009; Jorgensen *et al.* 2009). In this study, we examined how the dynamic nature of an Arctic sea ice ecosystem, with strong intra- and inter-annual variations in ice distribution, can affect the migration patterns and seasonal fidelity of an apex Arctic marine predator, the polar bear. Polar bear migratory behaviour between land and sea ice environments was linked to specific sea ice conditions that occurred during annual break-up and freeze-up periods. Previously, annual mean arrival ashore for polar bears in western Hudson Bay was found to be correlated with the timing of 50% ice concentration in regions approximated by the Western Hudson Bay population management

Table 4. Parameter estimates, S.E. and 95% confidence intervals (CI) for polar bear date ashore and departure from shore models with substantial evidence, $\Delta AIC < 2$ (Burnham & Anderson 2002)

Model I.D.	Parameter	Estimate	S.E.	95% CI		P-value
				Lower	Upper	
28 Date ashore	30% Sea ice	0.81	0.17	0.49	1.14	< 0.001
	30% to disappearance	-0.33	0.56	-1.43	0.77	> 0.05
	30% Sea ice \times 30% to disappearance	-0.21	0.08	-0.37	-0.05	< 0.01
	Constant	218.20	2.37	213.55	222.84	< 0.001
32 Date ashore	20% Sea ice	0.90	0.18	0.55	1.25	< 0.001
	20% to disappearance	-0.20	0.55	-1.27	0.88	> 0.05
	20% Sea ice \times 20% to disappearance	-0.14	0.07	-0.27	-0.02	< 0.05
	Constant	216.71	2.12	212.55	220.86	< 0.001
3 Departure from shore	10% Sea ice	0.72	0.11	0.51	0.93	< 0.001
	appearance to 10%	1.13	0.49	0.17	2.09	< 0.05
	Constant	329.99	0.67	328.68	331.31	< 0.001
4 Departure from shore	10% sea ice	0.65	0.13	0.38	0.91	< 0.001
	appearance to 10%	1.40	0.56	0.30	2.50	< 0.05
	10% sea ice* appearance to 10%	0.14	0.15	-0.15	0.44	> 0.05
	Constant	329.63	0.77	328.12	331.14	< 0.001

Table 5. AIC results for the best 5 of 26 candidate models to predict polar bear fidelity. AIC is the AIC score for each model, ΔAIC is the difference in AIC scores between different candidate models and the best model, and w is the AIC weight or the weight of evidence that a model is the best approximating model given the data and the set of models considered. Definitions of variables: SH/WH at 30% is ice concentration in the southern Hudson Bay zone relative to the western Hudson Bay zone on the date of 30% sea ice in the 95% MCP. Refer to Table 1 for all other variable definitions

Model I.D.	Model parameters	AIC	ΔAIC	w
9	30% to disappearance, SW/WH at 30%, 30% to disappearance \times SW/WH at 30%	959.24	0	0.31
22	20% to disappearance, SW/WH at 20%, 20% to disappearance \times SW/WH at 20%	960.92	1.68	0.13
13	30% sea ice, 30% to disappearance, SW/WH at 30%, 30% to disappearance \times SW/WH at 30%	961.10	1.86	0.12
26	20% sea ice, 20% to disappearance, SW/WH at 20%, 20% to disappearance \times SW/WH at 20%	961.66	2.42	0.09
11	30% sea ice, 30% to disappearance, SW/WH at 30%, 30% sea ice \times 30% to disappearance	961.90	2.66	0.08

zone (Stirling, Lunn & Iacozza 1999). However, in this study we tested a range of sea ice concentration increments and accounted for the rate of ice disappearance to determine a suite of factors that best predicted the timing

of polar bear migration on and off land. Using these multivariate methods that included the rate of ice disappearance and higher resolution (SSM/I) daily sea ice data, we found that polar bear dates ashore were best correlated with the timing of 30% sea ice concentration during break-up. We additionally determined that timing of 10% ice concentration during freeze-up, when considered with rate of ice appearance, was correlated with polar bear departure from shore dates (Fig. 2). These results represent the first quantitative evidence of the relationship between sea ice conditions and polar bear departure from onshore refugia anywhere in the Arctic.

In Hudson Bay, freeze-up typically occurs in the western portion first, with ice forming along the north-west shoreline and spreading south-east (Derocher & Stirling 1990; Gough, Cornwall & Tsuji 2004). When total ice cover in the 95% MCP was 10%, most of the existing ice was likely distributed along the western coast where polar bears aggregate to await freeze-up (Latour 1981; Derocher & Stirling 1990). Thus, the local ice concentrations that bears were exposed to when departing from shore were likely greater than 10%. Nevertheless, given that polar bears in this region congregate in coastal areas in anticipation of freeze-up, they should be expected to initiate migration at the minimum functional sea ice concentration. Such knowledge regarding how large-scale environmental factors are correlated to the timing of migration is important to conservation efforts for migratory species (Mueller *et al.* 2008; Harris *et al.* 2009; Jonker *et al.* 2010); particularly those inhabiting geographical regions greatly affected by climate change (Laidre *et al.* 2008). Future climate scenarios for Arctic and sub-Arctic environments forecast long-term increases in atmospheric temperatures coupled with changes to sea ice freeze-thaw cycles (Gagnon & Gough 2005b; Holland, Bitz & Tremblay 2006; Zhang & Walsh 2006). We have presented a

Table 6. Parameter estimates, S.E. and 95% confidence interval (CI) for parameters in polar bear fidelity models with substantial evidence, $\Delta AIC < 2$ (Burnham & Anderson 2002)

Model I.D.	Parameter	Estimate	S.E.	95% CI		P-value
				Lower	Upper	
9	30% to disappearance	-6.26	3.83	-13.77	1.25	> 0.05
	SW/WH at 30%	64.39	18.94	27.27	101.51	< 0.01
	30% to disappearance \times SW/WH at 30%	-10.66	4.90	-20.27	-1.04	< 0.05
	Constant	119.92	14.73	91.04	148.80	< 0.001
22	20% to disappearance	-9.63	4.94	-19.32	0.07	> 0.05
	SW/WH at 20%	39.14	10.71	18.15	60.14	< 0.001
	20% to disappearance \times SW/WH at 20%	-6.37	2.98	-12.22	-0.53	< 0.05
	Constant	125.21	15.07	95.67	154.73	< 0.001
13	30% sea ice	0.48	1.29	-2.06	3.01	> 0.05
	30% to disappearance	-6.81	4.13	-14.91	1.29	> 0.05
	SW/WH at 30%	63.81	19.12	26.33	101.28	< 0.01
	30% to disappearance \times SW/WH at 30%	-10.73	4.94	-20.41	-1.05	< 0.05
	Constant	120.26	14.85	91.15	149.37	< 0.001

mechanistic understanding of how sea ice dynamics affect polar bear migration that will provide a quantitative basis for predicting how future climate warming will affect the length of onshore fasting periods for polar bears in western Hudson Bay.

Changes to the timing of migration patterns as a result of varying environmental conditions have been observed in several species (Sims *et al.* 2004; Swanson & Palmer 2009; Srygley *et al.* 2010) and may lead to disruptions in the spatiotemporal overlap with key resources (Robinson *et al.* 2008). Throughout our study, collared polar bears showed trends towards arriving onshore earlier during break-up and departing from shore later during freeze-up. The consequent reductions to the amount of time polar bears had access to ice-associated seal prey likely resulted in negative effects on reproduction and survival (Derocher & Stirling 1995; Stirling, Lunn & Iacozza 1999; Regehr *et al.* 2007; Molnár *et al.* 2010, 2011). Subadult bears, with their smaller absolute fat stores, are likely to be the most severely affected by a prolonged fasting period and it is likely that the reduced survival of subadults, as identified by Regehr *et al.* (2007), has continued in more recent years. Furthermore, nutritional stress associated with later departures from shore during freeze-up has been linked to increases in human-bear conflicts, particularly among subadult bears, in the western Hudson Bay region (Townsend *et al.* 2009).

In addition to monitoring the timing of break-up and freeze-up, understanding the effects of climate change on other aspects of regional ice dynamics, such as the seasonal rate of ice formation and disappearance, will be especially relevant to predicting future polar bear migration patterns. In our study, earlier break-up combined with higher rates of ice disappearance resulted in polar bears arriving ashore earlier in the year, which was likely because they were forced to move towards familiar onshore regions more quickly. Timing and rate of ice disappearance and formation are dependent upon numerous

interacting factors related to trends in atmospheric circulation, temperatures and wind direction (Mysak *et al.* 1996; Wang *et al.* 2004; Hochheim & Barber 2010). Understanding how these factors are affected by anthropogenic greenhouse gases will be a crucial component of predicting future polar bear migration behaviour in relation to climate change. In addition to climate-induced shifts to annual patterns of sea ice cover, decreased ice thickness throughout Arctic regions is also likely to affect ice-dependent marine ecosystems (Moline *et al.* 2008). Decreases to ice thickness will probably hinder polar bear mobility through highly fractured ice during break-up, which may force bears to abandon the sea ice and head for land at an earlier date.

Climate-induced changes in the spatial or temporal distribution of resources also have the potential to negatively impact specialist species by reducing the benefits gained by previously formed patterns of seasonal fidelity; however, responses and adaptations to these environmental changes are likely to vary. For example, animals that demonstrate strong site fidelity may not alter their distribution despite decreases to habitat quality (Ganter & Cooke 1998; Laidre & Heide-Jørgensen 2005; Matthews & Haiganoush 2010). Conversely, some animals may shift their distribution to unfamiliar or poorer quality habitat (Ficke, Myrick & Hansen 2007; Stillman & Goss-Custard 2010). Because ice usually remains later in southern Hudson Bay (Wang, Mysak & Ingram 1994; Gough & Allakhverdova 1999; Saucier *et al.* 2004), we hypothesized polar bears would face a trade-off in years with early break-up: either come to shore early in the traditional summer range or attempt to remain on the ice longer but come to shore further south and east along the Ontario coast. We found that polar bears displayed high degrees of fidelity even when sea ice disappeared relatively early, suggesting that coming ashore in a familiar location may be more important than remaining longer on the ice (Derocher & Stirling 1990; Stirling *et al.* 2004). For many

wildlife species, the choice to abandon site fidelity represents a balance between risks associated with using unfamiliar habitat and benefits associated with potentially maximizing energy acquisition by moving to new areas (Greenwood 1980; Bensch & Hasselquist 1991; Bradshaw *et al.* 2004). For female polar bears, additional energy gained from foraging in the remaining seasonal habitat may not outweigh risks to reproductive success caused by spending shore-bound or maternity denning periods in unfamiliar areas. Similarly, energetic benefits gained from extended hunting in southerly locations may not outweigh the costs associated with walking on land back to familiar habitat, especially for pregnant adult females seeking a maternity den site. Observed lower fidelity in certain years was due to a combination of faster than normal ice disappearance and environmental factors, possibly wind, which forced ice away from the coastal regions of western Hudson Bay. When these conditions occurred some bears were likely unable to navigate towards land in the vicinity of their usual summer habitat. Climate change has been predicted to increase future high wind events and positive local temperature anomalies during break-up in Hudson Bay (Knippertz, Ulbrich & Speth 2000; Joly *et al.* 2010), which is likely to affect both the distribution of sea ice and rate of ice disappearance. Therefore, under current climate change scenarios, we expect the fidelity of polar bears to specific onshore regions during the ice-free period to decline.

Climate change is predicted to alter weather patterns and environmental conditions, not only in Arctic ecosystems, but globally (ACIA 2005). Understanding how large-scale seasonal environmental conditions affect the timing and geographical distribution of synchronized animal movement patterns is a central aspect of quantifying and predicting the effects of climate change on wide-ranging philopatric species. For polar bears in western Hudson Bay, changes to the timing and rate of sea ice break-up and formation are altering seasonal migration patterns and increasing the length of time they spend on land without access to calorie-rich marine mammal prey. Less access to high energy food sources will most likely result in additional reductions to body condition, reproductive success and population numbers.

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References

- ACIA. (2005) *Arctic Climate Impact Assessment*. Cambridge University Press, New York.
- Alerstam, T., Hedenström, A. & Åkesson, S. (2003) Long-distance migration: evolution and determinants. *Oikos*, **103**, 247–260.
- Allison, P.D. (1999) *Logistic regression using the SAS system: theory and application*. SAS Institute, Cary, North Carolina.
- Baker, J.D., Antonelis, G.A., Fowler, C.W. & York, A.E. (1995) Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behaviour*, **50**, 237–247.
- Bensch, S. & Hasselquist, D. (1991) Territory infidelity in the polygynous great reed warbler *Acrocephalus arundinaceus* the effect of variation in territory attractiveness. *Journal of Animal Ecology*, **60**, 857–871.
- Berthold, P. (1991) Recent advances in studies of bird migration. *Annual Review of Ecology, Evolution, and Systematics*, **22**, 357–378.
- Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81–83.
- Bradshaw, C.J.A., Hindell, M.A., Summer, M.D. & Michael, K.J. (2004) Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour*, **68**, 1349–1360.
- Bronson, F.H. (2009) Climate change and seasonal reproduction in mammals. *Philosophical Transactions of the Royal Society of London B*, **364**, 3331–3340.
- Brown, C.R., Brown, M.B. & Brazeal, K.R. (2008) Familiarity with breeding habitat improves daily survival in colonial cliff swallows. *Animal Behaviour*, **76**, 1201–1210.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd Edition. Springer-Verlag, New York, USA.
- Cotté, C., Taupier-Letage, I., Mate, B. & Petiau, E. (2009) Scale-dependent habitat use by a large free-ranging predator, the Mediterranean fin whale. *Deep-Sea Research Part 1 Oceanographic Research Papers*, **56**, 80–811.
- Dawson, A. (2008) Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philosophical Transaction of the Royal Society B*, **363**, 1621–1633.
- Derocher, A.E., Andriashek, D. & Arnould, J.P.Y. (1993) Aspects of milk composition and lactation in polar bears. *Canadian Journal of Zoology*, **71**, 561–567.
- Derocher, A.E., Lunn, N.J. & Stirling, I. (2004) Polar bears in a warming climate. *Integrative and Comparative Biology*, **44**, 163–176.
- Derocher, A.E. & Stirling, I. (1990) Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson-Bay. *Canadian Journal of Zoology*, **68**, 1395–1403.
- Derocher, A.E. & Stirling, I. (1995) Temporal variation in reproduction and body mass of polar bears in western Hudson Bay. *Canadian Journal of Zoology*, **73**, 1657–1665.
- Deutsch, C., Reid, J., Bonde, R., Easton, D., Kochman, H. & O'Shea, T. (2003) Seasonal movements, migratory behavior, and site fidelity of West Indian manatees along the Atlantic coast of the United States. *Wildlife Monographs*, **151**, 1–77.
- Dingle, H. & Drake, V. (2007) What is migration? *BioScience*, **57**, 113–121.
- Durner, G.M., Douglas, D.C., Nielson, R.M., Amstrup, S.C., McDonald, T.L., Stirling, I., Mauritzen, M., Born, E.W., Wiig, Ø., DeWeaver, E., Serreze, M.C., Belikov, S.E., Holland, M.M., Maslanik, J., Aars, J., Bailey, D.A. & Derocher, A.E. (2009) Predicting 21st-century polar bear habitat distribution from global climate models. *Ecological Monographs*, **79**, 25–58.
- Ferguson, S.H., Taylor, M.K. & Messier, F. (2000) Influence of sea ice dynamics on habitat selection by polar bears. *Ecology*, **81**, 761–772.
- Ficke, A., Myrick, C. & Hansen, L. (2007) Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries*, **17**, 581–613.
- Fryxell, J.M. & Sinclair, A.R.E. (1988) Causes and consequences of migration of large herbivores. *Trends in Ecology and Evolution*, **3**, 237–241.
- Gagnon, A.S. & Gough, W.A. (2005a) Trends in the dates of ice freeze-up and break-up over Hudson Bay, Canada. *Arctic*, **58**, 370–382.
- Gagnon, A.S. & Gough, W.A. (2005b) Climate change scenarios for the Hudson Bay region: an intermodel comparison. *Climate Change*, **69**, 269–297.
- Ganter, B. & Cooke, F. (1998) Colonial nesters in a deteriorating habitat: site fidelity and colony dynamics of lesser snow geese. *The Auk*, **115**, 642–652.

- Gough, W.A. & Allakhverdova, T. (1999) Limitations of using a coarse resolution model to assess the impact of climate change on sea ice in Hudson Bay. *The Canadian Geographer*, **43**, 415–422.
- Gough, W.A., Cornwall, A.R. & Tsuji, L.J.S. (2004) Trends in seasonal sea ice duration in southwestern Hudson Bay. *Arctic*, **57**, 299–305.
- Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.
- Greenwood, P.J. & Harvey, P.H. (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, **13**, 1–21.
- Gwinner, E. (1996) Circadian and circannual programmes in avian migration. *The Journal of Experimental Biology*, **199**, 39–48.
- Harris, G., Thirgood, S., Hopcraft, J., Cromsigt, J. & Berger, J. (2009) Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, **7**, 55–76.
- Hobson, K.A., Stirling, I. & Andriashek, D.S. (2009) Isotopic homogeneity of breath CO₂ from fasting and berry-eating polar bears: implications for tracing reliance on terrestrial foods in a changing Arctic. *Canadian Journal of Zoology*, **87**, 50–55.
- Hochheim, K.P. & Barber, D.G. (2010) Atmospheric forcing of sea ice in Hudson Bay during the fall period, 1980–2005. *Journal of Geophysical Research*, **115**, C05009.
- Holland, M.M., Bitz, C.M. & Tremblay, B. (2006) Future abrupt reductions in the summer Arctic sea ice. *Geophysical Research Letters*, **33**, L23503.
- Joly, S., Senneville, S., Caya, D. & Saucier, F.J. (2010) Sensitivity of Hudson Bay sea ice and ocean climate to atmospheric temperature forcing. *Climate Dynamics*, DOI: 10.1007/s00382-009-0731-4.
- Jonker, R.M., Eichhorn, G., van Langevelde, F. & Bauer, S. (2010) Predation danger can explain changes in timing of migration: the case of the barnacle goose. *PLoS ONE*, **5**, e11369.
- Jorgensen, S.J., Reeb, C.A., Chapple, T.K., Anderson, S., Perle, C., Van Sommeran, S.R., Fritz-Cope, C., Brown, A.C., Klimley, A.P. & Block, B.A. (2009) Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society B*, **277**, 679–688.
- Knippertz, P., Ulbrich, U. & Speth, P. (2000) Changing cyclones and surface wind speeds over the North Atlantic and Europe in a transient GHG experiment. *Climate Research*, **15**, 109–122.
- Laidre, K.L. & Heide-Jørgensen, M.P. (2005) Arctic sea ice trends and narwhal vulnerability. *Biological Conservation*, **121**, 509–517.
- Laidre, K.L., Heide-Jørgensen, M.P., Logsdon, M.L., Hobbs, R.C., Dietz, R. & VanBlaricom, G.R. (2004) Fractal analysis of narwhale space use patterns. *Zoology*, **107**, 3–11.
- Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, Ø., Heide-Jørgensen, M.P. & Ferguson, S.H. (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications*, **18**, S97–S125.
- Latour, P.B. (1981) Spatial relationships and behavior of polar bears (*Ursus maritimus* Phipps) concentrated on land during the ice-free season of Hudson Bay. *Canadian Journal of Zoology*, **59**, 1763–1774.
- Lunn, N.J. & Stirling, I. (1985) The significance of supplemental food to polar bears during the ice-free period of Hudson Bay. *Canadian Journal of Zoology*, **63**, 2291–2297.
- Lunn, N.J., Stirling, I. & Andriashek, D. (2004) Selection of maternity dens by female polar bears in western Hudson Bay, Canada and the effects of human disturbance. *Polar Biology*, **27**, 350–356.
- Mansfield, K.L., Saba, V.S., Keinath, J.A. & Musick, J.A. (2009) Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwest Atlantic. *Marine Biology*, **156**, 2555–2570.
- Marra, P.P., Francis, C.M., Mulvihill, R.S. & Moore, F.R. (2005) The influence of climate on the timing and rate of spring bird migration. *Oecologia*, **142**, 307–315.
- Matthews, K.R. & Haiganoush, H.K. (2010) Site fidelity of the declining amphibian *Rana sierrae* (Sierra Nevada yellow-legged frog). *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 243–255.
- Mauritzen, M., Belikov, S.E., Boltunov, A.N., Derocher, A.E., Hansen, E., Ims, R.A., Wiig, Ø. & Yoccoz, N. (2003) Functional responses in polar bear habitat selection. *Oikos*, **100**, 112–124.
- Milligan, S.R., Holt, W.V. & Lloyd, R. (2009) Impacts of climate change and environmental factors on reproduction and development in wildlife. *Philosophical Transactions of the Royal Society B*, **364**, 3313–3319.
- Moline, M.A., Karnovsky, N.J., Brown, Z., Divoky, G.J., Frazer, T.K., Jacoby, C.A., Torres, J.J. & Fraser, W.R. (2008) High latitude changes in ice dynamics and their impact on polar marine ecosystems. *Year in Ecology and Conservation Biology 2008*, **113**, 267–319.
- Molnár, P.K., Derocher, A.E., Thiemann, G.W. & Lewis, M.A. (2010) Predicting survival, reproduction, and abundance of polar bears under climate change. *Biological Conservation*, **143**, 1612–1622.
- Molnár, P.K., Derocher, A.E., Klanjscek, T. & Lewis, M.A. (2011) Predicting climate change impacts on polar bear litter size. *Nature Communications*, **2**, 186.
- Mueller, T., Olson, K.A., Fuller, T.K., Schaller, G.B., Murray, M.G. & Leimgruber, P. (2008) In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology*, **45**, 649–658.
- Mysak, L.A., Ingram, R.G., Wang, J. & Van Der Baaren, A. (1996) The anomalous sea-ice extent in Hudson Bay, Baffin Bay and the Labrador Sea during three simultaneous NAO and ENSO episodes. *Atmosphere-Ocean*, **34**, 313–343.
- PBSG (2006) *Polar Bears: proceedings of the 14th Working Meeting of the IUCN/SSC Polar Bear Specialist Group*, 20–24 June 2005, Seattle, Washington, USA. (eds J. Aars, N.J. Lunnand & A.E. Derocher), pp. 101–116. IUCN, Gland, Switzerland and Cambridge, UK.
- Peron, G., Lebreton, J.D. & Crochet, P.A. (2010) Breeding dispersal in black-headed gull: the value of familiarity in a contrasted environment. *Journal of Animal Ecology*, **79**, 317–326.
- Post, E. & Forchhammer, M.C. (2002) Synchronization of animal population dynamics by large-scale climate. *Nature*, **420**, 168–171.
- Post, E. & Forchhammer, M.C. (2008) Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B*, **363**, 2369–2375.
- Ramsay, M.A. & Hobson, K.A. (1991) Polar bears make little use of terrestrial food webs – evidence from stable-carbon isotope analysis. *Oecologia*, **86**, 598–600.
- Ramsay, M.A. & Stirling, I. (1988) Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of Zoology*, **214**, 601–634.
- Rasmussen, K., Palacios, D.M., Calambokidis, J., Saborio, M.T., Dalla Rosa, L., Secchi, E.R., Steiger, G.H., Allen, J.M. & Stone, G.S. (2007) Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biology Letters*, **3**, 302–305.
- Regehr, E.V., Lunn, N.J., Amstrup, S.C. & Stirling, I. (2007) Population decline of polar bears in western Hudson Bay in relation to climate change. *Journal of Wildlife Management*, **71**, 2673–2683.
- Robinson, R.A., Crick, H.Q., Learmonth, J.A., Maclean, I.M.D., Thomas, C.D., Bairlein, F., Forchhammer, M.C., Francis, C.M., Gill, J.A., Godley, B.J., Harwood, J., Hays, G.C., Huntley, B., Hutson, A.M., Pierce, G.J., Rehfish, M.M., Sims, D.W., Vieira dos Santos, M.C., Sparks, T.H., Stroud, D. & Visser, M.E. (2008) Travelling through a warming world: climate change and migratory species. *Endangered Species Research*, **7**, 87–99.
- Rojas-Martínez, A., Valiente-Banuet, A., Arizmendi, M.C., Alcántara-Eguren, A. & Arita, H.T. (1999) Seasonal distribution of the long-nosed bat (*Leptonycteris curasoae*) in North America: does a generalized migration pattern really exist? *Journal of Biogeography*, **26**, 1065–1077.
- Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S. & Imeson, A. (2008) Attributing physical and biological impacts to anthropogenic climate change. *Nature*, **453**, 353–358.
- Sabine, D.L., Morrison, S.F., Whitlaw, H.A., Ballard, W.B., Forbes, G.J. & Bowman, J. (2002) Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. *Journal of Wildlife Management*, **66**, 718–728.
- Saino, N., Rubolini, D., Lehikoinen, E., Sokolov, L.V., Bonisoli-Alquati, A., Ambrosini, R., Giuseppe, B. & Moller, A. (2009) Climate change effects on migration phenology may mismatch brood parasitic cuckoos and their hosts. *Biology Letters*, **5**, 593–541.
- Saucier, F.J., 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. *Climate Dynamics*, **23**, 303–326.
- Schliebe, S., Rode, K.D., Gleason, J.S., Wilder, J., Proffitt, K., Evans, T. J. & Miller, S. (2008) Effects of sea ice extent and food availability on spatial and temporal distribution of polar bears during the fall open-water period in the southern Beaufort Sea. *Polar Biology*, **31**, 999–1010.
- Scott, J.B.T. & Marshall, G.J. (2010) A step-change in the date of sea-ice breakup in western Hudson Bay. *Arctic*, **63**, 155–164.

- Sims, D.W., Wearmouth, V.J., Genner, M.J., Southward, A. & Hawkins, S.J. (2004) Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology*, **73**, 333–341.
- Singh, N.J. & Milner-Gulland, E.J. (2011) Conserving a moving target: planning protection for a migratory species as its distribution changes. *Journal of Applied Ecology*, **48**, 35–46.
- Smith, P.A., Elliott, K.H., Gaston, A.J. & Gilchrist, H.G. (2010) Has early ice clearance increased predation on breeding birds by polar bears? *Polar Biology*, **33**, 1149–1153.
- Srygley, R.B., Dudley, R., Oliveira, E.G., Aizprua, R., Pelaez, N.Z. & Riveros, A.J. (2010) El Niño and dry season rainfall influence hostplant phenology and an annual butterfly migration from neotropical wet to dry forests. *Global Change Biology*, **16**, 936–945.
- Stefanescu, C., Peñuelas, J. & Filella, I. (2003) Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology*, **9**, 1494–1506.
- Stempniewicz, L. (2006) Polar bear predatory behaviour toward molting barnacle geese and nesting glaucous gulls on Spitzbergen. *Arctic*, **59**, 247–251.
- Stillman, R.A. & Goss-Custard, J.D. (2010) Individual based ecology of coastline birds. *Biological Reviews*, **85**, 413–434.
- Stirling, I. & Derocher, A.E. (1993) Possible impacts of climatic warming on polar bears. *Arctic*, **46**, 240–245.
- Stirling, I., Lunn, N.J. & Iacozza, J. (1999) Long-term trends in the population ecology of polar bears in Western Hudson Bay in relation to climatic change. *Arctic*, **52**, 294–306.
- Stirling, I. & Parkinson, C.L. (2006) Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic*, **59**, 261–275.
- Stirling, I., Spencer, C. & Andriashek, D. (1989) Immobilization of polar bears (*Ursus maritimus*) with Telazol in the Canadian Arctic. *Journal of Wildlife Diseases*, **25**, 159–168.
- Stirling, I., Lunn, N.J., Iacozza, J., Elliott, C. & Obbard, M. (2004) Polar bear distribution and abundance on the southwestern Hudson Bay coast during open water season, in relation to population trends and annual ice patterns. *Arctic*, **57**, 15–26.
- Swanson, D.L. & Palmer, J.S. (2009) Spring migration phenology of birds in the Northern Prairie region is correlated with local climate change. *Journal of Field Ornithology*, **80**, 351–363.
- Switzer, P.V. (1993) Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, **7**, 533–555.
- Towns, L., Derocher, A.E., Stirling, I., Lunn, N.J. & Hedman, D. (2009) Spatial and temporal patterns of problem polar bears in Churchill, Manitoba. *Polar Biology*, **32**, 1529–1537.
- Tynan, C.T. & DeMaster, D.P. (1997) Observations and predictions of arctic climatic change: potential effects on marine mammals. *Arctic*, **50**, 308–322.
- Vibe, C. (1967) Arctic animals in relation to climatic fluctuations. *Meddelelser om Grønland*, **170**, 1–226.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Wang, J., Mysak, L.A. & Ingram, R.G. (1994) A numerical simulation of sea ice cover in Hudson Bay. *Journal of Physical Oceanography*, **24**, 2515–2533.
- Wang, J., Wu, B., Tang, C.L., Walsh, J.E. & Ikeda, M. (2004) Seesaw structure of subsurface temperature anomalies between the Barents Sea and the Labrador Sea. *Geophysical Research Letters*, **31**, L19301.
- Zhang, X. & Walsh, J.E. (2006) Toward a seasonally ice-covered Arctic Ocean: scenarios from the IPCC AR4 model simulations. *Journal of Climate*, **19**, 1730–1747.

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