

Determinants of Home Range Size for Polar Bears (*Ursus maritimus*)

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Abstract

The mean home range size of female polar bears (*Ursus maritimus*; $125\,100\text{ km}^2 \pm 11\,800$; $n = 93$) is substantially larger than the predicted value (514 km^2) for a terrestrial carnivore of similar weight. To understand this difference, we correlated home range size and sea ice characteristics. Home range size was related to (i) the ratio of land vs. sea within a given home range (42% of explained variance), and (ii) seasonal variation in ice cover (24%). Thus, bears using land during the ice-free season had larger home ranges and bears living in areas of great seasonal variation in ice cover also had larger home ranges. In another analysis we investigated how variation in a bear's environment in space and time affects its choice of home range. We found that polar bears adjusted the size of their home range according to the amount of annual and seasonal variation within the centre of their home range. For example, polar bears experiencing unpredictable seasonal and annual ice tended to increase their home range size if increasing home range size resulted in reducing variation in seasonal and annual ice. Polar bears make trade-offs between alternate space-use strategies. Large home ranges occur when variable ice cover is associated with more seals but also a more unpredictable distribution of those seals.

Keywords

Allometry, Arctic, body size, home range, polar bears, predictability, sea ice, seasonality, *Ursus maritimus*, variation

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INTRODUCTION

Environmental variation can have profound influences on population processes (Southwood 1988; Abrams 1997; Johst & Brandl 1997). Animals attempt to reduce variation in their life processes through space use (e.g. Wauters & Dhondt 1992) assuming that they can accurately assess environmental variation (Lima & Zollner 1996). Reducing variation in life processes can afford greater fitness provided that geometric mean fitness is greater than stochastic tracking of environmental perturbations (Yoshimura & Jansen 1996). This environmental unpredictability would explain the evolution of homeostatic adaptations by animals to reduce detrimental environmental variation on survival and reproduction. Similarly, animals may change behaviour through differential movement patterns and range use (e.g. seasonal movements) in an effort to control environmental heterogeneity and create more stable life history responses to external perturbations. This pattern of controlling

environmental influences is likely more pronounced in large animals because of their size.

Recent analyses suggest that polar environments are highly variable in both time and space (Ferguson & Messier 1996; Smith *et al.* 1998), but the implications of that variability for population processes are basically unknown. The sea-ice landscape is not only highly variable seasonally but also highly variable spatially (Walsh *et al.* 1979; Smith *et al.* 1998; Ferguson *et al.* 1999). Spatial variability, annual fluctuations, and extreme seasonality of sea ice coverage are linked to inherent variability characteristic of marine polar ecosystems (McGowan *et al.* 1998). External physical forces may play a more dominant role in causing variability in marine ecosystems compared to terrestrial ecosystems (Steele 1991; Underwood 1996; Smith *et al.* 1998). The annual advance and retreat of sea ice affects all levels of Arctic marine ecosystems, including the timing and magnitude of seasonal primary production, the abundance, distribution and recruitment of zooplankton, and the demography and

space-use patterns of top predators (Vibe 1967; Smith *et al.* 1995).

Polar bear (*Ursus maritimus*) is an apex predator living among the Arctic sea ice (Stirling & Derocher 1992). Polar bears may react to environmental fluctuations or environmental predictability with large home range size (e.g. Amstrup 1986; Garner *et al.* 1990). Here, we test whether large home range sizes of polar bears are due to spatial and temporal variation in sea ice. We assume that animals attempt to reduce variation in their life processes through space and time, and that they can accurately assess environmental variation. Thus, we predict that polar bears will adjust home range size to reduce environmental variation in space and time. For example, if the centre of their home range shows low temporal variation in ice characteristics relative to surrounding areas then we predict smaller home range size. This would include a space-use strategy whereby polar bears maintain a small home range within a predictable environment. In contrast, if the centre of their home range includes high temporal variation in ice characteristics relative to the surrounding area then we predict larger home range size. This would include a space-use strategy whereby polar bears extend their home range to reduce environmental variation in space and time. Hence, environmental variability affects decisions on the parts of the environment that a polar bear incorporates into its home range and the time that it is used.

METHODS

The arctic environment under study extends south (60°N), north (80°N), east (65°W), and west (110°W; Fig. 1). Of the study area (2.3×10^6 km²), 55% is covered by sea ice for at least 6 months of the year. More open water occurs in the Baffin Bay-Davis Strait area than other regions. The Arctic region of Canada and Greenland is dominated by a cycle of almost total ice cover in late winter and minimum ice extent in September (Collin & Dunbar 1964; Ferguson *et al.* 1999).

We used satellite telemetry (Argos Data Collection & Location System, Fancy *et al.* 1988) to obtain polar bear locations (1989–97) every 4 or 6 days (Messier *et al.* 1994) from 110 adult female bears equipped with radio collars (Telonics, Inc., Mesa, Arizona; Messier *et al.* 1992; Ferguson *et al.* 1997). Bears were captured from helicopter using darting equipment (Stirling *et al.* 1989) either in spring (April–May) or autumn (September–October) of 1989–96. The latitude-longitude coordinates received via satellite were transformed to Universal Transverse Mercator coordinates using SPANSTM GIS (Intera Tydac Technologies, Inc. 1994).

Nonparametric estimators (e.g. kernel contouring) are less influenced by outliers than other estimators of home

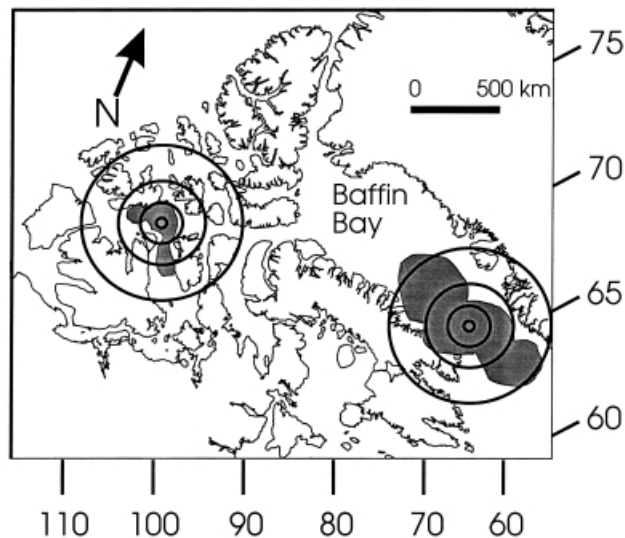


Figure 1 Arctic study area showing two examples of home ranges (95% kernel) of female polar bears in the Arctic Archipelago (left) and Baffin Bay region (right). Also shown are various radii (50, 100, 200, and 400 km) that circle the median location of bear home ranges.

range size (Silverman 1986; Worton 1989; Seaman & Powell 1996) which is a concern with nomadic animals such as polar bears. We chose to use the 95% adaptive kernel method with varying band width (CALHOME; Kie *et al.* 1996). CALHOME uses an adaptive Epanechnikov kernel with smoothing done by minimizing least-squares cross-validation scores. For comparative purposes we also calculated the 95% fixed kernel estimates of home range using “The Home Ranger”, Version 1.5 (F.W. Hovey, British Columbia Forest Service, Research Branch, Columbia Forest District, PO Box 9158, R.P.O. no. 3, Revelstoke, BC, V0E 3K0, Canada). The choice of home range estimator is probably not important as we compare home ranges among polar bears. Still, we considered the adaptive kernel to better represent the biological home range of a polar bear. Therefore, the adaptive kernel perimeter estimates were used in subsequent spatial analyses.

We refer to the estimated annual range as “home range”. As few as 20 locations are generally required for dependable kernel estimates of home range (Powell *et al.* 1997), although all home range estimators remain sensitive to increasing sample size up to at least $n = 500$ (Robertson *et al.* 1998). As a result, we restricted our analyses to a range in number of locations per bear-year from 25 to 100 (mean \pm SD: 61 ± 25 , $n = 93$) and to bears that provided more or less continuous locations (≤ 8 days between locations). Thus, denning bears were excluded (17 of 110 collared bears). As a check for sample

size bias affecting the observed effects, we included the number of locations as a covariate in analyses and found no effect ($P > 0.35$). In 13 instances we estimated a separate home range for the same bear. If the same bear provided two or three estimates of home range, we ensured that at least 1 year separated the calculated home ranges and that family status (e.g. with cubs or solitary) had changed to avoid dependence.

The perimeter coordinates for each kernel home range were overlaid upon monthly ice maps to determine percentage cover of the following habitat characteristics: land, annual ice (annually melts and reforms), multi-year ice (survives > 1 year), and water. The resolution of habitat (1 km²) matched the resolution of telemetry locations (Garner *et al.* 1990; Arthur *et al.* 1996; Ferguson *et al.* 1999). Ice characteristics were derived from ice maps (1:4 million) to assess seasonal variation (January to December 1994, $n = 12$) and annual variation (1987–97, $n = 10$). To assess the characteristics of available ice throughout the study area, we systematically sampled the intersection points of a 100 × 100 km grid ($n = 186$ points). Coastline habitat represents the relative amount of coastline within a home range and was measured as the distance of coastline (1 km wide) divided by the home range area.

First, we used SD as our variance descriptor and PROC REG of the Statistical Analysis System (SAS Institute, Inc. 1991) to compare annual home range size to environmental factors by multiple linear regression. We used stepwise selection with entry and exit criteria and model acceptance set at $P < 0.05$. Ten factors considered important as determinants of home range size included percentage cover of land, percentage cover of annual ice, percentage cover of multi-year ice, seasonal variation in three ice cover characteristics (SD within 12 months of a year), annual variation in three ice cover characteristics (SD within 10 years), and amount of coastline habitat. To avoid data dependence we eliminated percentage water cover from the sum of habitat proportions (see Aibischer *et al.* 1993). All data were log-transformed to meet model assumptions of normality and uniform variances. Data are presented as mean \pm standard error.

Next, we tested whether polar bears adjusted home range size to reduce unpredictability in sea-ice characteristics over time and space. We measured spatial variation using four distances (radii of buffers) from the centre of each polar bears' home range. We calculated habitat cover within buffers around the centre (i.e. median longitude and latitude values) of the home range of female polar bears (Fig. 1). Radius distances were 50 km (7900 km²), 100 km (31 400 km²), 200 km (125 700 km²) and 400 km (502 700 km²). Temporal variation was measured within each of these distance buffers as the SD in ice

characteristics (% annual ice, multi-year ice, open water) over seasons ($n = 12$ months, year = 1994) or years ($n = 10$, years 1987–97). To avoid data-dependence we did not use the percentage land habitat proportion and thus habitat proportions do not sum to unity (Aibischer *et al.* 1993).

If variation in time increases over distance then we predict polar bears will maintain relatively small home ranges. In contrast, we predicted larger home ranges if variation in ice characteristics decreased over distance (i.e. more predictable variation with larger buffers). We used the slope of the relationship between variation (SD) in ice characteristics and distance from the centre of the home range as a measure of predictability of ice characteristics. We assessed the variability in ice characteristics at the centre of a bears' home range as the y-intercept of this relationship. The calculated slope and intercept for the sample of bears was then correlated with home range size. For example, an increasing home range size with decreasing slope indicated that bears responded to greater temporal variability with larger home ranges and the result of a large home range was greater predictability (i.e. less seasonal and annual variation in ice characteristics). An increasing home range size with increasing intercept indicated that bears living in unpredictable ice over seasons and years had larger home ranges.

RESULTS

Home range size

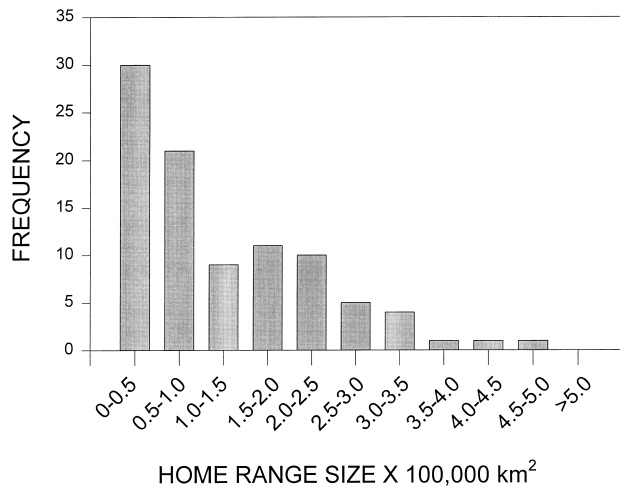
Female polar bears had a mean home range size of 125 500 \pm 11 800 km² ($n = 93$) and showed considerable variation in home range size (range 940–540 700 km², SD = 43 900; Fig. 2). Polar bears showed differences in home range size among populations (Table 1). For example, bears from the Kane Basin region had smaller home ranges (19 400 km² \pm 4200, $n = 11$, range = 5300–32 100 km²) than bears from the Baffin Bay region (192 000 km² \pm 16 500, $n = 14$, range = 63 300–332 500 km²; $t = 5.1$, $P < 0.001$). Data from 10 bears with more than one estimated home range showed that polar bears tended not to maintain similar sizes of annual home ranges from year to year ($r^2 = 0.23$, $n = 13$, year 1 vs. year 2, $P = 0.10$).

Home range size of polar bears estimated from telemetry data was significantly larger than predicted based on allometric regression of mammalian carnivore species living in terrestrial environments. We used 256 kg as the mean female polar bear weight (Cattet *et al.* 1997; $n = 255$). Polar bear home ranges estimated using adaptive or fixed kernel methods were almost two orders of magnitude greater than predicted by Lindstedt *et al.* (1986) allometric equation (Fig. 3). Estimated home range

Table 1 Home range size (km²) for female polar bears by population 1989–97 (ANOVA test: $F_{6,91} = 6.73$, $P < 0.001$)

Population	<i>n</i>	Mean	Standard error	Significance*
Davis Strait	5	228300	59400	a
Baffin Bay	32	192000	16500	a
Queen Elizabeth Islands	4	144800	109600	abc
Parry Channel	29	107700	20100	abc
Viscount-Melville Sound	9	53300	18700	bc
Gulf of Boothia	7	32500	8000	bc
Kane Basin	7	19400	4200	c
Total	93	125500	11800	

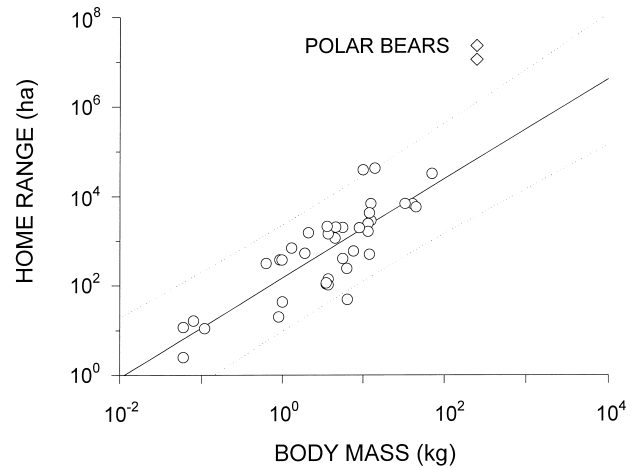
*Means with the same letter do not differ significantly from each other using Tukey's multiple comparison test ($P > 0.050$). Names of populations as per Taylor & Lee (1995).

**Figure 2** Frequency distribution of polar bear home ranges ($n = 93$) by intervals of 50 000 km² in the Canadian Arctic, including Baffin Bay and Davis Strait regions 1989–97.

sizes using fixed kernel estimators were $26 \pm 6.9\%$ smaller than adaptive kernel estimates of home range size (see also Powell *et al.* 1997).

Environmental correlates of home range size

The amount (% cover) of land, seasonal variation in annual ice, and coastline habitat contributed significantly to variation of home range size (Table 2). The amount of land in a polar bears' home range explained 42% of the variation in home range size. Polar bears living in areas where ice ablation occurred during late summer and autumn were forced to live on land for 2–3 months while awaiting the return of ice (e.g. Baffin Bay). In other areas where multi-year ice was available during summer, polar bears were able to use ice all year (e.g. Arctic Archipelago). Bears that lived on land during the late summer ice-free period had the largest home range sizes as

**Figure 3** Regression of home range area on body mass for terrestrial carnivores (○) (Lindstedt *et al.* 1986) showing 95% prediction interval relative to polar bear home range size calculated using adaptive kernel method (◇) and fixed kernel method (26% smaller). Both axis are presented in log-scales.

indicated by the strong positive correlation between percentage land and home range size. The amount of seasonal variation in sea ice explained 24% of the variation in home range size. Bears living in areas of great seasonal variation in ice cover had larger home ranges. The amount of coastline habitat explained 5% of the variation in home range size of polar bears. Bears living in areas with more coastline had smaller home ranges than bears living in areas of less coastline.

Sea-ice predictability and home range size

Seasonal variation in amount of annual ice, multi-year ice, and water varied with distance from the centre of home ranges of polar bears (Table 3). For example, polar bears with larger home ranges had greater seasonal variation in

Table 2 Multiple regression analysis of the relationship of mean and standard deviation of various sea-ice types on home range size of polar bears ($n = 93$) in the Canadian Arctic, including Baffin Bay and Davis Strait regions 1989–97. Partial correlations (r^2) express the unique contribution of a given factor (independent variable) as a proportion of the total variance explained on polar bear home range

Parameter	Proportion variation explained	F value	Significance (p)
Permanent attributes:			
Land cover (+)*	0.42	62.1	<0.001
Coastline habitat (-)	0.05	14.1	<0.001
Seasonal variability:			
Annual ice (+)	0.24	60.3	<0.001
Complete Model	0.71	68.6	<0.001

*(+) positive correlation, (-) negative correlation.

ice-free cover near the centre of their home range (i.e. high intercept value; $P = 0.04$). Also, polar bears with large home ranges tended to have a negative relationship between variation in ice-free cover and distance (i.e. high negative slope value; $P = 0.07$). This relationship indicates that by increasing home range size bears decreased unpredictability in ice-free cover.

A similar pattern was evident for seasonal variation in annual ice (Table 3), although the slope and home range size relationship was not significant ($P = 0.17$). A positive relationship between the intercept and seasonal variation in annual ice ($P = 0.02$) suggests that bears with a

relatively small amount of variation near the centre of their home range (i.e. small intercept value) had smaller home range size. In contrast, bears with unpredictable annual ice at the centre of their home range were likely to have larger home ranges. Larger home ranges had the effect of reducing seasonal variation in ice cover (i.e. reducing unpredictability).

Seasonal variation in multi-year ice over distance showed the opposite pattern relative to annual ice (Table 3). Polar bears with variation in multi-year ice that decreased with distance from the centre of their home range had smaller home ranges ($P = 0.04$).

Annual variation in ice characteristics was also correlated with distance (radius) from the centre of home ranges (Table 3). The same patterns observed for seasonal variation with distance were observed for annual variation. Polar bears had larger home ranges if they experienced (i) greater unpredictability in water/annual ice cover at the centre of their home range, or (ii) lower variation in water/annual ice cover with distance from the centre of their home range. Again, the opposite pattern was evident for multi-year ice.

DISCUSSION

Home range size of polar bears was larger than other mammalian carnivores which are adapted to terrestrial environments. To explain this discrepancy, we tested for determinants of home range size. Landscape, measured as the amount of land cover, contributed most (42%) of the variation in home range sizes. Previously, we showed

Table 3 Relationship between (i) the slope or intercept of the correlation between sea-ice parameter and distance from centre of polar bear home ranges, and (ii) home range size of polar bears from the Canadian Arctic, including the Baffin Bay and Davis Strait regions 1989–97 ($n = 93$). A significant negative correlation between home range and slope indicates that greater temporal variability in ice characteristics results in large home range size whereas a significant positive correlation between home range and intercept indicates that greater unpredictability in ice characteristics results in larger home range size

Ice characteristics	Slope		Intercept	
	r^*	p^\dagger	r^*	p^\dagger
Seasonal variability:				
Water	-0.21	0.07	+0.27	0.04
Annual ice	-0.17	0.17	+0.25	0.02
Multi-year ice	+0.24	0.04	-0.06	0.61
Annual variability:				
Water	-0.19	0.09	+0.28	0.03
Annual ice	-0.35	0.001	+0.19	0.09
Multi-year ice	+0.22	0.04	-0.29	0.01

*Pearsons product moment correlation coefficient.

†Probability of slope different from zero.

that polar bear movements were constrained by landscape pattern (Ferguson *et al.* 1998). Polar bears living in areas with many islands, such as the Arctic Archipelago, had more irregular movements and smaller seasonal home range sizes. In contrast, polar bears that lived in seasonal environments characterized by the annual ablation of ice during late summer had the largest home range sizes (e.g. Baffin Bay and Davis Strait populations). Larger home ranges may result from use of land during the ice-free period because bears remain with the ice as long as possible, resulting in large distances separating winter and summer range. Seasonal changes in the amount of annual ice explained a large amount (24%) of the variation in home range size of female polar bears. Annual ice is critical to the food base for arctic marine food webs and directly controls the availability and accessibility of food for polar bears (Savidge *et al.* 1996; Arrigo *et al.* 1997; Nicol & Allison 1997). In contrast, multi-year ice and zones of open water provide few seal hunting opportunities for polar bears (Stirling *et al.* 1993). Relative amount of coastline habitat contributed to an explanation of polar bear home range size. Polar bear home ranges that had more coastline likely encompassed a greater proportion of highly productive coastline habitat (Sakshaug *et al.* 1994; Arrigo *et al.* 1997; Stirling 1997) and, as a result, home ranges were smaller than many offshore home ranges.

The proportion of ice cover (e.g. annual ice) likely affects polar bear home range size but predictability of sea-ice characteristics across time and space ultimately affects the area required by polar bears to maintain life. Polar bears control for spatial and temporal variation in ice characteristics by making large-scale movements and selecting sea-ice landscape favourable for seal hunting (Garner *et al.* 1990; Ferguson *et al.* 1999). We found evidence that polar bears adjusted their home range size to reduce annual and seasonal variation in ice characteristics. For example, home ranges with unpredictable ice characteristics across seasons or years were larger than those associated with more predictable ice features.

Three factors important to polar bear predation of seals and home range size are the dispersion of land, the seasonal flux of ice, and the amount of edge habitat. At one extreme, bears living in areas with many large islands, multi-year ice, and extensive shoreline habitat (e.g. Arctic Archipelago) have more predictable access to seals, particularly in spring during seal pupping. Here, we predict a lower annual return on their hunting efforts but an annual return that is more constant year-to-year. The greater proportion of multi-year ice in these habitats provides for fewer seals, and hunting success by polar bears is likely lower. As a result these bears tend to have

smaller home ranges and their space-use strategy involves a trade-off between the mean availability of food (low) and the temporal and spatial variability associated with this food (low). At the other extreme, bears living in areas characterized by large expanses of ice and large seasonal flux of annual ice (e.g. Baffin Bay) have large home ranges. The space-use strategy adopted by these bears is to take greater risks to find patches of prey in a more variable environment. As a result, they move extensively and exploit larger home ranges. These bears travel far offshore searching the moving pack ice for concentrations of seals. The density of seals is greater offshore, but their distribution is more spatially and temporally unpredictable. Also, offshore bears have access to other food sources for a greater part of the year [e.g. narwhals (*Monodon monoceros*), beluga whales (*Delphinapterus leucas*), bearded (*Erignathus barbatus*) and hooded seals (*Cystophora cristata*; Stirling 1997)]. Therefore, some bears trade off greater food availability (high mean) for more variable food over time and space (greater unpredictability), whereas other bears live with lower but more constant food availability. Bears will adopt a strategy along this continuum that fits their local environment. Also, some bears likely switch strategies as indicated by the weak correlation between home range sizes comparing the same bears from year to year.

What is the cause of the large home range sizes characteristic of this species (see also Amstrup 1986; Garner *et al.* 1990; Wiig 1995; Born *et al.* 1997)? We propose that large home range size of polar bears is due to the distribution of their prey within the three-dimensional water environment and the ever-changing ice layer that their primary prey (ringed seals; *Phoca hispida*) live under. Sea-ice, like all interfaces, not only creates ecological diversity but it also selects for organisms adapted to environments that vary considerably with space and time (Holling 1992; Naiman & Décamps 1997). Polar bear morphology is that of a terrestrial mammal and they rely on the two-dimensional terrestrial-like platform of sea ice to move about and prey on ringed seals (Stirling & Archibald 1977). Large home range sizes have been documented for marine fish (Zeller 1997), marine turtles (Renaud & Carpenter 1994), marine otters (Bowyer *et al.* 1995), seals (Stewart & DeLong 1993), and whales (Whitehead 1996). Similarities that polar bears have with marine mammals, relative to terrestrial carnivores, include large size, long-distance travel, lack of territoriality, and physiological adaptations to extremes in seasonal fluctuations in food availability (e.g. periods of fasting). Thus, selection pressure to capture marine prey has resulted in polar bear adaptations that include movement patterns similar to a marine mammal living in a three-dimensional environment.

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Steven Ferguson has research interests in evolution of life-history traits and population biology, with particular emphasis on predator–prey relations.

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