PROCEEDINGS OF THE ROYAL SOCIETY B

rspb.royalsocietypublishing.org

Research

Cite this article: Laidre KL, Born EW, Gurarie E, Wiig Ø, Dietz R, Stern H. 2012 Females roam while males patrol: divergence in breeding season movements of pack-ice polar bears (*Ursus maritimus*). Proc R Soc B 280: 20122371.
http://dx.doi.org/10.1098/rspb.2012.2371

Received: 11 October 2012
Accepted: 9 November 2012

Subject Areas:
behaviour, ecology

Keywords:
ursids, polar bear, Greenland, breeding season, pair formation, tortuosity

Author for correspondence:
Kristin L. Laidre
e-mail: klaidre@apl.washington.edu

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2012.2371 or via http://rspb.royalsocietypublishing.org.

Females roam while males patrol: divergence in breeding season movements of pack-ice polar bears (*Ursus maritimus*)

Kristin L. Laidre[1,3], Erik W. Born[3], Eliezer Gurarie[2], Øystein Wiig[4], Rune Dietz[5] and Harry Stern[1]

[1]Polar Science Center, APL, and [2]Department of Statistics, University of Washington, Seattle, WA 98105, USA
[3]Greenland Institute of Natural Resources, PO Box 570, 3900 Nuuk, Greenland
[4]National Centre for Biosystematics, Natural History Museum, University of Oslo, PO Box 1172, Blindern, 0318 Oslo, Norway
[5]Institute of Bioscience, Arctic Research Centre, Aarhus University, PO Box 358, 4000 Roskilde, Denmark

Intraspecific differences in movement behaviour reflect different tactics used by individuals or sexes to favour strategies that maximize fitness. We report movement data collected from $n = 23$ adult male polar bears with novel ear-attached transmitters in two separate pack ice subpopulations over five breeding seasons. We compared movements with $n = 26$ concurrently tagged adult females, and analysed velocities, movement tortuosity, range sizes and habitat selection with respect to sex, reproductive status and body mass. There were no differences in 4-day displacements or sea ice habitat selection for sex or population. By contrast, adult females in all years and both populations had significantly more linear movements and significantly larger breeding range sizes than males. We hypothesized that differences were related to encounter rates, and used observed movement metrics to parametrize a simulation model of male–male and male–female encounter. The simulation showed that the more tortuous movement of males leads to significantly longer times to male–male encounter, while having little impact on male–female encounter. By contrast, linear movements of females are consistent with a prioritized search for sparsely distributed prey. These results suggest a possible mechanism for explaining the smaller breeding range sizes of some solitary male carnivores compared to females.

1. Introduction

Many species of solitary carnivores demonstrate differences in movement behaviour between sexes. These are related to strategies for acquiring and defending resources, territories, competition or mate searching [1], ultimately to maximize reproductive success and survival [2]. During the mating season, female distribution is often determined by food resources and optimal habitat, whereas male distribution is determined by the distribution of females [3].

Ursids are generally non-social mammals with large home ranges that vary with season and habitat. Thus, social interactions and consorting tend to be limited to the breeding season. Terrestrial male brown bears (*Ursus arctos*) are known to travel widely during the breeding season [4], and dispersal has been reported to be sex-biased, with highly philopatric females establishing breeding home ranges in or adjacent to natal areas and subadult males dispersing long distances from their mothers' home range [5–8]. The large breeding ranges of males often overlap with those of several females [8]. Within populations, home range sizes vary with age, sex, population density, reproductive status and the occurrence of temporally available foods.

Polar bears (*Ursus maritimus*) are non-territorial asocial ursids that occur at relatively low densities throughout their range [9–11]. During the breeding season, spatial distribution of mates, mating season length and time allocated for mate

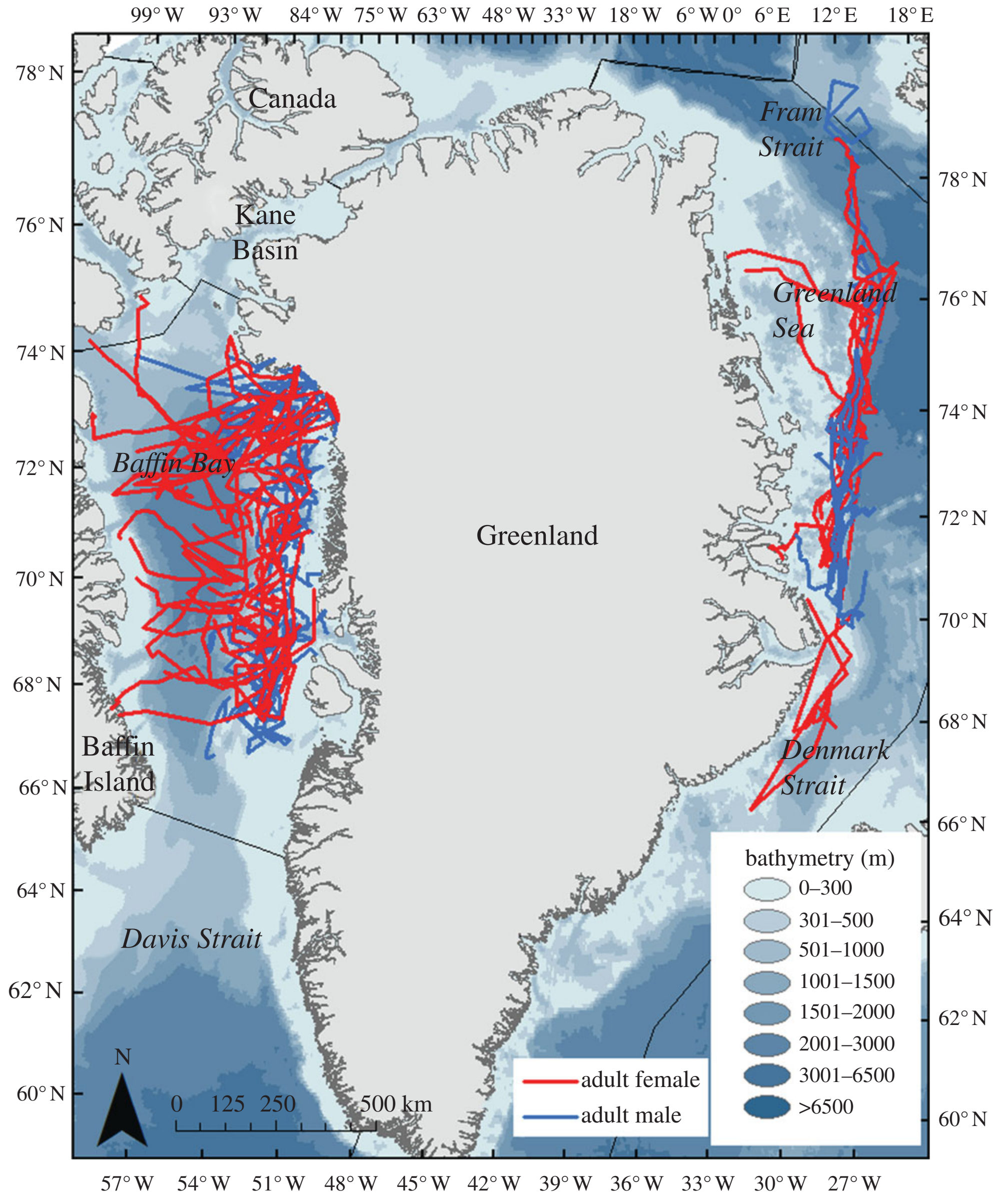

Figure 1. Map of movements of polar bears in two subpopulations (Baffin Bay and East Greenland) during the breeding period (April–May) on the pack ice, 2007–2011. IUCN Polar Bear Specialist Group subpopulation boundaries are shown with black lines.

searching limits the number of successful pairings [12]. Movements of individual polar bears have been studied using telemetry for decades [13–18]; however, data are almost exclusively from females with satellite collars because the conical shape of the neck and head of males precludes a collar attachment. With the exception of a study of seven males in Alaska with subcutaneously implanted transmitters [19], almost no data have been collected on male movements. Recent work has highlighted the need for data on male and female movements in an unpredictable sea ice environment in order to quantify the dynamics and rates of mating pair formation [12].

This study presents, to our knowledge, the first comparative data on the movements of adult female and adult male polar bears in two separate pack ice populations during five breeding seasons between 2007 and 2011. A novel satellite transmitter was attached to the ear of male bears in early spring to maximize the coverage of the breeding season. Movement data were analysed with respect to multiple sea ice habitat covariates, population, estimated body mass and reproductive condition, with an emphasis on differences between sexes. We interpret our results with respect to mammalian mating strategies of encounter theory with prey and potential mates. We hypothesized male polar bears, such as terrestrial ursids, would have longer-range linear movements and larger home ranges than receptive females during the breeding season in order to increase the number of mates.

2. Material and methods

(a) Baffin Bay and East Greenland polar bear habitat

We studied two geographically and genetically distinct polar bear subpopulations—Baffin Bay and East Greenland [20]—that occur on pack ice (moving sea ice unattached to land) for most of the year. The sea ice dynamics of Baffin Bay and East Greenland (figure 1) differ and are described in detail by Valeur *et al.* [21], Tang *et al.* [22] and Aagaard & Coachman [23]. In Baffin Bay, sea ice is seasonal and the region is almost ice-free in summer. East Greenland polar bear habitat is a convergent ice zone with ice formation along the coast driven by transport of multi-year pack ice from the Arctic Ocean [24]. The total area of pack ice in winter in East Greenland is generally narrower than the width of Baffin Bay; however, owing to the presence of multi-year ice, there is more sea ice habitat available over the entire year.

(b) Field methods

In East Greenland, polar bears were tagged in the fast and pack ice in the Greenland Sea based onboard R/V *Nordsyssel* (Institute of Marine Research, Tromsø, Norway) or R/V *Lance* (Norwegian Polar Institute, Tromsø, Norway) between 22 and 30 March 2007 and 2008. In Baffin Bay, West Greenland, polar bears were tagged on the fast and pack ice between 26 March and 18 April 2009, 2010 and 2011 operating out of coastal settlements.

Polar bears at all sites were darted and immobilized from an Ecureuil AS350 helicopter and handled according to procedures described in Stirling *et al.* [25]. Standard body measurements (standard length and axillary girth) were taken and total body mass was estimated using the approach by Derocher & Wiig [26]. Field estimates of age and reproductive status were recorded.

Adult female polar bears were fitted with A-3610 (East Greenland) and TAW-4610H (Baffin Bay) satellite radio collars (Telonics, Mesa, AZ, USA). Satellite collars provided information on geographical location, internal transmitter temperature and activity. Collars were programmed to transmit during one 6-hour period each day on 4-day intervals.

Adult male polar bears were fitted with SPOT-5 S227 satellite radio transmitters (Wildlife Computers, Redmond, Washington, USA) attached to the ear similar to numbered plastic ear tags used in conventional studies (right ear, except in four cases). The SPOT-5 transmitters weighed 32 g unmounted and 60 g with attachment system [27]. Ear transmitters were duty cycled to extend battery life, with most tags transmitting on 4-day intervals and others on daily intervals ($n = 8$). Satellite tags transmitted around noon local time each day and were programmed so that several locations were received per transmission day.

(c) Data filtering and subsampling

Data on locations and transmitter status from all polar bears were collected via the Argos Location Service Plus system (Toulouse, France). All locations were first filtered by a SAS-routine in the Douglas Filter V7.02 (7% of locations were removed). Filter settings included a maximum movement speed of 10 km h^{-1}. All locations of the highest accuracy (class 3) with an estimated location error less than 250 m were retained.

We created a strict 4-day interval time series for each individual by subsampling the portion of any adult male polar bear's time series that was initially transmitting on a 1-day duty cycle to match adult females. This ensured that the impact of serial autocorrelation was consistent between the sexes.

(d) Comparison between adult female and male movements

We analysed movement data during the 'spring breeding season' defined as the period from tagging (end of March or early April) to the end of May [28,29]. This period covered the post-mating season and included the peak of sea ice coverage and initiation of sea ice break-up. Ages of polar bears were estimated in the field and later confirmed from cementum layers of a pre-molar extracted during capture [30]. Adult females were defined as greater than or equal to 5 years old and adult males as greater than or equal to 6 years old.

We extracted two statistics for each bear using 4-day data: (i) the median 4-day displacement (total distance travelled in km), and (ii) the 'persistence index' (PI) or mean cosine of the turning angles between consecutive steps (unitless). As turning angles range from 0 to 2π, PI theoretically ranged from -1 to 1. PI-values close to 1 correspond to linear (more directed) movement while PI $= 0$ correspond to movements that are uncorrelated at the time-scale of the observations and therefore more tortuous. Negative values of PI are also possible, corresponding to movements that oscillate back and forth at the sampling time scale. The combination of displacements and PI are the basic components of correlated random walk models [31,32].

Consecutive sequences of three locations (two complete steps) were required to estimate a single turning angle; therefore, the number of steps used in determining PI was smaller than the number of steps used for displacements. Polar bears with more than 10 steps were used in the analysis, however, some bears had less than 10 obtainable turning angles owing to gaps. In these cases, we did not calculate PI. Four-day displacements were extracted from every possible 4-day interval (e.g. if data from an adult male were collected over days 1–6, displacements were extracted between day 1 and 5 and day 2 and 6). This strategy facilitated the use of all individuals' data and increased the sample size for males given tracking periods were relatively short and any gap would lead to the exclusion of two possible displacements. The lack of independence between overlapping turning angles sampled from male bears had no influence on the single-point estimate of PI. We confirmed this by simulating bear tracks with 50 positions with known PI, and estimating the 4-day PI using only a single set of 4-day subsamples and the overlapping data. In all cases, the estimates were statistically equivalent, with the only difference being the narrower standard deviation of the estimates using the overlapping method, as expected. Adult female bears with transmissions lasting over a year were treated separately in each year.

The hourly movement speeds were difficult to estimate directly from the 4-day displacements owing to the possibility of unobserved meandering [17]. However, there were multiple 1-day displacements (mean steps per bear $= 36$) for 25 bears, which provided a closer approximation to the actual movement speed. For these bears, we regressed the median 4-day displacements against the 1-day displacements, and used the slope of the regression to correct the remaining 4-day displacements to obtain estimates of speed. Note the single best daily location obtained with the filtering algorithm led to location error that was much smaller than the typical 4-day displacements, allowing us to neglect bias or error in the velocity estimates. Median 4-day displacements and PI were analysed with respect to population and sex/age main effects using linear regression and analysis of variance. A factorial analysis of the PI and the 4-day displacements was conducted with sex and population main effects and an interaction term. We also examined the effects of estimated body mass and reproductive status of adult females (with or without cub) on movement parameters. We classified adult females as 'available' to potential mates if they were alone, captured as a mating pair (e.g. with an adult male), or with any number of cubs that were 2 years old. 'Unavailable' females had cubs of the year (COYs) or yearlings.

We calculated 95 per cent kernel home ranges (km^2) using smoothed cross validation bandwidth selector [33] for each individual polar bear in each population for the combined breeding months [34]. We assumed these areas represented the area used by each individual during the breeding season.

(e) Habitat selection modelling

We tested for effects of sea ice habitat selection on movement behaviour by building habitat models for both sexes and populations. We used sea ice concentration (0–100%) products derived from the AMSR-E instrument on NASA's Aqua satellite (nominal pixel size 6.25×6.25 km; Centre for Marine and Atmospheric Sciences in Hamburg, Germany).

We linked sea ice concentration to each bear location at three scales: the sea ice concentration pixel value where the bear was located, and the mean sea ice concentration within circular regions of two sizes centred on the pixel occupied by the bear: a small region with 42.5 km radius consisting of 145 pixels (5664 km^2 in area) and a large region with 85.6 km radius consisting of 593 pixels (23164 km^2 in area). The large radius corresponded to the 75% percentile of 4-day displacements for both sexes.

We also calculated the distance (km) from each location to the sea ice edge and distance (km) to the coastline. Sea ice edge was defined as either less than 15 or less than 50 per cent ice concentration [35]. The parameter was defined as the distance (km) from the bear's location to the centre of the nearest pixel with the threshold sea ice concentration. Distances were calculated based on latitude and longitude, so were not subject to variable pixel size.

Using the 4-day data for each bear, we constructed a null set of pseudo-absence locations by creating a sample of potential movement locations around the observed daily locations for each bear. These potential locations were obtained by computing the distance and turning angle for 50 randomly selected movement steps, and adding those steps to the preceding location. This conservative pseudo-absence location set reflected those locations where a bear could potentially move based entirely on the movement behaviour of that bear, thereby accounting for autocorrelation [36]. Note the actual next location of the bear was a subset of the null set. For bears that had less than 30 movement steps, we generated possible movement steps by permuting all turning angles and movement steps that were available. All pseudo-absence polar bear locations were linked to the habitat covariates, and combined with true locations for modelling.

We modelled bear presence and pseudo-absences with respect to the habitat, sex and population covariates using mixed effect logistic regression models (glmmML package in R), with individual bears as a random effect and accounting for temporal autocorrelation.

(f) Simulation study

We performed a simulation study to explore the effect of PI on potential male–male and male–female encounter rates. We populated an area with male or female bears at a range of densities appropriate for our study areas (from 0.1 to 0.5 bears per 100 km^2). A focal male was released in a random location moving with a continuous random walk model [37] with an effective 4-day PI ranging from 0 to 0.5. When the focal male moved with a given encounter radius (5, 10 or 20 km in different simulation runs) of another bear, the time to encounter was recorded. Encounter radii are difficult to measure in the field, thus we chose a wide range of feasible values based on expert opinion. In the male–female simulations, all females moved with a 4-day PI of 0.4. In the male–male simulations, all males moved with the same PI as the focal male. The mean speed of movement for all bears was 12.2 (s.d. = 6) km d^{-1}, consistent with the empirical observations. For each combination of parameter values, we recorded the mean and standard error of the time to encounter, repeating the simulation 1600 times so that the standard errors were approximately 0.1 days. For further details on the simulation, including the parametrization of the movement model, see the electronic supplementary material. Simulations were performed using R [38].

3. Results

(a) Study animals

Sample sizes included 26 adult females and 23 adult males. In East Greenland, adult females' estimated body mass was on average 209.5 kg (s.d. = 29, $n = 6$) and adult males was 405.3 kg (s.d. = 72, $n = 6$). In Baffin Bay, adult female mass was 209.9 kg (s.d. = 27, $n = 20$), and adult males was 365.4 kg (s.d. = 69, $n = 17$). Body mass was significantly different between the two sexes (t-test, $p < 0.001$) but not between populations.

(b) Performance of satellite transmitters

SPOT5 transmitters on adult males in East Greenland transmitted an average of 115 days (s.d. = 38, range: 84–158 days) in 2007 and 76 days (s.d. = 26, range: 38–129 days) in 2008. In Baffin Bay, SPOT5 tags transmitted an average of 76 days (s.d. = 79, range: 29–196 days) in 2009, 49 days (s.d. = 17, range: 30–92 days) in 2010 and 63 days (s.d. = 16, range: 28–78 days) in 2011. Collars deployed on adult females in both areas transmitted for several years. In total, 26 individual females were followed for 40 unique breeding seasons (13 were followed for more than one breeding season). Only data overlapping with the transmission of males are reported here.

(c) Distribution of polar bears

Both Baffin Bay ($n = 20$ adult females, $n = 17$ adult males) and East Greenland ($n = 6$ adult females, $n = 6$ adult males) polar bears were distributed over fast ice and dense pack ice in April and May, occupying habitat with average sea ice concentrations greater than 95 per cent. The total area of habitat available to the two populations was similar.

East Greenland polar bears tagged in 2007 ($n = 4$ adult females, $n = 3$ adult males) and 2008 ($n = 2$ adult females, $n = 3$ adult males) ranged offshore between 200 and 500 km between 66° N and 82° N (*ca* 1779 km). In spring, polar bears used a clearly defined linear home range region along the sea ice edge nearest to the coast at *ca* 70° N and furthest from the coast at 79–80° N (figure 1).

Baffin Bay polar bears tagged in spring 2009 ($n = 4$ adult females, $n = 5$ adult males), 2010 ($n = 8$ adult females, $n = 3$ adult males) and 2011 ($n = 8$ adult females, $n = 9$ adult males) were concentrated on the eastern side of Baffin Bay (69°–74° N) but some adult females dispersed westward towards Baffin Island (figure 1). Some adult female bears tracked over several years were located off the coast of Baffin Island in early April subsequent to the tagging year and moved eastward towards West Greenland.

(d) Movement metrics

The mean 4-day displacement for all groups was 50 km (s.d. = 20.7), and all were greater than 16 km. The median 4-day displacement for all bears in Baffin Bay was 50.6 km (s.e. = 2.4, $n = 49$) and East Greenland was 60.1 km (s.e. = 5.7, $n = 14$), however, the difference was not significant (type III ANOVA, $p = 0.094$; table 1). The median 4-day displacements were similar between sexes within the populations ($p = 0.45$; table 1). Within each population, year was not a significant covariate in explaining variation in mean 4-day displacements ($p = 0.19$ Baffin Bay, $p = 0.12$ East Greenland).

There were no differences between populations for the PI (type III ANOVA, $p = 0.94$), however, there were highly significant differences in PI between sexes: females moved in significantly more directed (linear) paths than males ($p < 0.001$; table 1), with the difference in PI consistent across both populations. Within each population, year was not a significant covariate in explaining variation in PI ($p = 0.27$ Baffin Bay, $p = 0.10$ East Greenland). There were four females

Table 1. Summary statistics of polar bear movement data grouped by population, sex and female availability status. (We report total number of bears, total number of analysed tracks (including bears tracked over multiple breeding seasons) and means and standard deviations of median 4-day displacement (km), mean persistence index (PI) and 95% range. The total number of adult females is different than the sum of available and unavailable females because some females were tracked over several breeding seasons (years).)

population and sex	*n* bears	*n* tracks	*n* steps	4-day median displacement (km)	PI	95% kernel range (km^2)	hourly estimated speed (km h^{-1})
Baffin Bay							
all adult females	20	32	12.5 (1.1)	48.9 (16.4)	0.43 (0.25)	101 300 (70 300)	0.72 (0.24)
available	15	15	12.3 (1.3)	51.0 (15.0)	0.38 (0.28)	106 000 (63 400)	0.75 (0.22)
unavailable	7	8	12.6 (0.9)	44.8 (14.7)	0.40 (0.20)	66 100 (36 600)	0.66 (0.22)
adult males	17	17	29.2 (11.3)	53.7 (17.4)	0.10 (0.19)	43 900 (20 200)	0.79 (0.25)
East Greenland							
all adult females	6	8	34.2 (22.2)	60.3 (26.8)	0.45 (0.15)	86 300 (54 280)	0.89 (0.39)
available	3	4	34.8 (24.0)	62.1 (21.9)	0.54 (0.09)	105 500 (60 000)	0.91 (0.32)
unavailable	3	4	33.8 (24.1)	58.5 (34.4)	0.36 (0.17)	67 000 (47 800)	0.86 (0.50)
adult males	6	6	35.5 (23.6)	59.8 (13.8)	0.01 (0.24)	60 000 (30 300)	0.88 (0.20)

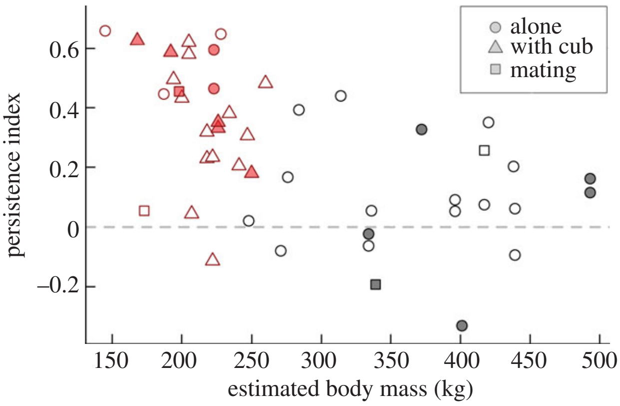

Figure 2. Persistence index plotted against estimated body mass of adult polar bears. Females are shown in red and males are shown in black. Bears in East Greenland are shown with filled symbols and bears in Baffin Bay are shown with open symbols.

in Baffin Bay tracked for multiple seasons known to be moving directly back to West Greenland from Baffin Island at the start of April. Their mean PI was 0.58 and after removing these females, the difference between remaining adult females ($PI = 0.42$) and adult males in Baffin Bay was still highly significant (Mann-Whitney $U = 93$, $p < 0.001$).

The regression of median 4-day displacements against median 1-day displacements yielded a slope of 2.83 (s.e. = 0.10, $r^2 = 0.96$), with no differences between populations or sexes (type III ANOVA, $p > 0.2$). Based on the high correlation and low standard error of the regression, the slope was determined to be a robust correction for velocity (km h^{-1}) based on 4-day displacements. Using this correction, polar bears in all categories moved on average between 0.72 (s.e. = 0.04) and 0.89 km h^{-1} (s.e. = 0.14; table 1). There were no significant differences between sexes or populations.

We further examined movement metrics against reproductive status and body mass, pooling bears from both populations. There were no significant differences in PI and 4-day median displacement between reproductive categories of females (type III ANOVA, $p > 0.3$; table 1). All reproductive categories of females moved in significantly more linear paths (higher PI) than males.

Two adult females had COYs and their 4-day median displacements were 16.8 and 45.7 km, the latter of which was comparable to displacements of other reproductive categories of females with yearlings (mean = 53.0, s.e. = 6.9, $n = 10$), adult females with 2-year olds (mean = 51.3 km, s.e. = 5, $n = 9$) or adult females with no cub (mean = 55.1 km, s.e. = 5.8, $n = 10$). Adult females with COYs had PIs of 0.18 and 0.23, in both cases lower than all other categories: adult females with yearlings (mean PI = 0.42, s.e. = 0.06, $n = 10$), adult females with 2-year olds (mean PI = 0.34, s.e. = 0.09, $n = 9$) and adult females without cubs, which had the most directed trajectories (mean PI = 0.51, s.e. = 0.07, $n = 10$), but the difference was not significant (Mann-Whitney $U = 120$, $p = 0.08$). There was no relationship between number of cubs and persistence or displacement.

There was no relationship between the estimated body mass (kg) of individual polar bears and 4-day displacements (figure 2). Although heavier females tended to move less linearly than leaner females, regression coefficients were not significant ($p = 0.18$). We note that unavailable females (with COYs and yearlings) had significantly higher body mass (mean = 229 kg, s.e. = 5.8,

Table 2. Linear mixed effect model coefficients from habitat selection analysis for bears in Baffin Bay and East Greenland during the breeding season.

		main effect		interaction with sex	
habitat covariates	**population**	**coefficient (β)**	***p*-value**	**coefficient (β)**	***p*-value**
ice concentration					
at bear	Baffin Bay	0.014	<0.001	−0.008	0.11
	East Greenland	0.017	<0.001	−0.003	0.61
within 42.5 km	Baffin Bay	0.011	0.005	−0.005	0.29
	East Greenland	0.011	0.001	−0.003	0.58
within 85.6 km	Baffin Bay	0.007	0.063	−0.004	0.39
	East Greenland	0.006	0.059	−0.002	0.76
distance to					
ice edge (15%)	Baffin Bay	0	0.656	0	0.94
	East Greenland	0.002	0.234	−0.002	0.35
ice edge (50%)	Baffin Bay	0	0.992	0	0.89
	East Greenland	0.001	0.528	−0.001	0.80
land	Baffin Bay	0	0.747	−0.001	0.54
	East Greenland	0	0.718	0	0.96

$n = 12$) than available females (mean $= 199$, s.e. $= 5.3$, $n = 19$, $p = 0.003$).

The mean 95 per cent kernel home range of adult females during the breeding season was significantly larger than for adult males in both populations ($p = 0.001$; table 1). There were no differences between the home range size for population or for an interaction term. When female reproductive availability was considered (both populations combined), available females had significantly higher 95 per cent kernel ranges than both unavailable females and adult males ($p < 0.001$). Available females had almost identical 95 per cent breeding ranges in both populations, as did unavailable females, albeit smaller (table 1).

(e) Comparison between male and female habitat selection

There were no differences in habitat selection between adult males or females in either population for sea ice concentration at three spatial scales, distance to sea ice edge, or distance to shore (interaction p-values > 0.1; table 2). The strongest preference pattern was for high sea ice concentrations, both at the bears' location and within the small radius (all p-values < 0.005 for both populations). There were no strong responses for distance to ice edge or distance to coast (all regression coefficients near 0, p-values > 0.23; table 2).

(f) Simulation results

Over the range of parameters explored, the expected time to male–female encounter ranged from 0.67 days (at 0.5 bears per 100 km^2 and 20 km radius) to 19.6 days (at 0.1 bears per 100 km^2 and 5 km radius). There were clear differences in the time to encounter for male–male and male–female encounters at different values of male PI (figure 3). At lowest values of male PI, the time to male–male encounter was on average 36 per cent (s.d. = 16%) longer than the time to male–female encounter. This effect was most prominent at lower bear densities (approx. 54% greater at 0.1 bears per 100 km^2 when compared with 21% for 0.5 bears per 100 km^2) and was relatively insensitive to different encounter radii. The male–male time to encounter was 44 per cent (s.d. = 20%) higher at low PI = 0 than high PI (greater than 0.1; figure 3). By contrast, the male–female time to encounter varied little across values of male PI (7.3% higher at low PI when compared with high PI, s.d. = 3.0%). Note that the observed values of 4-day male PI in this study were between 0 and 0.1, corresponding to the low range of simulated PIs (table 1).

4. Discussion

This study provides, to our knowledge, the first comparison of adult male and female polar bear movements using satellite telemetry in two subpopulations inhabiting pack ice. Data collection from males was made possible by the development of ear tags, which transmitted over 2.5–3.5 months, a short period compared with female collars that routinely transmit over several years. However, tracking durations covered the breeding season [28,29,39,40] when the movements of females and males have the most direct impact on population processes.

Polar bears used a large area corresponding to nearly the entire accessible habitat in Baffin Bay and East Greenland. They moved with a high degree of independence and individual variability. In both environments, the bears showed a strong preference for higher ice concentrations at several scales (table 2), with no preference or avoidance of ice edges or coastline. There was no difference between sexes in habitat selection.

The movement rates for the two sexes were also statistically indistinguishable. Rates (mean 0.72–0.89 km h^{-1}) were similar to those reported in other parts of the Arctic, where Amstrup *et al.* [19] reported speeds of 1.18–1.95 km h^{-1} in Alaska and Wiig *et al.* [16] reported rates of

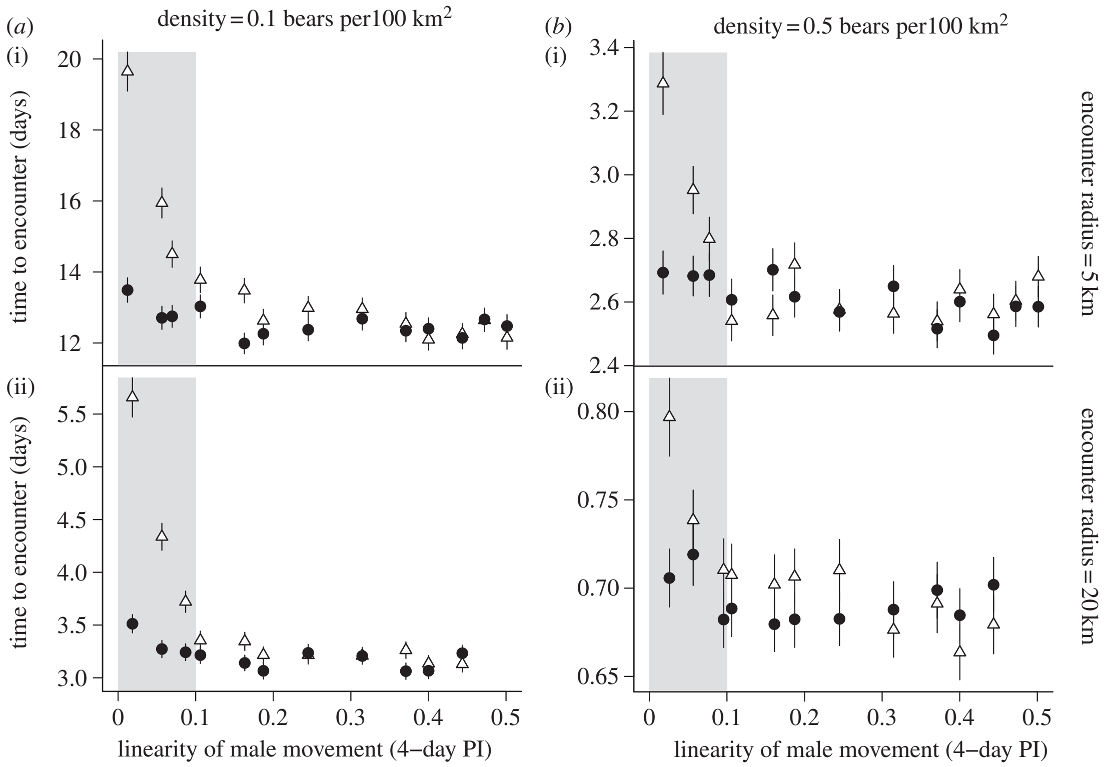

Figure 3. Time to encounters simulated against linearity of male polar bear movement (4-day PI) for two densities (0.1 and 0.5 bears per 100 km^2, (*a*,*b*) respectively) and two encounter radii (5 and 20 km, (i,ii), respectively). White triangles represent male–male encounters, black dots represent male–female encounters, and vertical bars represent 1 s.e. around the means over 1600 simulations. The shaded area represents the range of observed PI's for male polar bears in Baffin Bay and East Greenland.

0.54–0.65 km h^{-1} in East Greenland. We did not consider the impacts of sea ice movement on movement metrics of individuals, however the aggregate effect of moving sea ice is likely to have been similar for both adult males and females as they were located in the same areas over the comparison period.

In our study, the single most significant and consistent difference between male and female movements during the breeding season was in the linearity of movement. Adult females moved more linearly than males, a pattern consistent in both populations, across all years and independent of sea ice habitat selection (table 1). Furthermore, both reproductively available and non-available females demonstrated this pattern. By contrast, adult male polar bears used smaller regions and moved less linearly than females, often doubling back on their track in a particular area.

(a) Drivers of spring breeding season movements

Polar bears are generally solitary and independent predators, continuously searching for food throughout the year [11]. An exception to this is the spring breeding season, during which males actively seek females in oestrus to form mating pairs [40], often pursuing females by scent or following their tracks in the snow [10]. The breeding season overlaps with the spring feeding period when ice seals have formed lairs, given birth, and are vulnerable to predation.

All bears, especially females with cubs, must prioritize nutritional gain in spring to improve body condition before the summer, particularly in seasonal ice environments. The main prey of polar bears on the pack ice are ringed (*Phoca hispida*) and bearded seals (*Eriganthus barbatus*), or harp (*Pagophilus groenlandicus*) and hooded seals (*Cystophora cristata*) along the edge of the pack ice, which are distributed over large areas with few topographical constraints [41,42]. Several studies have shown that the optimal behaviour for animals which predate on stationary prey at low densities is linear movement [37,43,44]. Thus, the optimal foraging strategy for a polar bear on the pack ice is to continuously move in a roughly linear manner.

During the breeding season, male polar bears have the added imperative to search for receptive females [11,19,12], which could result in a divergence in the priorities and differences in movement behaviour. This is consistent with reviews of solitary carnivore behaviour and ecological theory, which indicate that during the breeding season female distributions are determined by food resources and optimal habitat, whereas male distributions are determined by the distribution of females [2,3].

We considered several possible factors that could explain more tortuous spring movement of male polar bears. First, we hypothesized that differences were owing to prey selection or habitat preference. Because of their larger size, adult male polar bears may be able to take larger prey such as bearded seals which, as benthic feeders tend to inhabit shallower waters than ringed seals [41]. However, there were no differences between sexes or populations in any of the habitat selection models, and distance to land in particular (a proxy for bathymetry) was a non-significant factor.

An alternative hypothesis is that differences in male movement are behavioural signals specific to the breeding season. Specifically, that tortuous male movements lead to reduced male–male interaction both pre-pair formation (when males are searching for receptive females) and post-pair formation (when males restrict movements of receptive females to small areas). This hypothesis is consistent with our observations, simulation study, and general encounter rate theory.

Pre-pair formation, male polar bears' encounter rates with females are not substantially improved by more linear movement, both because the females themselves are constantly moving (leading to a finite encounter probability even for a completely stationary male), and because the effective encounter radius is extended by the ability of males to follow a female's tracks or scent [10]. Furthermore, movement away from a general 'patrolling' area can increase the probability of encountering another male, and result in competitive interactions [11].

After a male locates a receptive female, the male remains with the female for up to three weeks to induce ovulation [12,16,40] and generally restricts the females' movements to a relatively small area. This nonlinear movement also reduces encounters with other males [11,45]. If a male is capable of locating a new female soon after completing activities with the previous female, he may not be required to move large distances. Mate switching has been observed in female polar bears [11,45] but duration between male mating attempts has not been documented.

In our study, there was a slight but non-significant surplus of adult males in both subpopulations. The mating system of polar bears is thought to be governed by the ratio of receptive females to adult males [11]. This surplus contributes to the potential for competition-driven conflicts, which may shape movement behaviour. Derocher *et al.* [40] suggested that body size and movement behaviour may be interacting factors in determining pairing success. Because we observed no relationship between estimated body mass and tortuosity among males, we can provide no additional support to these relationships (figure 2). This was largely owing to the high level of variability among individuals and the relatively small sample size in our study.

(b) Simulation study

The hypothesized relationship between tortuosity of movement and encounters was supported by the simulation study. When males move tortuously, the mean time to male–male encounter is much higher than when males move more linearly (figure 3). By contrast, the mean time to male–female encounter is insensitive to tortuosity, and depends almost entirely on population density, movement speed and encounter radius.

The numerical results of the simulation depend on two key variables: the magnitude of the encounter radii and the density of polar bears. The density range we selected is consistent with polar bear densities observed (or expected) in Baffin Bay and East Greenland based on pilot aerial surveys or assumed population sizes ([20,46,47], E. W. Born 2012, unpublished data). The range of encounter radii (5–20 km) was based on expert opinion. Importantly, however, the qualitative results of the simulation appear to be similar and robust across the ranges of both parameters. Quantitatively, at all the densities and encounter radii that we examined, the flux of females through the encounter area of a male is high enough that the expected time to encounter is no longer than two weeks, and as low as 1 day, regardless of the tortuosity of the male's movements. At higher densities (greater than 2 per 100 km^2) [47], and/or higher encounter radii, any given bear is almost constantly within the potential encounter radius of another bear. In these cases, encounter times may be insensitive to the statistical properties of a movement process, but depend more on details of behavioural interaction which were not captured in our simulation.

Our simple simulation assumes a homogeneous environment, a habitat-independent movement model, and no behavioural interactions (e.g. active avoidance or pursuit), all of which can additionally structure movement patterns. This was in part owing to the relatively coarse and sparsely sampled telemetry data used to parametrize the model. Despite these caveats, the robustness of the results suggests that at polar bear densities reasonable for our study area, the relationship between tortuosity and encounter rate is important.

(c) Comparison to other systems

The patterns we identified for polar bears contrast with our original expectation that behaviour would be similar to terrestrial male ursids, which expand their range during the breeding season in efforts to maximize female encounters [4,48,49]. The prey available for generalist feeders like brown bears in forest environments are widely distributed throughout the environment (e.g. insects and plants) or are highly mobile (e.g. ungulates) [49]. Thus, a restricted home range and more tortuous movements are a more viable strategy for female brown bears, in contrast to female polar bears, and male brown bears must range widely to mate with females. By contrast, it is more difficult for male polar bears to locate females at low densities over large areas in dynamic sea ice [40], especially while moving in pursuit of prey. Thus, a polar bear male's strategy may essentially be to wait for a flux of moving females to enter its encounter area.

It should be noted that polar bears inhabit a variety of ecoregions and occur at widely varying densities across their range [18]. Different male and female movement strategies may be more optimal under different conditions. For example, Amstrup *et al.* [19] reported movements of $n = 7$ male bears tracked in Alaska did not differ greatly from movements of females, however, male bears tended to move in a more linear manner than females. This suggests that movement and breeding strategies may be regionally variable and perhaps related to population density, though more data are needed to explore this hypothesis.

There are several other wide ranging, solitary mammals for which males during the breeding season have smaller ranges than females. These include several other marine carnivores, such as sea otters, (*Enhydra lutris*) and harbour seals (*Phoca vitulina*) where males defend small territories and attempt to attract females [2,50,51]. A somewhat analogous terrestrial system is that of the white rhinoceros (*Ceratotherium simum*). Owing to lengthy inter-calf intervals, females enter a receptive period approximately every 3 years similar to the polar bear [52]. Males defend mutually exclusive territories that are much smaller than females' ranges and territories are constrained by fierce male–male competition. White *et al.* [52] suggested that female white rhinoceros ranging patterns may be designed in part to access, and assess, multiple males for mating purposes and resources. The females tend to visit the same number of male territories regardless of their reproductive status, and select good quality habitat in the male territory over active mate choice. Male mating success is positively correlated with the number of females using a male territory, and therefore an optimal strategy is to maintain a territory in a preferred habitat [53–55]. White *et al.* [54] further suggested that one plausible explanation for large female ranges is that females have the ability to interact with several males, which may be part of an assessment strategy to identify and evaluate potential mates. The case for male polar bears could be similar, where males remain in optimal habitat waiting for receptive females. Female polar bears are known to mate with several males and have litters sired by several fathers [11,45], so there may be some active mate sampling or mate choice.

5. Conclusion

Molnár *et al.* [12] illustrated that the rate of pair formation is among the most important parameters in determining the eventual likelihood of reproductive success of polar bears, particularly at low population density. The dynamics of polar bear pair formation is ultimately controlled by movement behaviour, population densities, and biological and physical constraints in a dynamic Arctic environment. The integrated movement analysis presented here is a step towards a framework [56] by which individual movement data can inform population processes.

All permits for the study were provided by the Greenland Institute of Natural Resources and the Government of Greenland.

Studies were funded by the Bureau of Mineral and Petroleum (Nuuk), the Danish Ministry of the Environment, The Greenland Institute of Natural Resources, Åarhus University Department of Bioscience, University of Oslo and a NASA ROSES grant (NNX11AO63G). Thanks to Ib Larsen, Ilannguaq Egede, Jørgen Adam Fisker, Hans Christian Schmidt, Dennis Andriashek, Inge Mortensen, Mikkel Villum Jensen, Sigga Joensen, Lasø and Upernavik Sea Food, Tore Haug, Kit Kovacs, Christian Lydersen, Jon Aars, and Magnus Anderson for valuable help. Two anonymous reviewers improved the paper.

References

1. Ruckstuhl K, Neuhaus P (eds) 2005 *Sexual segregation in vertebrates*. Cambridge, UK: Cambridge University Press.
2. Sandell M. 1989 The mating tactics and spacing patterns of solitary carnivores. In *Carnivore behavior, ecology, and evolution* (ed. JL Gittleman), pp. 164–182. London, UK: Chapman and Hall.
3. Sandell M, Liberg O. 1992 Roamers and stayers: a model on male mating tactics and mating systems. *Am. Nat.* **139**, 177–189. (doi:10.1086/285319)
4. Ciarniello LA, Boyce MS, Seip DR, Heard DC. 2007 Grizzly bear habitat selection is scale dependent. *Ecol. Appl.* **17**, 1424–1440. (doi:10.1890/06-1100.1)
5. Bunnell FL, Tait DEN. 1981 Population dynamics of bears: implication. In *The dynamics of large mammal populations* (eds CW Fowler, TD Smith), pp. 75–98. New York, NY: John Wiley and Sons.
6. McLellan BN, Hovey FW. 2001 Natal dispersal of grizzly bears. *Can. J. Zool.* **79**, 838–844. (doi:10.1139/z01-051)
7. Kojola I, Danilov PI, Laitala H-M, Belkin V, Yakimov A. 2003 Brown bear population structure in core and periphery: analysis of hunting statistics from Russian Karelia and Finland. *Ursus* **14**, 17–20.
8. Støen O-G, Zedrosser A, Swenson JE, Sæbø S. 2006 Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia* **148**, 356–364. (doi:10.1007/s00442-006-0384-5)
9. Stirling I, Øritsland NA. 1995 Relationships between estimates of ringed seal and polar bear populations in the Canadian Arctic. *Can. J. Fish. Aquat. Sci.* **53**, 2594–2612. (doi:10.1139/f95-849)
10. Stirling I. 2011 *Polar bears: a natural history of a threatened species*. Markham, Canada: Fitzhenry & Whiteside.
11. Ramsay MA, Stirling I. 1986 On the mating system of polar bears. *Can. J. Zool.* **64**, 2142–2151. (doi:10.1139/z86-329)
12. Molnár P, Derocher AE, Lewis MA, Taylor MK. 2008 Modelling the mating system of polar bears: a mechanistic approach to the Allee effect. *Proc. R. Soc. B* **275**, 217–226. (doi:10.1098/rspb.2007.1307)
13. Larsen T, Jonkel C, Vibe C. 1983 Satellite radio-tracking of polar bears between Svalbard and Greenland. *Int. Conf. Bear Res. Manag.* **5**, 230–237.
14. Amstrup SD, Durner GM, Stirling I, Lunn NJ, Messier F. 2000 Movements and distribution of polar bears in the Beaufort Sea. *Can. J. Zool.* **78**, 948–966. (doi:10.1139/z00-016)
15. Taylor MK *et al*. 2001 Delineation of Canadian and Greenland polar bear (*Ursus maritimus*) populations by cluster analysis of movements. *Can. J. Zool.* **79**, 690–709.
16. Wiig Ø, Born EW, Pedersen LT. 2003 Movements of female polar bears (*Ursus maritimus*) in the East Greenland pack ice. *Polar Biol.* **26**, 509–516. (doi:10.1007/s00300-003-0513-0)
17. Andersen M, Derocher AE, Wiig Ø, Aars J. 2008 Movements of two Svalbard polar bears recorded using geographical positioning system satellite transmitters. *Polar Biol.* **31**, 905–911. (doi:10.1007/s00300-008-0428-x)
18. Durner GM *et al*. 2009 Predicting 21st-century polar bear habitat distribution from global climate models. *Ecol. Monogr.* **79**, 25–58. (doi:10.1890/07-2089.1)
19. Amstrup SC, Durner GM, McDonald TL, Mulcahy DM, Garner GW. 2001 Comparing the movement patterns of satellite tracked male and female polar bears. *Can. J. Zool.* **79**, 2147–2158. (doi:10.1139/z01-174)
20. Obbard ME, Thiemann GW, Peacock E, DeBruyn TD. (eds) 2010 *Polar bears. Proc. of the 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, Copenhagen, Denmark, 29 June–3 July 2009*, pp. 235. Gland, Switzerland: IUCN.
21. Valeur HH, Hansen C, Hansen KQ, Rasmussen L, Thingvad E. 1996 Weather, sea and ice conditions in eastern Baffin Bay, offshore Northwest Greenland. Danish Meteorological Institute Technical Report no. 96–12, Copenhagen, Denmark.
22. Tang CCL, Ross CK, Yao T, Petrie B, DeTracey BM, Dunlap E. 2004 The circulation, water masses and sea ice of Baffin Bay. *Progr. Oceanogr.* **53**, 183–228. (doi:10.1016/j.pocean.2004.09.005)
23. Aagaard K, Coachman LK. 1968 The East Greenland Current north of Denmark Strait. Part 1. *Arctic* **21**, 1181–2000.
24. Martin T, Wadhams P. 1999 Sea-ice flux in the East Greenland Current. *Deep-Sea Res. Part II* **46**, 1063–1082. (doi:10.1016/S0967-0645(99)00016-8)
25. Stirling I, Spencer C, Andriashek D. 1989 Immobilization of polar bears (*Ursus maritimus*) with Telazol in the Canadian Arctic. *J. Wildlife Dis.* **25**, 159–168.
26. Derocher AE, Ø Wiig. 2002 Postnatal growth in body length and mass of polar bears at Svalbard. *J. Zool.* **256**, 343–349. (doi:10.1017/S0952836902000377)
27. Born EW, Sonne C, Dietz R. 2010 Research on polar bears in Greenland, 2005–2009, p. 135–149. In *Polar Bears: Proc. 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group* (eds ME Obbard, GW Thiemann, E Peacock, TD DeBruyn), *Copenhagen, Denmark, 29 June–3 July 2009*. Gland, Switzerland: IUCN.
28. Rosing-Asvid A, Born EW, Kingsley MCS. 2002 Age at sexual maturity of males and timing of the mating season of polar bears (*Ursus maritimus*) in Greenland. *Polar Biol.* **25**, 878–883.
29. Born EW, Heilmann A, Kielsen Holm L, Laidre KL. 2011 Polar bears in Northwest Greenland: an interview survey about the catch and the climate. *Monogr. Greenland Meddelelser om Grønland* **351**, 250.
30. Calvert W, Ramsay MA. 1998 Evaluation of age determination of polar bears by counts of cementum growth layer groups. *Ursus* **19**, 449–453.

31. Kareiva PM, Shigesada N. 1983 Analyzing insect movement as a correlated random walk. *Oecologia* **56**, 234–238. (doi:10.1007/BF00379695)
32. Morales JM, Haydon DT, Frair J, Holsinger KE, Fryxell JM. 2004 Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* **5**, 2436–2445. (doi:10.1890/03-0269)
33. Duong T. 2011 Ks: Kernel smoothing. R package version 1.8.2. See http://CRAN.R-project.org/package=ks.
34. Hooge PN, Eichenlaub B. 1997 *Animal movement extension to arcview*. v. 1.1. Anchorage, AK, USA: Alaska Science Center—Biological Science Office, U.S. Geological Survey.
35. Stirling I, Parkinson CL. 2006 Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* **59**, 261–275.
36. Gurarie E, Suutarinen J, Kojola I, Ovaskainen O. 2011 Wolf (*Canis lupus*) movement and kill behaviors with respect to human-influenced habitat features in Finland. *Oecologia* **165**, 891–903. (doi:10.1007/s00442-010-1883-y)
37. Gurarie E, Ovaskainen O. 2011 Characteristic spatial and temporal scales unify models of animal movement. *Am. Nat.* **17**, 113–123. (doi:10.1086/660285)
38. R Development Core Team 2011 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. (http://www.R-project.org/)
39. Palmer SS, Nelson RA, Ramsay MA, Stirling I, Bahr JM. 1988 Annual changes in serum sex steroids in male and female black (*Ursus americanus*) and polar (*Ursus maritimus*) bears. *Biol. Reprod.* **38**, 1044–1050. (doi:10.1095/biolreprod38.5.1044)
40. Derocher AE, Andersen M, Wiig Ø, Aars J. 2010 Sexual dimorphism and the mating ecology of polar bears (*Ursus maritimus*) at Svalbard. *Behav. Ecol. Sociobiol.* **64**, 939–946. (doi:10.1007/s00265-010-0909-0)
41. Finley KJ, Miller GW, Davis RA, Koski WR. 1983 A distinctive large breeding population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. *Arctic* **36**, 162–173.
42. Thiemann GW, Iverson SJ, Stirling I. 2008 Polar bear diets and Arctic marine food webs: insights from fatty acid analysis. *Ecol. Monogr.* **78**, 591–613. (doi:10.1890/07-1050.1)
43. Visser A, Kiørboe T. 2006 Plankton motility patterns and encounter rates. Oecologia (*Berlin*) **148**, 538–546. (doi:10.1007/s00442-006-0385-4)
44. Bartumeus F, Catalan J, Viswanathan G, Raposo E, da Luz M. 2008 The influence of turning angles on the success of nonoriented animal searches. *J. Theor. Biol.* **252**, 43–55. (doi:10.1016/j.jtbi.2008.01.009)
45. Wiig Ø, Gjertz I, Hansson R, Thomassen J. 1992 Breeding behaviour of polar bears in Hornsund, Svalbard. *Polar Rec.* **28**, 157–159. (doi:10.1017/S0032247400013474)
46. Wiig Ø, Derocher AE. 1999 Application of aerial survey methods to polar bears in the Barents Sea. In *Marine mammal survey and assessment methods* (eds GW Garner, SC Amstrup, JL Laake, BFJ Manly, LL McDonald, DG Robertsen), pp. 27–36. Rotterdam, The Netherlands: Balkema.
47. Aars J, Marques TALO, Andersen M, Belikov S, Boltunov A, Buckland ST, Ø Wiig. 2009 Estimating the Barents Sea polar bear subpopulation size. *Mar. Mamm. Sci.* **25**, 35–52. (doi:10.1111/j.1748-7692.2008.00228.x)
48. Dahle B, Swenson JE. 2003 Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *J. Anim. Ecol.* **72**, 660–667. (doi:10.1046/j.1365-2656.2003.00737.x)
49. Steyaert SMJG, Endrestøl A, Hackländer K, Swenson JE, Zedrosser A. 2012 The mating system of the brown bear *Ursus maritimus*. *Mamm. Rev.* **42**, 12–34. (doi:10.1111/j.1365-2907.2011.00184.x)
50. Jameson RJ. 1989 Movement, home range, and territories of male sea otters off central California. *Mar. Mamm. Sci.* **5**, 159–172. (doi:10.1111/j.1748-7692.1989.tb00330.x)
51. Van Parijs SM, Jannik VM, Thompson PM. 2000 Display area size, tenure and site fidelity in the aquatic mating male harbour seal. *Can. J. Zool.* **78**, 2209–2217.
52. Owen-Smith RN. 1988 *Megaherbivores: the influence of very large body size on ecology*. Cambridge, UK: Cambridge University Press.
53. Rachlow JL, Berkeley EV, Berger J. 1998 Correlates of male mating strategies in white rhinos (*Ceratotherium simum*). *J. Mammal.* **79**, 1317–1324. (doi:10.2307/1383023)
54. White AM, Swaisgood RR, Czekala N. 2007 Ranging patterns in white rhinoceros, *Ceratotherium simum simum*: implications for mating strategies. *Anim. Behav.* **74**, 349–356. (doi:10.1016/j.anbehav.2006.12.011)
55. Guerier AS, Bishop JM, Crawford SJ, Schmidt-Küntzel A, Stratford KJ. 2012 Parentage analysis in a managed free ranging population of southern white rhinoceros: genetic diversity, pedigrees and management. *Conserv. Genetics* **13**, 1–14. (doi:10.1007/s10592-011-0274-1)
56. Gurarie E, Ovaskainen O. 2012 Towards a general formalization of encounter rates in ecology. *Theor. Ecol.* (doi:10.1007/s12080-012-0170-4)