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Home ranges in moving habitats: polar bears and sea ice

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Home range size estimates are often used to assess the amount of space required for animals to perform the activities essential for their survival and reproduction. However, in moving environments, traditional home range estimates may be ill suited to this task. In particular, traditional home range estimates are inaccurate representations of the space required by polar bears *Ursus maritimus*. The sea ice is the prime foraging platform of polar bears, and estimating the amount of ice encountered by bears may provide a better approximation of space use. We develop a technique to make these estimates. Our results confirm that polar bears use more space than terrestrial carnivores to find the resources and conditions they require. We also show that the traditional geographic home range can underestimate both the movement of bears and the amount of space encountered. Moreover, area of ice encountered increased with ice drift, indicating that bears living on highly mobile ice might be exposed to higher energetic costs, and potentially larger energetic gains, than bears inhabiting more stable ice. The methods and concepts presented here can serve as a foundation for new approaches to study the space use of the many species living in moving environments.

The formation of a home range is a ubiquitous property of animal space use that affects many of the fundamental ecological processes influencing their abundance and distribution (Börger et al. 2008). As such, the concept of home range has become an important part of ecological research and wildlife management. Burt (1943) formalised the definition of home range as the 'area traversed by the individual in its normal activities of food gathering, mating, and caring for young'. Although this basic definition is imprecise (Cooper 1978, White and Garrott 1990), two notions emerge as central to the home range concept. First, home ranges are associated with site fidelity and an animal's familiarity with an area (Cooper 1978, Spencer et al. 1990, Powell and Mitchell 2012). This familiarity may provide knowledge that confers fitness benefits (Powell and Mitchell 2012). Second, home ranges have long been used to represent the amount of space required by animals to acquire the resources necessary for their survival and reproduction (McNab 1963, Reiss 1988, Kelt and Van Vuren 1999). This second aspect of home ranges is at the heart of studies that explain variation in home range size across species or individuals (McNab 1963, Kelt and Van Vuren 1999, Tucker et al. 2014). This second aspect is also essential to studies assessing optimal home range dimensions in terms of the costs and benefits of reaching spatially distributed resources (Mitchell and Powell 2004, 2007), and those that seek to identify important characteristics of an animal's habitat (Tufto et al. 1996, Millspaugh et al. 2006, Edwards et al. 2013). While home ranges cannot be equated to habitat (sensu Hall et al. 1997), they can be used to identify the areas containing the conditions and resources with the potential to promote occupancy.

The two central aspects of home ranges are spatially linked for terrestrial species, and can be assessed simultaneously using statistical tools such as the simple kernel-based utilisation distribution (Worton 1989) or more sophisticated mechanistic modeling techniques (Moorcroft et al. 1999, 2006). By delineating the geographic area repeatedly visited by an individual, these statistical tools also capture the area of the landscape used by the animal to gather resources. However, for many species that live in drifting environments (e.g. oceans, rivers, sea ice, and the atmosphere), the direct spatial link between the geographic area and the conditions and resources encountered is lost. If resources are drifting in and out of a geographic area, the area cannot be assigned a fixed habitat quality, which is needed to relate its size to the amount of resources it provides. In marine environments, the amount of resources encountered in a given location will depend on the strength of currents and the productivity in the areas from which currents emerge. Because large changes in current strength and direction occur frequently, the resources provided by a particular geographic area are likely to have more extreme temporal variation in marine than in terrestrial environments. The movement direction of an animal in relation to the drift direction will affect the costs and benefits of space use in two important ways. First, whether an animal is passively drifting with the current or actively moving against the flow will influence how much of the medium it encounters, and thus the amount of resources it may find. Second, because moving with or against a current significantly affects the energy expenditure of an animal (Gaspar et al. 2006), we can no longer use distance moved as a proxy for the energetic cost of reaching resources.

Here, we incorporate drift in home range analysis and demonstrate the potential benefits of this approach. We use polar bears *Ursus maritimus* as our study species because their interaction with the two-dimensional sea ice platform provides a simple illustration of the challenges associated with studying home ranges in drifting environments. Polar bears hunt seals on the sea ice, and many bears spend a significant part of the year on drifting pack ice (Stirling et al. 1993, Amstrup et al. 2000, Mauritzen et al. 2003). Sea ice can move many kilometres per day (Hakkinen et al. 2008). Individual polar bears return to the same geographic region annually, use the same core area across years, and follow similar movement patterns between seasonally important regions (Amstrup et al. 2000, Mauritzen et al. 2001, Stirling 2002). Thus, the geographic area used by bears corresponds to the site fidelity aspect of their home range. However, aspects linked to resources, such as the amount of sea ice visited, amount of prey encountered, and energy expended cannot be related to this geographic area without incorporating ice drift. This is particularly important for polar bears because the distribution of their main prey, the ringed seal *Pusa hispida*, is linked to the sea ice. Ringed seals must maintain breathing holes and lairs to prevent them from freezing closed, and thus are tied to a specific piece of ice from freeze-up to melting (Smith and Stirling 1975, Kelly et al. 2010). Many ringed seals choose stable landfast ice to construct their lairs, but others inhabit drifting pack ice (Smith and Stirling 1975, Wiig et al. 1999, Kelly et al. 2010, Pilfold et al. 2014b). Thus, for polar bears, the area of sea ice visited will represent the resource aspect of their home ranges better than the geographic area.

In this paper, we develop a method to estimate the area of sea ice visited by polar bears. We refer to this estimate as the 'area of habitat encountered', by which we mean the amount of icescape animals use to find the resources and conditions they require. We compare these estimates to the sizes of bears' geographic home ranges. First, we show that mean area of habitat encountered is significantly larger than that of the geographic home range. Second, we show that the area of habitat encountered is correlated with the amount of ice drift and discuss how the influence of drift on polar bear space use has implications on both their energy expenditure and food intake. Finally, we discuss how incorporating drift in home range analyses of other marine species could help investigate a series of questions, including why territory formation is less common in the ocean and why animals in drifting environments have larger home ranges than terrestrial species. We highlight how comparing estimates of area of habitat encountered to geographic home range size is the first step towards understanding the trade-offs of using drifting rather geographically-fixed resources.

Methods

Polar bear GPS data

We used the movement data from 21 polar bears collared in the Beaufort Sea from April and May 2007–2011 to estimate annual home ranges. We located bears by helicopter and immobilized them using standard methods (Stirling et al. 1989). Collars (Telonics, Mesa, AZ) were programmed to collect a GPS location every 4 h for one or two years. Following immobilisation, most bears recover their normal movement within three days of capture (Thiemann et al. 2013). Thus, we excluded locations during this three-day period. Any subsequent capture event ended the data series for that bear. We limited the analysis to individuals that had data for close to a whole year (i.e. collar functioned for ≥ 343 d and with ≤ 8 consecutive days of missing data). As the calculation of our home range depended on daily sea ice drift data at the location of the bear, we also excluded any bear year that was missing more than 150 d of drift data (see below for sea ice data description). We had sufficient data from five individuals to create multiple annual home ranges. For these, we selected the year that had the least missing sea ice data.

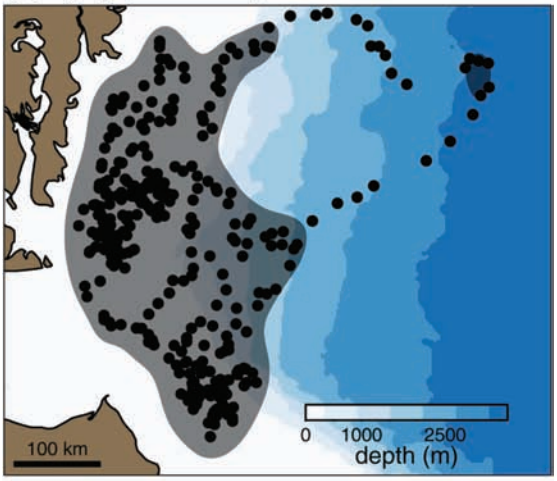
Sea ice movement data and differentiating drift from voluntary movement

One of our primary objectives was to incorporate ice drift into our home range analyses. We used Polar Pathfinder Daily 25 km Ease-Grid Sea Ice Motion Vectors, which are calculated using various satellite sensors and the movement paths of ice buoys (Fowler 2003). These 25 by 25 km pixel rasters provide estimates of the daily movement of sea ice as displacement in the x and y direction. We interpolated the ice drift value at each bear location with the 'iwd' function of the R package 'gstat' (Pebesma 2004), setting the distance weighting power to 3. All locations with fewer than three pixels with drift data within 36 km were categorized as missing data. Pixels lacked sea ice movement data because of low ice concentration or proximity to the coast, which makes the estimation of sea ice movement by satellite imagery difficult (Schwegmann et al. 2011). Ice movement data are often missing in areas where stationary landfast ice is found in winter and spring. We identified these instances using regional sea ice charts (Canadian Ice Service 2009) and assigned a drift of 0 to these locations.

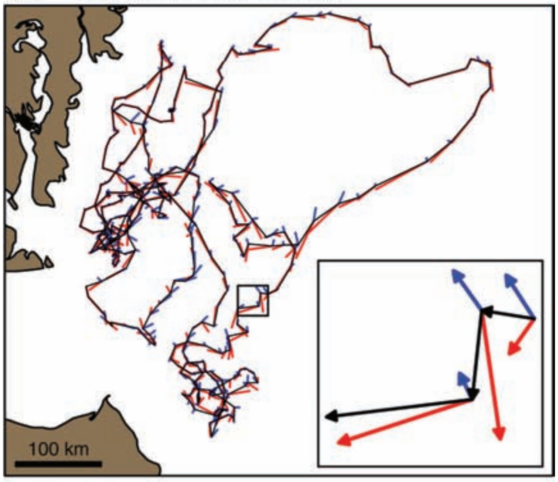
To incorporate drift in our home range analysis, it was important to differentiate the voluntary movement of the bear from movement caused by sea ice drift. To estimate the voluntary movement, we used vector subtraction to calculate the difference between the daily displacement of the sea ice and the observed daily collar displacement (Fig. 1b). Both missing collar locations and missing sea ice data precluded the estimation of the daily voluntary movement of a bear. We interpolated collar locations for missing days using the straight-line distance between the two most recent locations. For days when we had missing sea ice data, we used the observed displacement of the collar as an estimate of the voluntary movement of the bear. This procedure may underestimate the difference between the geographic home range size and area of habitat encountered.

Estimating the area of the geographic home range and of the habitat encountered

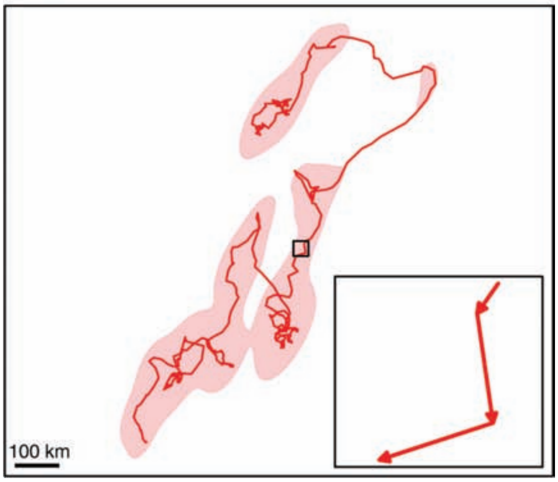
Both the area of the geographic home range and of the habitat encountered were estimated using a utilisation distribution



(a) geographic home range



(b) voluntary movement vs ice drift



(c) area of habitat encountered

Figure 1. Representation of (a) the geographic home range (dark polygons) based on the locations given by the collar (●) of one bear, (b) the decomposition of the observed displacements of the bear (black lines and arrows) into their ice drift (blue lines and arrows) and voluntary movement (red lines and arrows) components, and (c) an estimate of the area of habitat encountered (polygons) based on the reconstructed voluntary movement path (lines and arrows). The map projection is the Northern Hemisphere azimuthal equal-area EASE-Grid developed for polar sea ice data (Brodzik and Knowles 2002).

with fixed bivariate normal kernel (Worton 1989), one of the most common methods to estimate home range size. For the smoothing parameter, we used the plug-in method (Sheather and Jones 1991, Fieberg 2007). We chose the plug-in method because other commonly used methods did not converge or resulted in nonsensical results. The smoothing parameters estimated with the reference bandwidth method were much larger than the maximum observed displacement, resulting in over-smoothed home ranges. The least-square cross-validation method had convergence problems for many individuals and under-smoothed the home range of the others. The problems associated with these methods have been discussed elsewhere (Hemson et al. 2005, Kie 2013). The smoothing parameter affects the absolute size of estimates. However, our study is focused on comparing estimates across individuals and between the geographic home range size and the area of habitat encountered. To produce reliable results in comparative studies, a standardized sampling regime overrides the importance of potential bias in the absolute size of the estimates (Börger et al. 2006, Fieberg and Börger 2012). Our estimates are based on movement paths with similar sample size, sampling rate, and sampling period. We used the 95% contour of the utilisation distribution to delineate the home range. These calculations were made using the package ‘ks’ (Duong 2007).

The main difference between the two area estimates lies in the locations used to calculate the utilisation distributions. For the geographic home range, we used the observed and interpolated collar locations (Fig. 1a). For the habitat encountered, we used the locations associated with a movement path recreated from the voluntary movement of the bear (Fig. 1c). We determined whether the area of ice habitat encountered by bears differed from their geographic home range using a Wilcoxon signed rank test for paired samples ($H_{0:}$ $\text{area}_{HE} = \text{area}_{GHR}$, $H_{a:}$ $\text{area}_{HE} > \text{area}_{GHR}$).

Identifying the determinants of home range size

To assess the determinants of home range size, and whether these differed between the geographic home range and the area of ice habitat encountered, we used multiple linear regressions with a variety of intrinsic and extrinsic variables. The intrinsic variables were age class (adult, subadult), sex, and whether or not dependent cubs accompanied the individual at the beginning of the time series. We included age class and sex because similar factors have been associated with the movement of individuals (Amstrup et al. 2000, Mauritzen et al. 2001, Laidre et al. 2013). The majority of the individuals collared were adult females, however some were subadults of both sexes. We included the presence of cubs because caring for young can alter home ranges (Tufto et al. 1996, Mitchell and Powell 2007). In two instances, we could not ascertain from field observations whether cubs accompanied the females at the beginning of the year. Following Mauritzen et al. (2003), we assigned cub status in these cases based on the normal reproductive cycle of polar bears and whether there was evidence for denning in the movement path. Polar bears only den to give birth to cubs and females from the Beaufort Sea normally weaned their young at 2.5 yr of age (Stirling 2002). As bears with cubs-of-the-year have different movement patterns and habitat preference than other females (Amstrup et al. 2000, Pilfold et al. 2014a), cub age might be an important explanatory variable. However, our small sample size of cubs in certain age classes limited our analysis to presence/absence of cubs.

The extrinsic factors we assessed included both static and dynamic features of the habitat. The static features were the mean ocean depth within the geographic home range and whether the bears spend more than a week on land. We estimated the mean ocean depth using the International Bathymetric Chart of the Arctic Ocean ver. 2.23 with 2 by 2 km grid cells (Jakobsson et al. 2008). A binary variable, denoting whether a bear spent more than a week on land, was used to differentiate the bears remaining most of the year on the sea ice from those staying long periods on land. Bears can use land for maternity denning or to take refuge during the low-ice season. Our two dynamic covariates were associated with sea ice features: mean daily drift experienced by a bear (described above) and a proxy for the proportion of prime sea ice conditions that an individual encountered. To assess the quality of the sea ice conditions, while also accounting for the daily changes in sea ice quality, we used the proportion of days that a bear spent at sea in ice concentration $> 85\%$ (i.e. 'best' conditions for polar bears following Sahanatien and Derocher (2012), see also Pilfold et al. 2014a). We also examined a threshold of 60% (i.e. 'good' conditions for polar bears, Sahanatien and Derocher 2012), but excluded it from final analyses because it was highly correlated with the other variable and performed less well. We used daily estimates of sea ice concentration for 25 by 25 km pixels generated from satellite brightness temperature data (Cavalieri et al. 1996). For the analysis of the area of sea ice encountered, we used an additional variable, the number of days with missing ice drift data, to account for its potential effect on our estimates.

Before conducting our analyses, we assessed collinearity between our predictor variables, using the correlation coefficient, r, as an indicator and the commonly used threshold of $|r| > 0.7$ (Dormann et al. 2013). None of the variables in our final analysis were collinear. To identify which covariates were important determinants, we fit a series of linear regression models. We compared the relative fit of the models using AICc and assessed the relative importance of variables using AICc-based importance weights (Burnham and Anderson 2002). As an additional check of variable importance, we carried out random forest analyses (Breiman 2001). We used 500 trees with two candidate variables randomly selected per split and the permutation-based mean square error (MSE) reduction (Grömping 2009). We used the R package 'randomForest' (Liaw and Wiener 2002). Because many of the models were within two ΔAICc from the best model (see Results), the estimated coefficients for the variables were based on model averaging. We evaluated the absolute fit of models using R^2 and the statistical significance of a variable using the 95% confidence interval (CI) of its model-averaged coefficient (Lukacs et al. 2010).

Because we had no a priori expectation for combinations that would produce the best model, we conducted pre-analyses that selected the best combinations within two sets of variables: intrinsic and extrinsic variables. Similar to Mellin et al. (2012), only the variable combinations that outperformed the null model and had an Akaike weight > 0.001 were retained in the final model comparisons and in the model-averaged coefficients. Note, however, that all combinations of the pre-selected variables were used when assessing the AICc-based importance weight, because this measure requires that all variables be used in an equal number of models (Burnham and Anderson 2002). Because of our small sample size, we did not include interactions between covariates.

Post-hoc movement analyses

To gain further insight into our home range results, we investigated a few polar bear movement characteristics. First, we investigated whether the determinants of the ice habitat encountered were similar to those explaining the total voluntary bear displacement. We use the same covariates and methods as for the ice habitat encountered (see above), but use the annual total voluntary displacement as the response variable. Because estimating the voluntary movement of the bear requires ice drift data, the total voluntary displacement estimates excluded days with missing ice drift data. However, we retained the number of days with missing data as a predictor variable to determine whether this exclusion affected the analysis. Second, we investigated whether the direction of the voluntary movement of bears was in the opposite direction to ice drift, as suggested by our home range results. To investigate whether the difference in angle between the voluntary movement and the ice drift may have a unimodal peak, we used a modified Rayleigh test of uniformity with alternative mean angle of 180° (Zar 2014). To test whether the mean angle was significantly different from 180°, we used the one-sample test for the mean angle (Zar 2014). For these circular analyses, we only used the movement of bears when they were experiencing drift (i.e. remove all days when the bear is on land, on land fast ice, or on other non-moving sea ice).

All analyses and spatial data manipulations were performed in R 3.1.1 (R Core Team), and relied on the 'sp', 'raster', and 'rgdal' packages (Pebesma and Bivand 2005, Bivand et al. 2013, Hijmans 2013). All spatial analyses used the Northern Hemisphere azimuthal equal-area EASE-Grid map projection developed for polar sea ice data (Brodzik and Knowles 2002).

Data available from the Univ. of Alberta Education and Research Archive: <https://era.library.ualberta.ca/public/home>.

Results

On average, the annual area of habitat encountered (178 040 km^2, range: 3766–367 547 km^2) was significantly larger than that of the annual geographic home range (142 332 km^2, range: 3528–381 947 km^2; Wilcoxon test, $V = 27$, $p < 0.01$). However, the magnitude of the difference between these two area estimates ranged widely among individuals (range: 238–138 400 km^2). Although most individuals (17/21) had larger areas of habitat encountered, a few (4/21) had larger

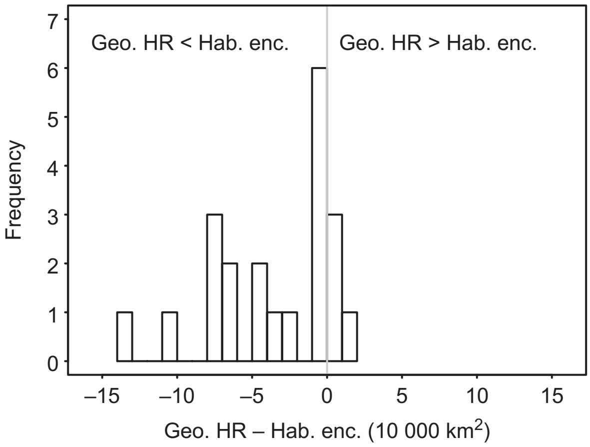


Figure 2. Histogram of the individual differences between the size of the geographic home range (Geo. HR) and area of habitat encountered (Hab. enc.).

geographic home range areas (Fig. 2). When travelling on ice, the annual average drift experienced by individual bears ranged between 2.3 and 8.0 km d^{-1} (mean = 4.5 km d^{-1}). The annual average of individuals' voluntary movement ranged from 4.1 to 21.5 km d^{-1} (mean = 13.9 km d^{-1}).

The variation in geographic home range area was largely explained by mean ocean depth, the only variable for which the model-averaged CI did not include 0. Depth was in the best model and had the highest importance according to Akaike weights and random forest MSE reduction (Supplementary material Appendix 1, Table A1 and A2). Geographic home range size increased with mean depth (Supplementary material Appendix 1, Fig. A1).

The variation in area of habitat encountered was largely explained by mean ocean depth, time on land, and mean daily ice drift. Depth, land, and drift were the only variables for which the model-averaged CI did not include 0, the only three covariates of the best model, and had the highest importance according to both importance measures (Table 1 and 2). As was the case for the geographic home range area, the area of habitat encountered increased with depth (Fig. 3a and Table 2). The area of habitat encountered also increased if the bear spent ≤ 1 week on land and with increasing ice drift (Fig. 3b, c, Table 2). These three variables explained a large part of the variation in the area of habitat encountered by different bears ($R^2 = 0.69$).

Table 1. Relative and absolute fit of the best models ($\Delta AICc \leq 4$) explaining the area of the ice habitat encountered. The intrinsic and extrinsic variables were first considered separately. For each separate analysis, only the models that outperformed the null model and with an Akaike weight greater than 0.001 were retained for the final analysis. None of the combinations of intrinsic covariates outperformed the null model and thus only models with extrinsic covariates are presented.

Covariates included	DF	ΔAICc	Akaike weight	R²
depth + drift + land	5	0.00	0.238	0.68
depth + land	4	0.58	0.178	0.61
depth + drift + best ice	5	1.34	0.121	0.66
depth + drift + best ice + iceNA	6	1.35	0.121	0.72
depth + drift + land + iceNA	6	1.48	0.114	0.72
depth + drift	4	2.46	0.069	0.58
depth + drift + land + best ice	6	3.43	0.043	0.69
depth + land + iceNA	5	3.52	0.041	0.62
depth + best ice	4	3.65	0.038	0.55
depth + land + best ice	5	3.67	0.038	0.62

Table 2. Estimates of the covariates' coefficient and their relative importance in the habitat encountered models. The average coefficients and associated CIs are based only on covariate combinations retained by the final analysis. In contrast, the AICc-based importance weight relies on all possible combinations of the pre-selected covariates (see Methods). The non-normalised random forest importance scores are also presented for the pre-selected covariates. Note that the values of the two importance measures are not directly comparable but the ordering is similar. The variables for which the CI excluded 0 are bolded.

			Importance	
Covariate	Coef	CI	AICc-based	Random forest-based
depth	**0.007**	**0.002–0.012**	**0.93**	**10.65**
drift	**2.66**	**0.09–5.23**	**0.72**	**6.47**
best ice	24.35	−8.85–57.55	0.38	3.72
iceNA	0.056	−0.033–0.145	0.32	2.74
land (True)	**−8.76**	**−17.37–−0.15**	**0.61**	**5.40**

Consistent with our analysis of habitat encountered, the total voluntary displacement of bears decreased with time spent on land and increased with ice drift (Supplementary material Appendix 1, Table A3, A4). However, there was no relationship between total voluntary displacement and depth (Supplementary material Appendix 1, Table A3, A4). The circular tests and visual inspection suggested that the annual average voluntary movement of polar bears was in the opposite direction to the ice drift (Fig. 4). According to the modified Rayleigh test with alternative mean angle of 180°, the distribution of the angle between the voluntary movement and ice drift was significantly different from the uniform distribution ($u = 0.645$, $p < 0.01$). According to the one-sample test of mean angle, the mean difference between the voluntary movement and drift was not significantly different from 180° (mean angle = 167°, CI = 136°–197°).

Discussion

For species that inhabit drifting environments, analyses of space use based on geographic locations can capture the fidelity of an individual to a region, but can be inadequate to quantify the amount of habitat an individual encounters. In particular, because sea ice drifts in and out of polar bears' geographic home ranges and is the prime platform they use to forage (Stirling et al. 1993, Derocher et al. 2004), home range size cannot be used as an indicator of a polar bear's habitat requirements and energy expenditure without considering ice drift. Thus, the geographic home range of animals in drifting environment cannot be used to represent the balance between the costs and benefits arising from the use of spatially distributed resources (Kelt and Van Vuren 1999, Mitchell and Powell 2004). We have presented a new means to estimate the area of habitat encountered for animals that inhabit drifting sea ice. Our results indicate that most polar bears encountered more habitat than estimated by the geographic home range and, in extreme cases,

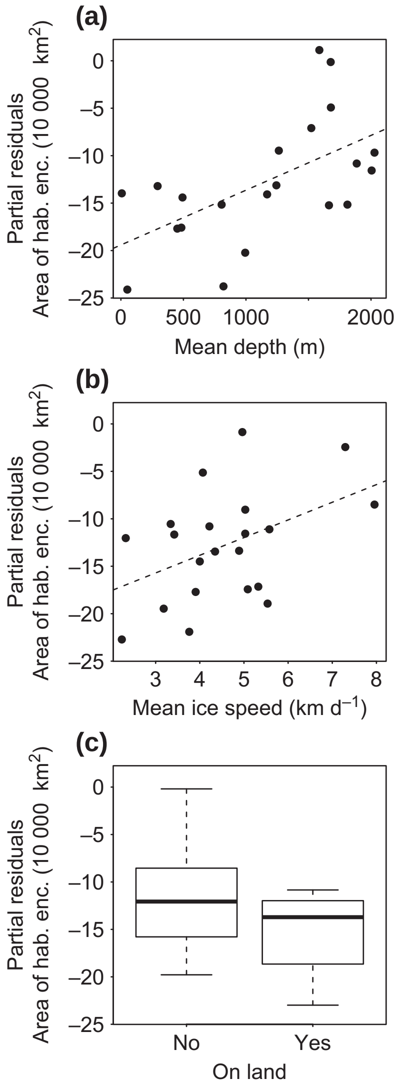


Figure 3. Relationships between the area of habitat encountered and the only three variables for which the model-averaged CIs excluded 0: (a) mean depth, (b) whether the bear spend more than a week on land, and (c) mean daily ice speed. The points represent the partial residuals of the final averaged model and the dashed lines represent the components (i.e. the modeled relationships).

the difference between these two estimates was greater than 100 000 km^2 (i.e. >70% of the mean geographic home range size). In addition, the individual variation in area of the habitat encountered and that of the geographic home range were explained by different covariates. This suggests that correcting home range area estimates with drift information is important in facilitating our understanding of the factors that govern polar bear space use.

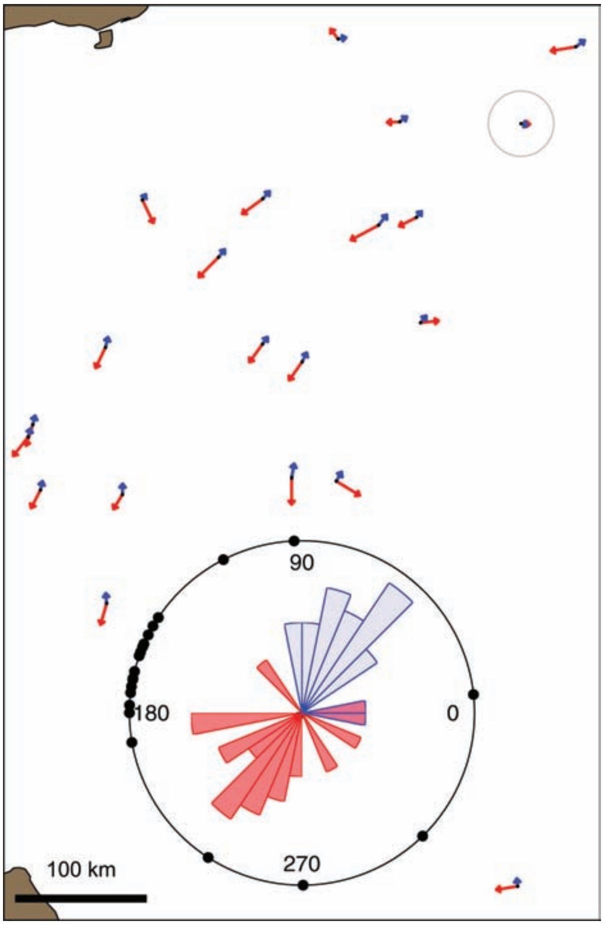


Figure 4. Comparison between the voluntary movement of bears and the drift they experience when they are on moving sea ice. The red arrows represent the mean voluntary movement of an individual, while the blue arrows represent the mean ice drift experienced. The length of the arrows (arrowhead excluded) represents the annual average speed for an individual. Except for one exception, the start of arrows represents the center of the geographic home range of each individual. The individual circled in grey was too far from the others to be nicely displayed (close to Wrangel Island) and the start of its arrows does not represent its home range center. In the rose diagram, the area of the red and blue bars represents the relative frequency of the direction of the voluntary and drift movement, respectively. The black dots around the circular graph represent the mean difference in angle between the voluntary movement of a bear and the drift it experiences. A dot at 180° represents an individual moving, on average, in the opposite direction to ice drift.

Population and individual differences in area estimates

Polar bears have geographic home ranges orders of magnitude larger than expected for terrestrial carnivores of similar weight (Ferguson et al. 1999). This suggests that polar bears require more space than terrestrial carnivores to acquire resources. It also suggests that they can energetically afford to travel long distances to reach resources, even though the metabolic cost of walking is unusually high for polar bears (Hurst et al. 1982). Because previous home range size estimates did not correct for ice drift, the larger home ranges of polar bears could have resulted from bears passively drifting over large geographic areas. Thus, accounting for ice drift could have revealed that polar bears use a similar amount of space to terrestrial carnivores. Our results suggest that this is not the case. Our estimates of the area of habitat encountered were generally larger than our estimates of geographic home range size, and both mean estimates fell within the range estimated by others (Ferguson et al. 1999, Amstrup et al. 2000). Our findings confirm that polar bears require a larger area of habitat than terrestrial carnivores, and that factors such as large seasonal changes in habitat quality might force polar bears to travel long distances to maintain access to resources (Ferguson et al. 1999).

The larger size of the area of habitat encountered compared to the geographic home range suggests that bears generally move in the opposite direction to the ice, which was supported by our post-hoc movement analyses. In the Barents Sea, where there is a continuous southward ice drift, this behaviour appears to be necessary for polar bears to remain in ice-covered environments (Mauritzen et al. 2003). In the Beaufort Sea, moving against the clockwise sea ice drift, caused by the Beaufort gyre (Coachman and Aagaard 1974), would not necessarily help bears avoid ice-free regions. Polar bears exhibit site fidelity (Amstrup et al. 2000, Mauritzen et al. 2001, Stirling 2002), and bears may walk against sea ice drift to remain within a familiar geographic region. Alternatively, movement against ice drift may be the result of bears tracking the cyclical changes in the spatial distribution of habitat of high quality (Mauritzen et al. 2003).

Regardless of what causes bears to move against the sea ice, our results indicate that most bears encounter more habitat than their geographic home range would suggest. Thus, the geographic home range is often an inadequate representation of the ice habitat a bear covers in a year. The difference between the estimates of area of habitat encountered and geographic home range area spanned three orders of magnitude, with some individuals displaying the opposite pattern from the majority (i.e. encountered less ice habitat than estimated with geographic locations). This variation further emphasizes that studies of the physiological and ecological factors affecting home range size should account for the drift experienced by each bear.

Determinants of home range area

The annual home range sizes of polar bears are highly variable, ranging from a few hundred to several hundred thousand square kilometres (Ferguson et al. 1999, Mauritzen et al. 2001). This variability was explained by both large regional differences in the amplitude of the seasonal change in ice extent, and whether an individual responds to the sea ice retreat by taking refuge on land (Ferguson et al. 1999, Mauritzen et al. 2001). These relationships reflect polar bears' use of sea ice as a platform to hunt seals and requirement for high ice concentration to travel effectively (Derocher et al. 2004, Cherry et al. 2013), as well as the high cub mortality risk and decline in body condition associated with long-distance swims (Blix and Lentfer1979, Monnett and Gleason 2006, Durner et al. 2011). The highly dynamic ice of the Beaufort Sea likely explains why our home range estimates, and those of Amstrup et al. (2000), are at the higher end of the size spectrum. We investigated the covariates that might explain the subtler differences in home range size of Beaufort Sea polar bears.

Ocean depth was positively correlated with both the geographic home range area and area of habitat encountered. Two mechanisms may explain this relationship. First, the relationship could result from individual differences in strategies used to cope with seasonal ice loss. None of our bears used land as a refuge during the low sea-ice season. However, some remained close to the coast, while others ranged far offshore. These differences might involve a trade-off. Bears staying in shallower regions travel less and have smaller home ranges, but they might be exposed to low ice concentration and the risk of being caught in open water. Second, the relationship may result from a decrease in foraging habitat quality with depth. The diet of polar bears in the Beaufort Sea comprises seal species that are most abundant in the shallow waters of the continental shelf (Stirling et al. 1977, Frost et al. 2004, Pilfold et al. 2012). Theory predicts that individuals in poor quality habitat should compensate for lower resource density with larger home ranges (Ford 1983). Our results are consistent with this hypothesis, but seal density is not linearly related to depth. A better test of this hypothesis would require extensive data on seal distributions. The relative importance of these two mechanisms is unclear. Nevertheless, there is a clear relationship between depth and polar bears' space use patterns. While it is not an important variable for the total voluntary displacement, it is a strong predictor of polar bear habitat use (Durner et al. 2009) and the most important covariate in our analyses of both geographic home range and habitat encountered.

The analysis of area of habitat encountered revealed two important secondary covariates not present in the analysis of the geographic home range: time spent on land and ice drift. Bears that spent more than a week on land had smaller area of habitat encountered and smaller total voluntary displacement than those remaining on the sea ice for almost the entire year. In our study, land use was mainly associated with denning. Of the four bears that made extensive use of land, two entered a maternal den and one had a movement pattern consistent with denning. The fourth remained in the same location from 10 December to 9 February, which is suggestive of a failed reproductive event (Amstrup and Gardner 1994). These females had small home ranges because they spent multiple months immobile on land.

Area of habitat encountered increased with ice drift. These results, as well as the post-hoc movement analyses, suggest that polar bears compensate for ice drift, which has two implications. First, bears travelling against higher levels of ice drift have to walk more than bears in lower drift environments to cover the same-sized geographic area. If food resources are geographically fixed, such bears expend more energy to acquire the same amount of food. Second, with increased movement, there is an increase in the amount of ice habitat encountered. Polar bears make extensive use of drifting ice, where they kill many seals (Stirling et al. 1993, Pilfold et al. 2014b). Bears walking against faster moving ice will encounter more resources if the ice encountered has the same seal density and the seals are confined to specific ice floes (e.g. ringed seals maintaining breathing holes, Smith and Stirling 1975, Kelly et al. 2010). This increase in foraging opportunities may counteract the cost of walking against ice drift. Thus, the costs and benefits of compensating for ice drift will depend on whether seals are more tightly linked to particular geographic areas or particular ice floes, as well as how seals' space use strategies are affected by ice drift. Nevertheless, the influence of drift on polar bear space use identified with our estimates of habitat encountered has implications on both their energy expenditure and food intake. The importance of drift on polar bear space use is also emphasized by its large magnitude (4.5 km d^{-1}) relative to the bears' voluntary movement (13.9 km d^{-1}).

Challenges involved in incorporating drift in home range analyses

We presented a new method to incorporate drift into home range analyses. Our estimate better approximates the ice habitat encountered, and the movement required to access resources, than if we were to assume that the sea ice is immobile, which the geographic home range does. However, this approach could be developed further. Our estimate is based on the simplifying assumption that ice drifts as one large piece, or many pieces moving in unison, and thus that the voluntary movement of the bears maps the amount of ice encountered. This assumption may be met for large parts of the year when the Beaufort Sea is composed of westward moving floes wider than 2 km (Canadian Ice Service 2009). However, sea ice fractures and compresses, wind affects the direction of ice drift, and sea ice configuration can change rapidly during break up (Comiso 2010). Although logistically challenging, further developments could account for these factors by modelling the movement of individual floes. Any estimates of ice habitat encountered will depend on the availability, accuracy, and spatiotemporal scale of ice drift data. Ice drift data is often limited to coarse spatiotemporal scales and is inaccurate or unavailable close to the coast and where ice concentration is low (Fowler 2003, Schwegmann et al. 2011). Improved ice drift data would allow us to refine estimates of the area of ice habitat encountered.

Polar bears are thought to have large and variable home ranges because they depend on the marine environment, which is highly variable in space and time (Ferguson et al. 1999). Based on conventional geographic home ranges, other marine mammals also have larger home ranges than their terrestrial counterparts (Tucker et al. 2014). Other marine taxa ranging from zooplankton to loggerhead turtles *Caretta caretta* move in the reverse direction to the current (Genin et al. 2005, Kobayashi et al. 2014). For fish, orienting towards prevailing flow facilitates the capture of drifting prey and is a vital component of olfactory search (Montgomery et al. 2000). These examples indicate that polar bears may not be the only marine species to encounter more habitat than estimated through traditional home range methods. Thus, the habitat encountered by marine species might be even larger relative to terrestrial species than currently thought.

Perhaps because of the complexity associated with studying the space use patterns of marine animals, comparatively fewer home range studies have been performed on marine than terrestrial species. While the effects of drift on the movement of marine animals is increasingly recognised as important (Gaspar et al. 2006, Kobayashi et al. 2014), its effects on broader-scale home range analysis has been ignored. Recent studies of marine home range sizes used geographic area estimated by kernel density and minimum convex polygon (Schofield et al. 2010, Welsh et al. 2013, Tucker et al. 2014). In the terrestrial literature, more sophisticated methods to model space use patterns have been developed (Benhamou 2011, Potts and Lewis 2014, Potts et al. 2014). Unlike kernel-based home range analyses, some of these methods can describe the mechanistic behaviours associated with territory formation and predict observed shifts in space use patterns (Moorcroft et al. 1999, 2006). These frameworks are amenable to the incorporation of drift, and doing so could help us understand why territory formation is less common in drifting environments. A larger challenge will be to incorporate drift in the newly developed 3D home ranges (e.g. km^3 rather than km^2), which account for depth in addition to horizontal space use (Kelly et al. 2010, Tracey et al. 2014). While these 3D home ranges are not necessary for polar bears, which spend most of their life at the sea level, using home range estimates that account for vertical movement is crucial for many marine species. As for drift, ignoring depth is likely to underestimate home range size and misrepresent the behaviour of marine species with complex diving patterns. Thus, simultaneously accounting for drift and the third dimension is a crucial future direction for understanding marine home ranges.

For some marine animals, such as benthic and demersal species, ignoring the third spatial dimension may be an acceptable simplification. In such case, the method presented here may be adequate to incorporate drift in home range analysis. However, caution is required with respect to the spatiotemporal scale of the home range relative to currents. Because we map the area encountered using the voluntary movement of the animal, the water/ice masses need to move in a predictable manner according to the prevailing currents. This implies that the scale of the turbulent flow is smaller than the scale of the prevailing drift. To affect the area of habitat encountered, the scale of the prevailing drift needs to be similar to, or larger than, the voluntary movement of the animal studied. In areas with oceanic gyres, where water recirculates, it is important to choose a temporal scale for the home range analysis that is shorter than the time it takes the gyre to complete one cycle. This will prevent recirculating water/ice masses from being included twice in the estimate of habitat encountered. As oceanic gyres require multiple years to complete their cycle (Richardson 1983, Archer and Humayun 2001), the common annual and seasonal home range analysis should remain possible for many species.

Studying the home range of marine animals will require us to differentiate between the trade-offs of using resources that are geographically fixed and those that are drifting. Using our method to compare geographic home ranges to estimates of area of habitat encountered is the first step towards this goal. Our method is directly applicable to other species walking on the sea ice (e.g. arctic fox *Vulpes lagopus*; Pamperin et al. 2008) and useful for other ice-dependent species, such as ringed seals and bearded seals *Erignathus barbatus*. The more fluid and three-dimensional ocean present additional challenges. However, the concepts presented here can serve as a foundation for new approaches to study the space use of marine species.

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Supplementary material (Appendix ECOG-01260 at <www.ecography.org/appendix/ecog-01260>). Appendix 1.