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Assessing spatial discreteness of Hudson Bay polar bear populations using telemetry and genetics

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Abstract. Identifying biologically meaningful populations is essential to the conservation and management of at-risk species. Natural populations can be delineated using a variety of methods including tag recoveries, telemetry, stable isotopes, and population genetics, but understanding the processes that lead to and maintain the demographic and genetic distinctiveness of populations is also important. We combined telemetric and genetic data from three adjacent polar bear (*Ursus maritimus*) populations in Hudson Bay, Canada, to compare two methods of defining structure. We compared the population structure inferred from utilization distributions (UDs) of 62 adult female polar bears tracked by satellite telemetry during the mating season by grouping individuals in two ways: (1) by the management population in which individuals were sampled (capture location), and (2) by population genetic assignment of individuals using marker data (genetic assignment). We found that space-use overlap varied depending on how individuals were grouped. We found 19.1–34.4% UD overlap when capture locations were used to group individuals, but there was no UD overlap for bears across different genetic groupings. Wildlife management objectives should include consideration of genetic diversity and differentiation, and we found that using genetic assignment to augment analyses from telemetric data provided additional insights on population delineation.

Key words: genetics; polar bear; population; single nucleotide polymorphism; telemetry; *Ursus maritimus*; utilization distribution.

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INTRODUCTION

Effectively delineating populations to establish meaningful divisions is a critical but challenging task for wildlife managers. Part of the challenge stems from a rigorous definition of what is meant by the term "population" (Berryman 2002, Camus and Lima 2002), but identifying spatially discrete groups of individuals that have demographic processes largely constrained to those groups may suffice for most management and conservation objectives. Populations and their boundaries have been determined using various methods including mark–recapture (Lentfer 1983, Kohler and Turner 2001), telemetry (Bethke et al. 1996, Iverson et al. 1996, Nagy et al. 2011), stable isotopes (Hobson and Wassenaar 2001, Newman et al. 2010), and genetics (Baker and Palumbi

1997, Paetkau et al. 1999, Barr et al. 2008). Each method has its advantages and shortcomings, varying in temporal and spatial scales, and may emphasize different aspects of population processes. However, combinations of more than one method can often assist interpretation of results (Ayvazian et al. 2004, Prochazka et al. 2013). If conservation goals include maintenance of demographic parameters, spatial distribution, and genetic diversity, then integrated methods may be more informative for delineating populations than any single approach.

Telemetry data provide tracking of individuals over a short period, compared to molecular markers that provide insights into population structure over longer time spans (Haig et al. 1997). Despite the potential gain of integrating telemetric data with genetic marker information, their combination is uncommon, though some studies have investigated space use and genetic relatedness (Støen et al. 2005, Shafer et al. 2014), and migration patterns considering genetic assignments (Östergren et al. 2012). From a population genetics perspective, telemetric data collected during the mating season may be of particular interest as it pertains to the potential for genetic differentiation if individuals have fidelity to different non-overlapping mating areas. Mating can involve variable movement behavior within and between different groups (Bradford and Taylor 1997, Bowne and Bowers 2004, Van Dyck and Baguette 2005), leading to different levels of genetic structure. Integrating telemetric and genetic data may provide an alternative perspective for delineation of biologically meaningful units for wide-ranging species with continuous distributions. For the highly mobile polar bear (*Ursus maritimus*), both telemetric and genetic data are available, but have never been combined. Combining both data sources may be useful for polar bears where harvest management, conservation of genetic resources, and climate change pose challenges for the long-term conservation of the species (Vongraven et al. 2012, Derocher et al. 2013).

Independently, polar bear space use (Bethke et al. 1996, Obbard and Middel 2012, Sahanatien et al. 2015) and genetic structure (Paetkau et al. 1995, 1999, Peacock et al. 2015, Malenfant et al. 2016) have been extensively studied. Polar bears are capable of long-distance movement (Durner and Amstrup 1995, Johnson et al. 2017) but show fidelity to specific areas (Derocher and Stirling 1990, Amstrup et al. 2000, Mauritzen et al. 2001). Polar bears are managed using 19 defined populations across the Arctic that are based on mark–recapture, harvest recoveries, and telemetry data (IUCN/SSC Polar Bear Specialist Group 2010). There are low levels of genetic heterogeneity across the range, and the circumpolar population genetic structure of polar bears inferred using microsatellite markers was largely in agreement with these 19 populations (Paetkau et al. 1999, Peacock et al. 2015, Malenfant et al. 2016). One of four large-scale genetic clusters identified by Paetkau et al. (1999) occurs in Hudson Bay, Canada, and included individuals from the Western Hudson Bay (WH) and Foxe Basin (FB) populations which have a close association with Davis Strait individuals that are found eastward of FB. Although no samples were analyzed from the Southern Hudson Bay population (SH) in the Paetkau et al. (1999) study, it was assumed to be part of the Hudson Bay genetic unit due to its spatial proximity (IUCN/SSC Polar Bear Specialist Group 2010, Peacock et al. 2010). However, how these designated populations in Hudson Bay relate to mating ecology, on-ice distribution, and foraging areas remains poorly understood.

Hudson Bay is ice-free in summer–autumn, but ice-covered in winter–spring (Markham 1984). During the ice-free period, polar bears are forced ashore into three areas that have been defined as populations (WH, SH, FB; IUCN/SSC Polar Bear Specialist Group 2010) based on fidelity to geographically distinct areas (Derocher and Stirling 1990, Stirling et al. 2004, Obbard and Middel 2012, Sahanatien et al. 2015). Considerable overlap of bears from these three populations occurs while they are on the sea ice (Peacock et al. 2010). This may reduce the utility of the defined populations from a genetics perspective if mating is random.

Mating occurs on the sea ice in spring (Ramsay and Stirling 1986, Rosing-Asvid et al. 2002) which may lead to genetic structure if individuals mate non-randomly and does not necessarily involve the same grouping of individuals found during the onshore period. Analysis of polar bears using single nucleotide polymorphisms (SNPs) in Hudson Bay identified four genetic units that differed from the current population designations with a

Western cluster including bears from WH, SH, and southern FB, a Northern cluster with bears from northern FB and Davis Strait near Labrador, a Southeast cluster of SH bears living in James Bay (JB), and a Northeast cluster of bears from Davis Strait near Baffin Island (Viengkone et al. 2016). Three notable differences between current population designations and genetic structure are (1) the identification of a previously unknown genetic cluster in JB, (2) the lack of genetic differentiation between WH and SH (excluding JB), and (3) a more northerly division between Hudson Bay (WH and SH) and FB individuals (hence the inclusion of southern FB bears in the western genetic cluster with WH and SH bears). The differences between current population designations and genetic groupings may be due to the small number of observations of bears in JB and near the WH/FB border making boundaries inaccurate, shifting distributions, or differences in the timescale of analysis. As current populations contain individuals from different genetic stocks, we expect that space use will overlap during the mating season if individuals are grouped by capture location but may not overlap when individuals are grouped by genetic assignment.

Here, we use utilization distributions (UDs) of female polar bears tracked by satellite telemetry in Hudson Bay during the mating season to compare space-use overlap of bears grouped by capture location using existing population boundary structure to bears grouped by genetic cluster. We used home-range overlap to provide a measure of discreteness of populations defined using capture location and genetic assignment. The population definition that displays the lowest interpopulation overlap could be considered preferable because low overlap indicates greater spatial segregation and therefore defines a population with potential discrete demographic processes (e.g., birth rates, age structure) and genetic variation.

METHODS

The Hudson Bay area in Canada contains three polar bear populations (SH, WH, and FB; Fig. 1). Adult female polar bears (≥5 yr old) were caught on land during late summer and autumn in 2004–2011 by remote injection (Stirling et al. 1989) and fitted with Global Positioning System (GPS) satellite-linked collars (Telonics, Mesa, Arizona, USA) that provided a location every four hours. Telemetric data were collected from 1 February to 31 May during 2005–2013, which represents most of the mating season (Lønø 1970, Lentfer et al. 1980, Rosing-Asvid et al. 2002) when gene flow may occur but ends to exclude the shoreward migration period (Cherry et al. 2013). Capture and handling protocols were approved by the University of Alberta Animal Care and Use Committee for Biosciences, the Environment Canada Prairie and Northern Region Animal Care Committee, and the Animal Care Committee of Ontario Ministry of Natural Resources. Each collared bear was grouped into (1) one of three capture location populations (i.e., where they were caught, FB, SH, or WH), and (2) a genetic cluster based on the population genetic analysis in Viengkone et al. (2016) based on both males and females: one of Western, Northern, Southeast, or Northeast (Fig. 1). We do not include Davis Strait bears in this study because tracking data were unavailable.

Only bears with telemetric data and SNP genotype population assignments were used to generate mating season home ranges for each bear. We used the first location acquired each day and included all individuals with ≥10 locations/month and ≥40 locations over the mating season. Mating season home ranges were quantified as UDs, which describe the home-range boundary and intensity of use throughout the home range (Millspaugh et al. 2004). We estimated UDs with fixed-kernel analysis using the KS package (Duong 2007) for the R Statistical Environment (R Core Team 2015) and the plug-in method for choosing smoothing factors (Gitzen et al. 2006). We estimated UDs for each bear individually and for each population of bears defined either by capture location using existing geographic boundaries ($n_{\mathrm{SH}} = 18$; $n_{\mathrm{WH}} = 36$; $n_{\mathrm{FB}} = 8$) or by genetic assignment ($n_{\mathrm{Western}} = 55$; $n_{\mathrm{Northern}} = 5$; $n_{\mathrm{Southeast}} = 2$; see Viengkone et al. 2016 for genetic assignments). Home-range overlap between each pair of bears' UD and each pair of bear populations' UD was estimated using the volume of intersection index (VI), which estimates the volume of overlap between two UDs; VI ranges from 0 (no overlap) to 1 (complete overlap; Fieberg and Kochanny 2005).

We used beta regression, which allows the dependent variable to be continuous and bounded between 0 and 1, to determine whether

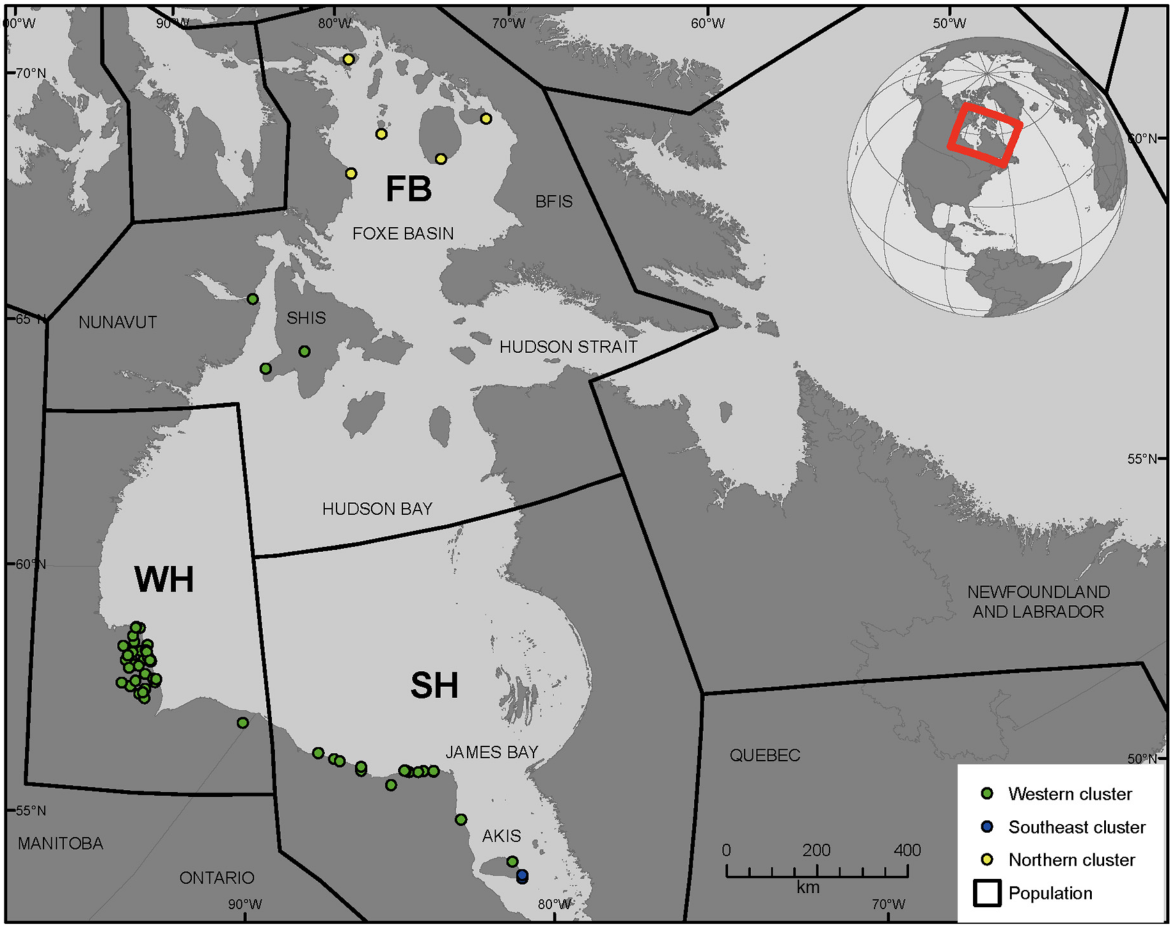

Fig. 1. Capture locations of 62 female polar bears within the Hudson Bay region color-coded to the genetic cluster they strongly assign to. The populations following the IUCN/SSC Polar Bear Specialist Group (2018) are outlined in solid black lines with the names shown in bold: Western Hudson Bay (WH), Southern Hudson Bay (SH), and Foxe Basin (FB). Two islands are identified: Akimiski Island (AKIS) and Southampton Island (SHIS).

interpopulation VI values were significantly lower when individual bears were defined by genetic assignment than by capture location; we also included intrapopulation VI values in our model. Dummy variables were used to define each pairwise comparison with interpopulation overlap defined by genetics cluster as the reference category. We implemented beta regression models using the betareg package in R (Cribari-Neto and Zeileis 2009) using the model:

$$\mathrm{VI} = \alpha + \beta 1 * \mathrm{InterM} + \beta 2 * \mathrm{IntraM} + \beta 3 * \mathrm{IntraG}$$

where VI was the amount of overlap between each pair of bears and each covariate was a dummy variable (InterM = overlap (VI) between individuals from different populations defined geographically, IntraM = VI between individuals within a population defined geographically, and IntraG = VI between individuals within a population defined by genetic cluster). The reference category is VI between individuals from different populations defined by genetic cluster. A significant and positive β would indicate that overlap is significantly higher for the above three dummy variables relative to the reference category (i.e., overlap is lowest between individuals from different populations defined by genetic cluster).

When bears were pooled and only a single UD was created per population, we could not compare interpopulation overlap statistically due to lack of replication; instead, we present these data

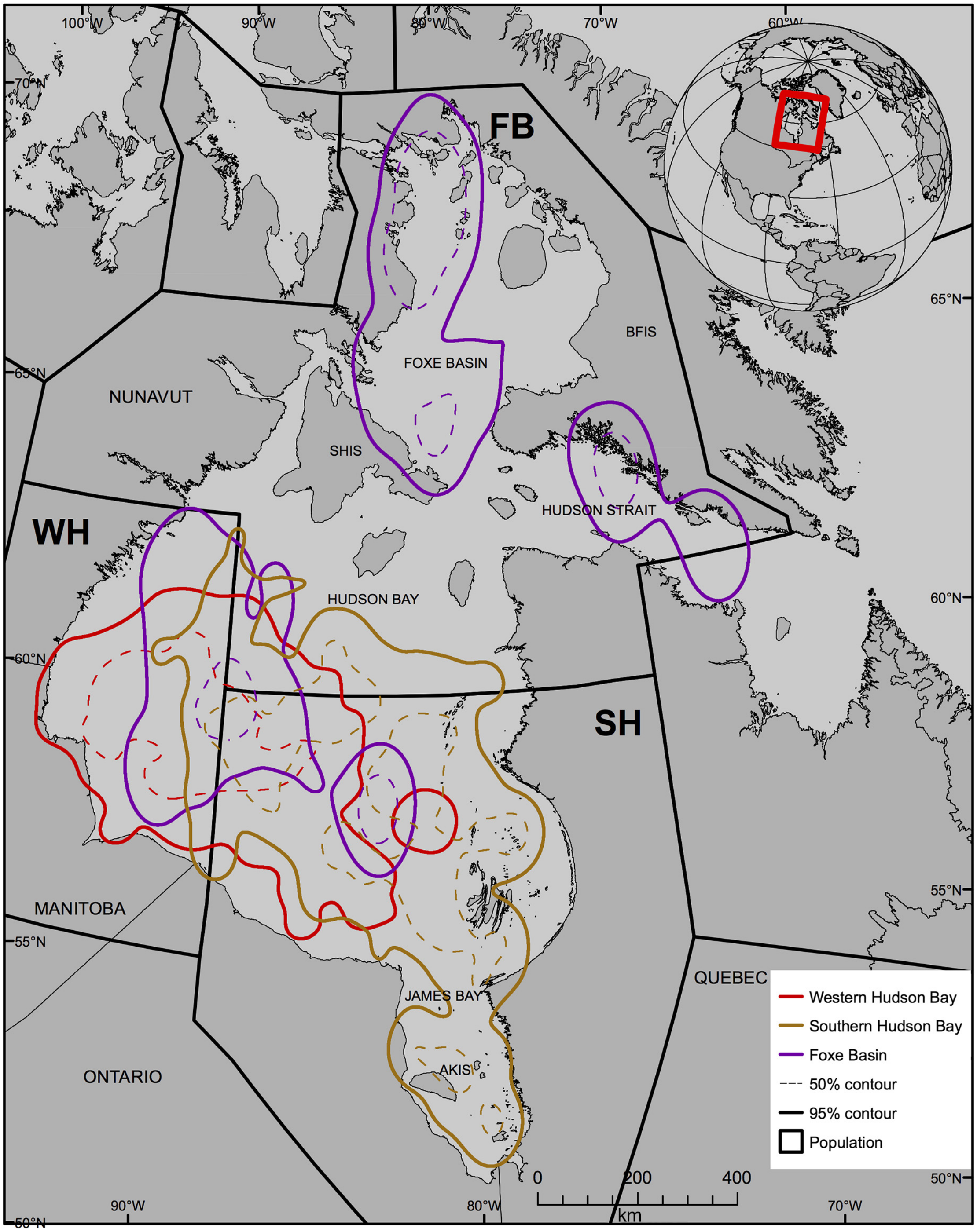

Fig. 2. Utilization distributions of mating season (1 February–31 May) home ranges of 62 female polar bears based on capture locations in Hudson Bay. General space use is represented by 95% contours (outer, solid line), and core areas are represented by 50% contours (inner, dashed line). Hudson Bay populations following the IUCN/SSC Polar Bear Specialist Group (2018) are outlined in solid black lines with the names in bold: Western Hudson Bay (WH), Southern Hudson Bay (SH), and Foxe Basin (FB). Two islands are identified: Akimiski Island (AKIS) and Southampton Island (SHIS).

as a qualitative comparison of interpopulation overlap between the different population definitions.

RESULTS

Telemetric and genetic data were available for 62 female polar bears (Fig. 1). Sample sizes varied for bears in a geographic population and in a genetic group. Of 18 SH females, 16 were genetically assigned to the Western group and 2 to the Southeast. Of 36 WH females, all 36 were genetically assigned to Western group. Of the eight FB females, three were genetically assigned to the Western group and five to the Northern. We had a mean of 102 ± 2 (SE) locations/bear. The 95% UD areas based on grouping by capture location varied in size: $\text{area}_{WH} = 307{,}868\ \text{km}^2$; $\text{area}_{SH} = 453{,}628\ \text{km}^2$; and $\text{area}_{FB} = 419{,}557\ \text{km}^2$ (Fig. 2). By capture location, the UD in northern Foxe Basin consisted of bears sampled only in FB. UDs of bears sampled in WH, SH, and some from FB overlapped extensively in Hudson Bay. The UD in James Bay included only bears with capture locations in SH. Pairwise comparisons of VI between the capture locations ranged from 19.1% to 34.4% (Table 1).

In comparison, 95% UDs for individuals grouped by genetic assignment showed greater variation than using capture location: Western (454,024 km^2), Southeast (39,220 km^2), and Northern (142,428 km^2; Fig. 3). The Western UD overlapped with both the currently accepted WH and SH populations. The Northern UD was concentrated in northern and eastern FB and extended slightly eastward. The Southeast UD was found only within James Bay.

We compared the mean VI values representing interpopulation and intrapopulation home-range overlap when defining polar bear populations in Hudson Bay defined by capture location (interpopulation = 0.043 ± 0.003, N = 1151; intrapopulation = 0.118 ± 0.004, N = 865) and genetic assignment (interpopulation = $<0.001 \pm 2.22 \times 10^{-7}$, N = 1553; intrapopulation = 0.097 ± 0.003, N = 463). Pairwise interpopulation VI values were lower when populations were defined by genetic assignment, than by capture location (Table 1). Both measures of intrapopulation VI were significantly higher than interpopulation VI defined by genetic assignment (Table 2).

When bears were pooled and one UD was created per population, there was no overlap between populations defined by genetic assignment (Fig. 3). However, there was overlap when populations were defined by capture locations (Fig. 2).

DISCUSSION

We detected spatial and genetic structure in Hudson Bay that differs from current population boundaries in Hudson Bay used for management and research. Using capture location to analyze population structure, we found significant overlap on the sea ice, and this suggests that using terrestrial capture locations does not reflect population structure on the sea ice during the mating season. In contrast, we found virtually no overlap in space use during the mating season when bears were grouped by genetic assignment. Using genetic assignment with telemetric data provided novel insight into population structure and identified areas used for mating by the different genetic clusters that could not be identified using genetic analysis alone. This information may aid conservation and management of the species by informing protection of such areas from development or industrial activity.

Table 1. Comparison of volume of intersection values based on capture location (left) and genetic assignment (right) of adult female polar bear telemetry data during the mating season, 2005–2013 (WH, Western Hudson Bay; SH, Southern Hudson Bay; FB, Foxe Basin).

Capture location	WH	SH	FB	Genetic assignment	Western	Southeast	Northern
WH	1.000	0.344	0.251	Western	1.000	<0.001	<0.001
SH	–	1.000	0.191	Southeast	–	1.000	<0.001
FB	–	–	1.000	Northern	–	–	1.000

Note: Volume of intersection index estimates the volume of overlap between two utilization distributions and ranges from 0 (no overlap) to 1 (complete overlap).

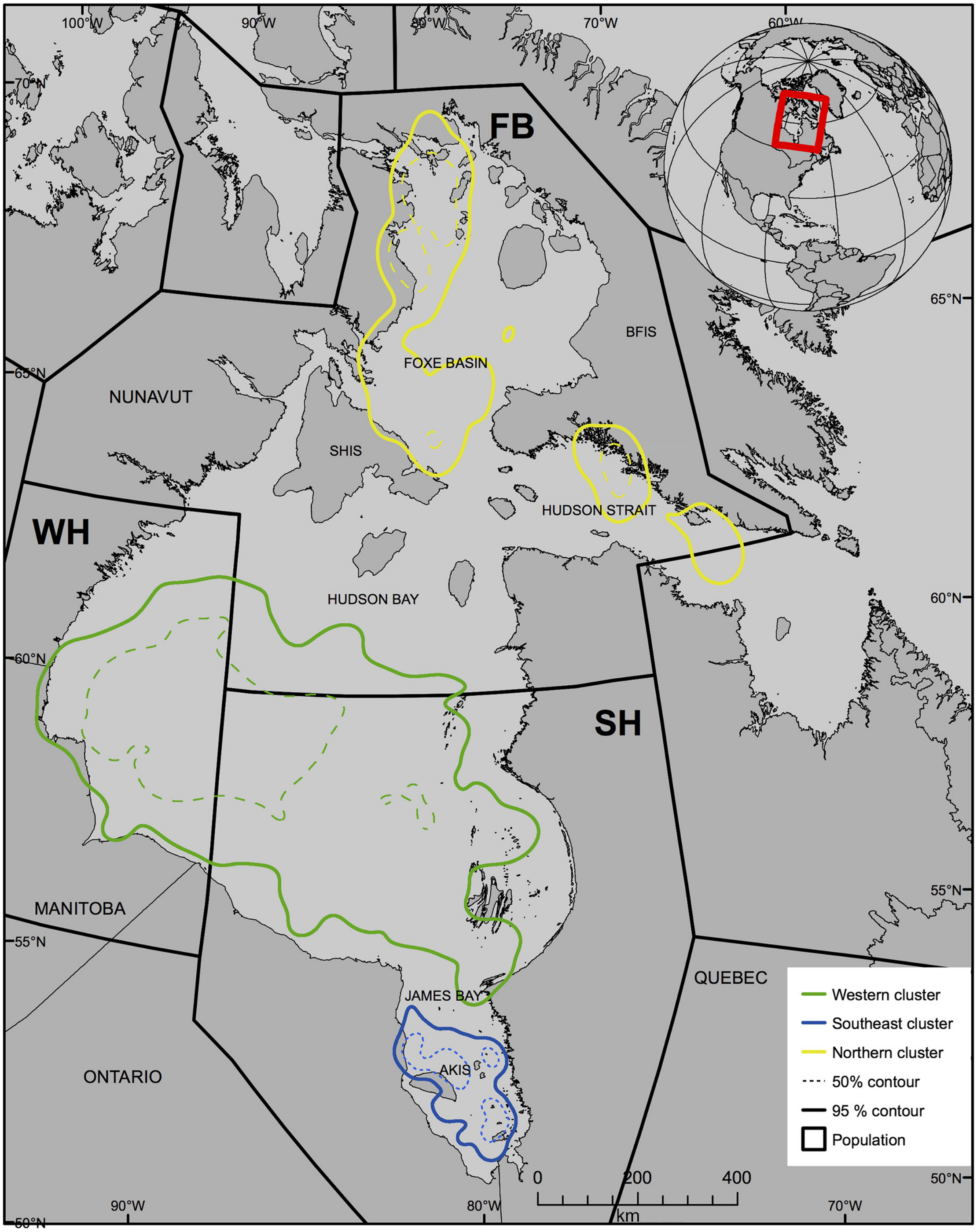

Fig. 3. Utilization distributions of mating season (1 February–31 May) home ranges of 62 female polar bears based on genetic assignment in Hudson Bay. General space use is represented by 95% contours (outer, solid line), and core areas are represented by 50% contours (inner, dashed line). Hudson Bay populations following the IUCN/SSC Polar Bear Specialist Group (2018) are outlined in solid black lines with the names in bold: Western Hudson Bay (WH), Southern Hudson Bay (SH), and Foxe Basin. Two islands are identified: Akimiski Island (AKIS) and Southampton Island (SHIS).

Table 2. Parameter estimates, standard deviations, and *P*-values associated with coefficients within a beta regression model estimating pairwise volume of intersection (VI) of home ranges within (intra) and between (inter) polar bear populations defined by capture location and genetic assignment.

Coefficient	Estimate	Standard deviation	*P*-values
Intercept	−3.53	0.06	<0.01
Interpopulation, capture location	0.46	0.06	<0.01
Intrapopulation, capture location	1.18	0.06	<0.01
Intrapopulation, genetic assignment	1.07	0.05	<0.01

Note: Dummy variables were used with interpopulation VI defined by genetic assignment as the reference categories.

To date, polar bear populations defined for management purposes have focused on discontinuities that reflect seasonal site fidelity of individuals inferred from a combination of mark–recapture studies, return of harvest tags, and telemetric data (Bethke et al. 1996, Taylor et al. 2001, Mauritzen et al. 2002). The resultant designations have been used as biologically meaningful populations; however, we found differences in spatial structure determined by capture location and by genetic assignment. Our delineated populations differ markedly from those currently used (IUCN/SSC Polar Bear Specialist Group 2018). Population structure in polar bears can be influenced by site fidelity, habitat quality, prey availability, physical barriers (e.g., landmasses, polynyas), and learned movement patterns (Ramsay and Stirling 1990, Paetkau et al. 1999, Mauritzen et al. 2001). The relationship between genetic assignment and mating season space-use patterns that we found suggests that the genetic structure detected by Viengkone et al. (2016) is due to different groups mating in discrete non-overlapping regions of Hudson Bay during the on-ice mating season. When the capture locations of bears were used and spatial distribution assessed using the existing polar bear populations in Hudson Bay (i.e., IUCN/SSC Polar Bear Specialist Group 2018), there is little spatial separation during the mating season. In contrast, we provide evidence that individuals who are assigned to different genetic clusters have negligible amounts of home-range overlap during the mating season. While the existing classification system may function for harvest management and estimating population sizes, it ignores the importance of genetic diversity and differentiation and the possibility of different demographic contributions of mating groups.

In the Southeast genetic assignment, polar bears have small home ranges as noted in other populations (Ferguson et al. 1999, Mauritzen et al. 2001). These authors postulated that a small home range may be a result of a high abundance of resources or low food availability with high predictability. In either case, the small mating season home ranges coupled with geographic isolation in James Bay may have contributed to genetic distinctiveness of this group of bears. Our results suggest that neither sex enters or exits James Bay during the mating season, which was supported by the movement patterns of adult females in James Bay (Obbard and Middel 2012) and the genetic uniqueness demonstrated by Viengkone et al. (2016) and Crompton et al. (2008, 2014). Thus, our results support the management of bears in James Bay as separate from the rest of SH.

Division of the north and south of FB was only recently identified genetically (Viengkone et al. 2016) and was supported by movement analysis (Sahanatien et al. 2015). Bears from northern FB differ in space use from bears in southern FB during the mating season. FB bears on Southampton Island were assigned to the Western cluster and shared similar space-use patterns with other Western cluster bears from WH and SH in the central-western areas of Hudson Bay during the mating season. The Northern cluster used the ice north of Southampton Island and east into Hudson Strait. In addition to our findings, a separate movement group was noted in Hudson Strait (Sahanatien et al. 2015). We were unable to detect this group due to our lack of sampling in southeastern FB. The genetic and spatial differentiation within FB suggests the revision of management where the bears north of Southampton Island are separate from those to the south.

Although our sampling was unbalanced, we used all our data to maximize resolution. The addition of more telemetry data from adjacent areas could increase the amount of overlap between populations categorized by capture location. Tracking data on males would also add additional insights, but few studies have tracked male polar bears. In general, male space use appears similar to females during the mating season (Ramsay and Stirling 1986, Amstrup et al. 2001, Laidre et al. 2012, Pilfold et al. 2014). Because the polar bear mating system is described as a female defense polygyny (Derocher et al. 2010), males should be found near females, so adding males to the analysis may not alter our interpretation. Our analyses also included uncertainties associated with the timing of the mating season, which is poorly understood in Hudson Bay. We believe, however, that our approach has merit given the similarity in the mating season across the range of polar bears. In addition, not all females we sampled would have mated in the years we tracked them. However, site fidelity of female polar bears across years (Mauritzen et al. 2001) would likely minimize any influence. Lastly, our small sample size in James Bay limits insights on our understanding of the Southeast cluster.

Population delineation for polar bears has largely focused on estimating abundance for use in harvest management and identifying demographically independent units (Bethke et al. 1996). We provide an example for an alternative approach to delineating populations using genetic data incorporated with mating season telemetry information. Deployment of radio telemetry devices requires the handling of wildlife and thus allows for concurrent collection of genetic samples. Therefore, genetic data should be available for telemetric studies and combining both sources of information may aid effective conservation. Our approach provides an example of the differences in perspectives that can arise depending on how telemetry data are examined.

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