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Revisiting Western Hudson Bay: Using aerial surveys to update polar bear abundance in a sentinel population

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ABSTRACT

Capture-based studies of the Western Hudson Bay (WH) polar bear population in Canada have reported declines in abundance, survival, and body condition, but these findings are inconsistent with the perceptions of local people. To address this uncertainty about current status, we conducted a comprehensive aerial survey of this population during August, 2011, when the region was ice-free and bears were on shore. We flew a combination of overland transects oriented perpendicular to the coastline, coastal transects parallel to shore, and transects across small islands. We used distance sampling and sight–resight protocols to estimate abundance. Bears were concentrated along the coast in central and southern Manitoba and Ontario portions of the population, although sightings >10 km inland were not uncommon in central Manitoba. We analyzed 2 combinations of data and derived an abundance estimate of 1030 bears (95% CI: ~754–1406). This figure is similar to a 2004 mark–recapture estimate but higher than projections indicating declining abundance since then. Our results suggest that mark–recapture estimates may have been negatively biased due to limited spatial sampling. We observed large numbers of bears summering in southeastern WH, an area not regularly sampled by mark–recapture. Consequently, previous mark–recapture estimates are not directly comparable to our aerial survey of the entire population. Whereas our results do not necessarily contradict the reported declines in this population, we believe that improvements are needed in monitoring, and methodological limitations and inconsistencies must be resolved to accurately assess status and the impacts of climate change.

1. Introduction

Polar bears (*Ursus maritimus*) span the circumpolar Arctic, with an estimated 20,000–25,000 bears inhabiting 19 populations across 5 range states (Obbard et al., 2010). Although there are significant gaps in basic demographic information from portions of their range (Obbard et al., 2010), the Western Hudson Bay population (WH) in Canada ranks as one of the most intensively studied large mammal populations worldwide, with a research program dating back more than 4 decades (Jonkel et al., 1972; Stirling et al., 1977; Derocher and Stirling, 1995a; Regehr et al., 2007).

Scientific evidence from the long-term capture and tagging program in WH suggests that the abundance of polar bears increased during the 1970s, remained stable for a period in the 1980s, and decreased by about 22% between 1984 and 2004 (Derocher and Stirling, 1995a; Lunn et al., 1997; Regehr et al., 2007). The recent decline in abundance has been attributed to earlier sea ice breakup in Hudson Bay (Regehr et al., 2007). This trend in sea ice breakup and the resultant extension of the ice-free season have forced bears to spend longer periods on land without access to seals, their primary food source, leading to declines in survival, reproductive output, and body condition (Stirling et al., 1999; Regehr et al., 2007). Concurrently, an increase in incidences of human–polar bear conflicts in WH has been interpreted as a sign that the population is undergoing significant change and has created public safety concerns (Stirling and Parkinson, 2006; Towns et al., 2009; Peacock et al., 2010; Government of Nunavut, unpublished data). Bears in poor condition may exhibit an increased tendency to seek alternative food sources such as those around settlements and camps (Stirling and Parkinson, 2006). Population viability analysis based on 2004 demographic data (Regehr et al., 2007) predicts that WH abundance has continued to decline over the past decade (Obbard et al., 2010). Additionally, climate models project that sea ice habitats in Hudson Bay will deteriorate, resulting in further impacts on polar bears (Amstrup et al., 2008).

There is general consensus between science and the traditional ecological knowledge (TEK) and observations of Inuit living along

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Hudson Bay that polar bear abundance in WH increased during the 1970s (Tyrrell, 2006). There is also agreement that polar bear distribution has changed, bear sightings have increased around communities, sea ice breakup is occurring earlier, and climate change is negatively influencing seal populations (Nunavut Wildlife Management Board [NWMB], 2007). However, in contrast to scientific evidence, Inuit perceptions do not support the notion that abundance in WH has declined since the 1980s (Tyrrell, 2006). Reports of more bears summering on land in northwestern Hudson Bay and increased incidences of problem bears around camps and communities instead have been attributed to several factors including increased abundance and an overpopulation of bears (Stirling and Parkinson, 2006; NWMB, 2007). This disparity between scientific findings and TEK has generated significant debate over the management and conservation of WH and led to calls for new research to inform status assessment and resolve apparent differences between knowledge sources.

Physical capture forms the basis for our current understanding of polar bear ecology and facilitates a variety of research initiatives (e.g., habitat use and movements via satellite telemetry). However, among Inuit in the region, requests for new information also have included a desire to see alternative research methods employed. These concerns fall into 3 categories. First, although several studies have failed to detect impacts on body condition, survival, and reproduction resulting from polar bear capture and handling (Ramsay and Stirling, 1986; Amstrup, 1993; Derocher and Stirling, 1995b; Messier, 2000), concerns remain about the invasiveness of

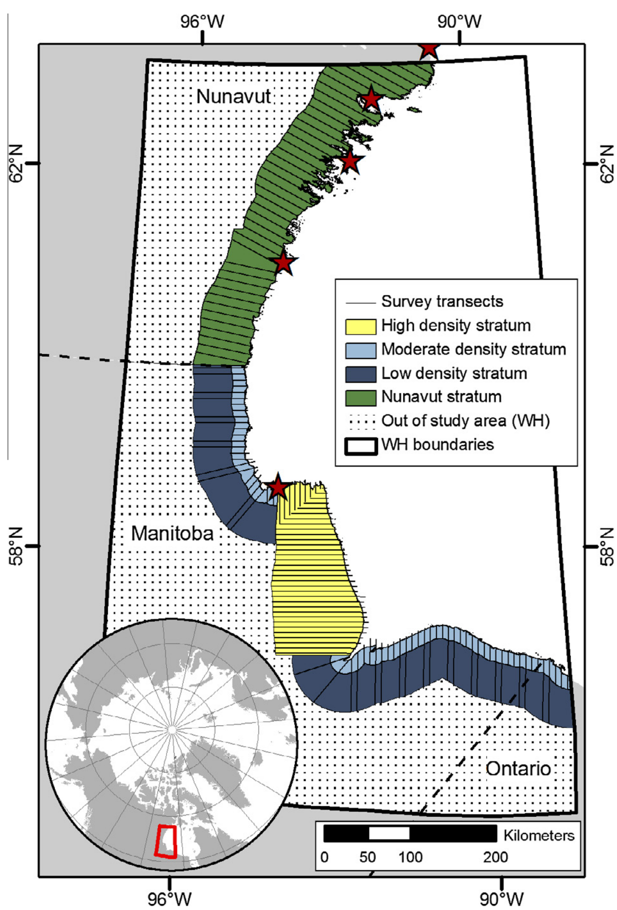

Fig. 1. Strata and planned survey transects for the Western Hudson Bay polar bear aerial survey, August, 2011. The Western Hudson Bay population is highlighted in red in the inset. Hashed lines denote territorial and provincial borders, and red stars mark communities.

this method (e.g., Dyck et al., 2007 but see Stirling et al., 2008). Second, the capture and marking of polar bears is viewed by many Inuit to be inconsistent with their cultural beliefs regarding human interactions with animals. Third, most polar bear research in WH has focused on the capture of bears in Manitoba, within a core study area that comprises the central and most densely occupied portion of the population's summer range (Fig. 1). Multiple capture-based studies suggest that focusing research in this region has not significantly biased mark–recapture (MR) estimates of abundance and survival (e.g., Lunn et al., 1997; Regehr et al., 2007). Nevertheless, Inuit contend that a significant and increasing number of bears are spending the ice-free period outside the core study site; if true, failure to extend sampling across the entire WH would have negatively biased abundance and survival estimates (NWMB, 2007).

To better inform status assessment, we conducted a comprehensive aerial survey of WH during the 2011, late summer ice-free period. Whereas aerial surveys are well-established and widely used to estimate abundance of other species, their application to polar bears has been limited. Recent studies in the Barents Sea (Aars et al., 2009) and Foxe Basin (Stapleton et al., 2012) suggest that aerial surveys may be used to successfully estimate polar bear abundance in certain conditions. Because WH has been the site of an intensive capture program, it provides the opportunity to advance aerial survey development. Specifically, although capture research has focused in a core study area, MR estimates are considered to represent the entire WH population (e.g., Obbard et al., 2010). Direct comparison of aerial survey and capture-based estimates enables an assessment of the methods' potential biases and precision, promotes the acceptance of new techniques in the scientific community, and may suggest possible modifications in monitoring methods.

2. Methods

2.1. Study area

WH, located at the southern extent of the global polar bear distribution, stretches across roughly 435,000 km^2 of Hudson Bay and the adjacent coastal regions including portions of the Nunavut Territory and the provinces of Manitoba and Ontario (Fig. 1). The region is seasonally free of sea ice, the primary habitat of polar bears, from about July to November.

WH shares borders with the Southern Hudson Bay and Foxe Basin populations. Boundary delineation was based on data derived from a variety of sources, including capture and recovery (Stirling et al., 1977; Derocher and Stirling, 1990; Kolenosky et al., 1992; Taylor and Lee, 1995; Derocher et al., 1997; Lunn et al., 1997), aerial surveys (Stirling et al., 2004), satellite telemetry (Stirling et al., 1999; Peacock et al., 2010), and genetic analysis (Paetkau et al., 1995, 1999; Crompton et al., 2008). Although the boundaries are semi-discrete and interchange occurs among neighboring populations (Stirling et al., 1999; Crompton et al., 2008), their separation is most complete during the late summer and early fall ice-free period (Peacock et al., 2010).

2.2. Survey design and field methods

We conducted an aerial survey during August, 2011, early in Hudson Bay's ice-free season. This period was selected for a number of reasons. First, bears are largely confined to land at this time, minimizing the survey area. Second, overlap with neighboring populations is at a minimum, since polar bears exhibit a high degree of site fidelity when ashore (Derocher and Stirling, 1990; Lunn et al., 1997; Stirling et al., 2004; Parks et al., 2006). Third, the absence of ice and snow in late summer makes polar bears readily observable against a dark landscape. Finally, during August, few bears were likely to have started maternity denning (Clark et al., 1997; Clark and Stirling, 1998; Lunn et al., 2004; Richardson et al., 2005) or making the seasonal, directional movements that typically occur prior to the formation of new sea ice (e.g., Stirling et al., 1977, 2004; Derocher and Stirling, 1990).

We implemented a systematic, stratified study design. We considered multiple sources of information to define the inland extent of the study area and delineate strata, including: (1) published information on the distribution of bears (e.g., Derocher and Stirling, 1990; Lunn et al., 1997; Stirling et al., 2004; Richardson et al., 2005; Towns et al., 2010); (2) pilot aerial survey data collected during 2010 in northern WH, outside the historical core study area (Stapleton et al., unpublished data); (3) local knowledge about bear distribution in northern WH provided by Inuit hunters from Nunavut; (4) capture records in Manitoba from 2003 to 2010 ($n = \sim 700$ records of independent bears; Environment Canada, unpublished data); (5) coastal and denning aerial surveys of portions of central and southern WH (Stirling et al., 2004; Manitoba Conservation, unpublished data); and (6) recent satellite telemetry data on the movements of collared polar bears ($n = 12$ bears in summer, 2010; A. Derocher, University of Alberta, and Environment Canada, unpublished data).

We defined 4 strata based on expected polar bear densities: (1) a high density zone corresponding to the historical core study area, including Wapusk National Park and extending up to 100 km inland; (2) a moderate density stratum, extending from the shoreline to 15 km inland elsewhere in Manitoba as well as Ontario; (3) a low density zone, from 15 km to 60 km inland in Manitoba and Ontario; and (4) a low density Nunavut stratum, extending from the coastline to 60 km inland from the Nunavut–Manitoba border to the community of Arviat, and from the shoreline to 50 km inland from Arviat to the northern boundary of WH (Fig. 1). The Nunavut stratum also included 2 large islands.

We used a combination of overland transects, coastal contour transects, and small island sampling to survey WH. Polar bears tend to congregate along or near the shoreline during the ice-free season (Derocher and Stirling, 1990; Towns et al., 2010), so overland transects were oriented roughly perpendicular to the coast (i.e., against the coastal density gradient; hereafter perpendicular transects) to improve precision and minimize potential biases using distance sampling (Fig. 1; Buckland et al., 2001). Transects also were extended over any exposed tidal flats. Because it was not possible to accurately delineate exposed flats in a GIS, polar bears sighted on tidal flats were considered to have occurred on the closest land for analysis. Sampling of tidal flats with perpendicular transects occurred at the same intensity as the nearshore inland strata, so any effect on the abundance estimate was negligible.

Perpendicular transects spanned from the shoreline up to 50–100 km inland. After reaching the most inland point, we flew roughly parallel to the shoreline to join the adjacent perpendicular transect and returned to the coast. Data collected during this cross-leg were generally not included in analyses. However, for 3 pairs of transects, we were unable to reach the far inland extent of the stratum due to logistical constraints. To incorporate sampling in the far inland portions of the strata in these instances, we included data collected along this cross leg.

Survey effort was allocated to maximize encounters while ensuring adequate coverage of all strata. Because polar bears are concentrated along the coast, we focused sampling in the nearshore inland zone. We also heavily sampled the high density stratum, which is a well-documented denning site (e.g., Richardson et al., 2005). Perpendicular transects were systematically spaced at 6, 7, and 10-km intervals in the high density, moderate density, and Nunavut low density strata, respectively (Fig. 1). Every other pair of transects in the moderate density zone in Manitoba and Ontario was extended through the low density (far inland) stratum, such that transect spacing there averaged 14 km.

We also conducted separate surveys following the contour of the entire WH coastline. These coastal contour transects were flown at or slightly below the high water line with one side of the aircraft dedicated to monitoring tidal flats and nearshore waters as the other side surveyed the strip of land along the shoreline. We flew coastal contours as close to high tide as possible to minimize tidal flat exposure. Because perpendicular transects were extended to the shoreline and over tidal flats, some bears along the shore could be sighted from both perpendicular and coastal transects. This design enabled us to estimate the abundance of bears in the coastal region with either perpendicular transects or coastal contour transects. Independent coastal and perpendicular transect data were treated separately to ensure that bears were not double-counted in abundance estimates (see Analyses). As with perpendicular transects, bears sighted on tidal flats or in nearshore waters were considered to be on land in order to calculate density and extrapolate to unsurveyed areas. We additionally sampled as many small islands as possible.

We surveyed the Nunavut and Manitoba–Ontario portions of the aerial survey from fixed wing (de Havilland DHC-2 MKIII Turbo Beaver) and helicopter (Bell 206L) platforms, respectively. Separate platforms were used to complete the survey within a narrow window of time and to enhance opportunities for participation by local people. The fixed wing survey crew consisted of 4 dedicated observers, with front and rear observer teams each comprised of 2 spotters, as well as a data recorder. With the helicopter, the pilot and observer in the co-pilot seat comprised the first team, and 2 individuals seated in the rear comprised the second team.

For each aircraft, we employed sampling protocols that facilitated the collection of data for both distance sampling (Buckland et al., 2001) and sight–resight (i.e., double observer; Pollock and Kendall, 1987) analyses. Front and rear seat observers could not see each other, and their sightings were not announced until both teams were afforded a full opportunity to independently spot a bear. Transects were flown at an above-ground level altitude of about 120 m and groundspeed of roughly 160 km/h with both platforms.

We recorded flight paths and bear locations at the time of first observation via GPS and measured perpendicular distances from sighted bears to the flight path in a GIS (adapted from Marques et al. (2006)). We recorded group size and estimated sex and age class based on morphological characteristics. We defined a group as multiple individuals whose detections were non-independent (e.g., a family group including an adult female and her cubs or a fraternity of 2 or more adult males). For each sighting, we also recorded factors that may have influenced detection probability, including weather conditions, activity when first observed, and habitat characteristics (e.g., habitat structure within 30 m of an individual bear that may impede detection; qualitative 1–3 scale).

During the late summer and early fall, polar bears in WH, particularly pregnant females, may retreat to earthen dens (Jonkel et al., 1972; Lunn et al., 2004). Denning bears that are completely unavailable for sighting would be excluded from an aerial survey abundance estimate. We flew close to dens with recent digging or other signs of activity to determine if a bear was present.

2.3. Analyses

2.3.1. Perpendicular transects

We used distance sampling (Buckland et al., 2001) to estimate abundance with data collected from perpendicular transects. We created 2 perpendicular transect datasets that (1) included sampling in the coastal zone and (2) excluded data from the coastal zone (bears instead were estimated with coastal contour transects). Histograms of sighting distances from the flight path suggested that detection declined predictably with increasing distance from the aircraft, indicating that distance sampling was an appropriate analytical method (Fig. 2).

A key assumption of distance sampling is that sampling is random with respect to the distribution of bears (Buckland et al., 2001). Since polar bears concentrate along the shore during the ice-free season, we only used distance sampling to analyze data from perpendicular transects, which cut across this density gradient. Sighting distances from coastal contour transects may partially reflect the bears' density gradient, not just their sightability, and thus were inappropriate for distance sampling.

Detection of all objects on the transect line is another fundamental assumption of distance sampling (Buckland et al., 2001); violation of this assumption yields a negatively biased abundance estimate. Whereas conventional distance sampling and multiple covariate distance sampling (Marques and Buckland, 2003) require perfect detection at distance 0 (i.e., from the flight path) to generate reliable abundance estimates, mark–recapture distance sampling (MRDS; Laake and Borchers, 2004) can correct for imperfect detection on the line using sight–resight data. In the helicopter, front observers could see the flight path, but rear observers had a 75-m blind spot on either side of the aircraft. Therefore, we initially examined a left-truncated dataset in which observations within 75 m of the helicopter were censored and 75 m was subtracted from all other sighting distances (Borchers et al., 2006). This procedure established the transect line such that all bears were available to both teams of observers. Both teams of observers in the fixed wing had a blind spot of nearly 170 m on either side of the aircraft, so 170 m was subtracted from all observations to establish the transect line. Preliminary analyses of left-truncated double-observer data indicated that the probability of a bear near the transect line being detected by at least 1 observer was >97%. We thus considered the assumption of perfect detection at distance 0 to be approximately valid and proceeded with conventional and multiple covariate distance sampling analyses. By using the untruncated helicopter data, we were able to incorporate all sightings from perpendicular transects (i.e., including those within the rear observer blind spot), thereby increasing the number of observations and improving estimation of the detection function.

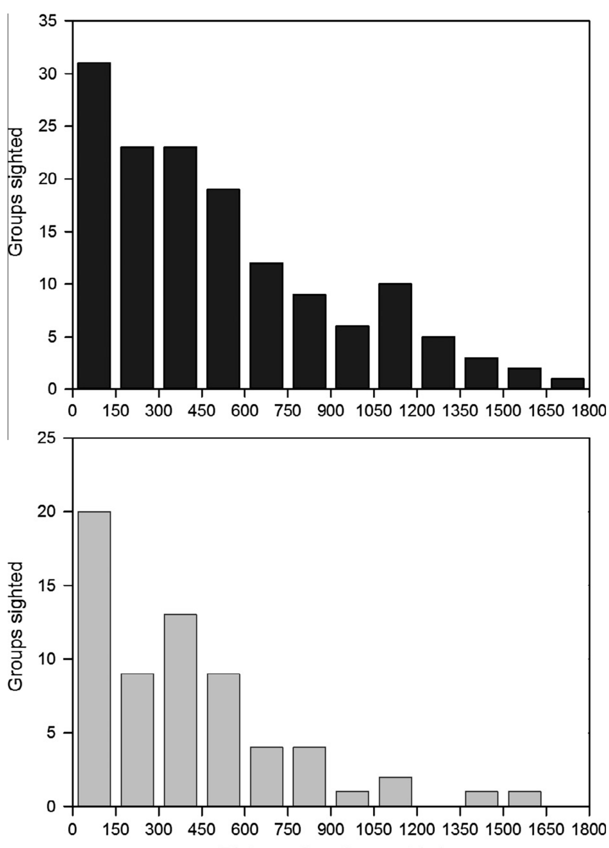

Fig. 2. Distribution of polar bear sighting distances from the original transect line on perpendicular transects, Western Hudson Bay, August, 2011. All strata are pooled. The top histogram includes all sightings, including perpendicular transects extending through the coastal zone. The bottom only includes sightings inland of the coastal zone.

We initially fit detection functions using only data collected from the helicopter. We had insufficient data from the fixed wing to model a separate detection function, so we pooled sighting data from the helicopter with left-truncated data from the fixed wing (because none of the observers could sight bears within 170 m of the flight path). For the most highly supported models, this pooling had a negligible impact on average detection probability and abundance estimates for the strata surveyed only from a helicopter. Hence, we proceeded with analyses incorporating untruncated data collected from the helicopter and the left-truncated data from the fixed wing. Additionally, we condensed the Nunavut stratum and the low density, far inland zone in Manitoba and Ontario into a single stratum due to limited encounters in these areas. Although sampling intensity was greater in Nunavut, estimated densities were very low in these strata and individual encounter rates were similar.

We fit conventional distance sampling models in program Distance (Version 6.0, Release 2; Thomas et al., 2010) to evaluate detection functions and to assess whether group size influenced detection. Following this preliminary review, we fit all distance sampling models in the MRDS engine of Distance. Both datasets were modeled as single observer studies. Data were right-truncated at roughly 5% to smooth the tail of the detection function and improve model fit and parsimony (Buckland et al., 2001).

We fit distance sampling models with hazard and half-normal key functions, and we considered visibility (weather) and habitat structure within 30 m of a sighting as covariates in these models. We evaluated all combinations of key functions and covariates. Covariates were scored in the field on a 3-point scale, but we condensed these into binary categories because of underrepresentation of some values. We specified a global detection function and used stratum-specific encounter rates and group sizes to estimate density and abundance by stratum. Stratum abundance estimates were subsequently summed to obtain an overall abundance estimate.

We employed Akaike's Information Criteria for model selection (Burnham and Anderson, 2002) and examined q–q plots and chi-square, Kolmogorov–Smirnov, and Cramér–von Mises tests to evaluate goodness of fit. Individual transects, within stratum, were considered sampling units for variance estimation. We used the Innes et al. (2002) method to estimate variance, since this technique does not require independence among variance components (i.e., stratum-specific abundance estimates were not fully independent because we estimated a global detection function). We obtained model-averaged estimates for models within 2 ΔAIC for each dataset combination (Burnham and Anderson, 2002). Model-averaging enabled us to account for variability in the estimation of the detection functions and associated densities.

2.3.2. Coastal transects and small islands

We used mark–recapture models to obtain a separate estimate of coastal zone abundance from coastal contour transects with sight–resight data. We employed the Huggins model (Huggins, 1989, 1991) to facilitate the inclusion of covariates to model variability in detection probabilities.

Front and rear observer teams comprised our first and second sampling periods, respectively, and we considered discrete groups of polar bears (as defined above) as the sampling unit. We sampled the coastal zone 500 m inland of the high-water line (since coastal contour transects were often flown below this line to improve coverage of the tidal flats) and censored sightings farther inland. We allowed detection probabilities to remain constant or vary between observers and used forward stepwise selection to evaluate covariates [habitat structure (binary); group size (1, 2, 3, ⩾4); activity (binary)] potentially impacting detection. There was insufficient variability in other covariates to warrant their inclusion in modeling. Models were fit in Program MARK (White and Burnham, 1999) and AIC adjusted for small sample sizes (AIC_c) was employed for model selection. We used detection probabilities from the most supported model and a generalized Horvitz–Thompson estimator to estimate the number of groups present in the sampled areas.

For small islands, the front team of observers spotted all groups that were sighted within the surveyed strip half-width of 750 m. Therefore, it was unnecessary to estimate individual detection probabilities via the Huggins model. For both the coastal contour transects and the small island sampling, we extrapolated group density estimates across the coastal zone and small islands and multiplied estimates by mean group sizes. We calculated group sampling variance following Buckland et al. (2001) and extrapolated and multiplied variances via the delta method (Powell, 2007).

2.3.3. Total abundance

Sampling and analytical protocols enabled us to generate 2 abundance estimates. One estimate was based on the complete set of perpendicular transects plus the small islands. The second was derived by summing estimates from perpendicular transects excluding coastal zone data, coastal contour transects, and small island sampling. We added point estimates from these components and summed their variances to obtain 2 population-wide abundance estimates. We averaged them with equal weighting to obtain a final abundance estimate for WH, and estimated unconditional variance in a model averaging framework.

3. Results

3.1. Sightings

During the 14–29 August, 2011, survey, we recorded 711 total polar bears, including 41 and 670 observations in the Nunavut and Manitoba–Ontario sections of WH, respectively (Fig. 3). Sampling in Manitoba and Ontario, where >90% of sightings occurred, was completed within an 11-day period. Because the coastal contour and perpendicular transects both covered the coastal zone, some bears were undoubtedly seen twice, but we were unable to calculate the number of unique bears that were sighted. However, sampling itineraries in Nunavut enabled us to estimate that no more than 31 unique bears were sighted there. Several aggregations of 4 or more bears, including 5 groups with 8–10 bears and a group with 21 individuals, were documented in southeastern WH (i.e., Area 2 in Fig. 3) and near Cape Churchill (in Area 1). We calculated litter sizes and cub observations from all observations in Manitoba and Ontario and only unique bears in Nunavut; 50 cubs-of-the-year (coy) and 22 yearlings were observed. Mean litter sizes were 1.43 (SD: 0.50; $n = 35$) and 1.22 (SD: 0.43; $n = 18$) for coy and yearlings, respectively.

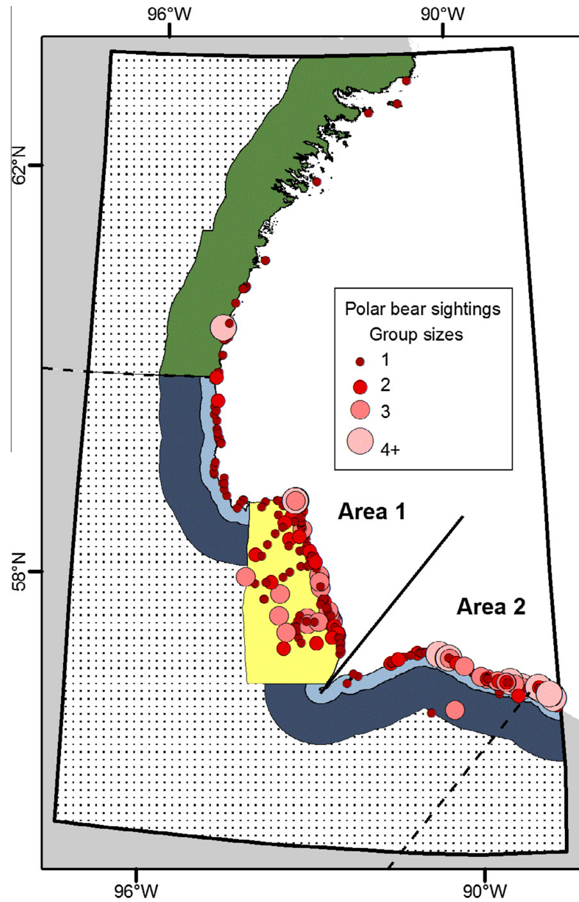

Fig. 3. Polar bear sightings recorded during the Western Hudson Bay aerial survey, August, 2011.

3.2. Distribution

Polar bear sightings were not uniformly distributed across WH (Fig. 3). The greatest densities of bears occurred in the high density stratum (Area 1) and along the coast of southeastern WH. In general, observations were highly concentrated along or near the coast throughout the population (Fig. 3). However, bears >10 km from the coastline were often recorded in the high density stratum ($n = 49$; 43% of bears sighted from perpendicular transects in the stratum) and less frequently observed in the southeastern portion of WH ($n = 6$; 8% of bears sighted from perpendicular transects in that region).

3.3. Abundance estimation

3.3.1. Perpendicular transects

We flew >7800 km along perpendicular transects, including >2750 km in the high-density stratum, nearly 1100 km in the moderate density Manitoba–Ontario zone, and about 4000 km in the Nunavut and low density (far inland) Manitoba–Ontario strata. After right truncation at about 5%, we included 139 and 62 polar bear groups in distance sampling analysis for the datasets that included and excluded the coastal zone, respectively.

Observed group sizes along perpendicular transects ranged from 1 to 8 ($\bar{x}$: 1.44; SD: 0.94). A group of 6 bears, including 2 family groups and 2 independent bears, was sighted in Nunavut, congregating around harvested whale carcasses. Because the low density Manitoba–Ontario and the Nunavut strata were pooled and we viewed this aggregation as an anomaly that would not reflect group sizes in interior Manitoba–Ontario, we instead substituted the stratum mean group size for this observation. Preliminary analyses did not indicate an effect of group size on detection probabilities, a finding that was consistent with our field observations. Goodness of fit metrics suggested adequate model fit for all highly supported models ($P > 0.05$ for all tests).

Model selection was similar among analyses and supported the inclusion of covariates to explain variability in detection probabilities (Table 1). Model-averaging yielded abundance estimates of $\widehat{N}$: 929 (SE: 186) and $\widehat{N}$: 561 (SE: 124) that included the coastal zone and excluded this region, respectively.

3.3.2. Coastal transects and small islands

Nunavut's coastline is highly irregular in portions of northern WH, making it challenging to conduct and analyze a comprehensive coastal contour transect. This reality, coupled with the low number of groups observed in the pooled low density stratum ($n = 6$), compelled us to rely exclusively on perpendicular transects to estimate coastal zone abundance in Nunavut. In Manitoba and Ontario, however, we sampled >95% of the coastline and included 190 polar bear groups in sight–resight analysis. Our highest ranked model incorporated separate detection probabilities for the front and rear observers and covariates for habitat structure and group size. Detection and abundance estimates were very consistent among the best supported models. Thus, we used detection probabilities from the most highly supported model ($\bar{p}_{\text{front}}$: 0.97, SE: 0.014; $\bar{p}_{\text{rear}}$: 0.86, SE: 0.027) to generate a group abundance estimate ($\widehat{N}$: 192 groups; SE: 1.7) for the sampled areas and inflated across the entire coastal zone. Multiplying by mean group size ($\bar{x}$: 1.45; SD: 1.6) yielded a coastal zone abundance estimate of 291 (SE: 23.8) polar bears in Manitoba and Ontario.

We sampled about 85% and 60% of total island area in Manitoba–Ontario and Nunavut, respectively, observed 102 and 9 bears and obtained estimates of 120 (SE: 19.8) and 15 (SE: 1.6) bears on and near small islands in the 2 areas. Additionally, 2 groups totaling 4 bears were sighted beyond the maximum inland extent of the defined study site (>75 km and >60 km inland, respectively) during ferry flights between transects. Because we were unable to incorporate these individuals elsewhere in the analysis, these bears were added to final calculations. We observed no bears in dens during the survey.

3.3.3. Total abundance

Summing estimates from the perpendicular transects including the coastal zone, small island sampling, and the bears observed beyond the extent of the inland strata yielded an abundance estimate of 1068 (SE: 187) bears. Estimates from coastal contour transects, perpendicular transects excluding the coastal zone data, and small island sampling, as well as the bears sighted beyond the extent of the inland strata, produced a total abundance of 991 (SE: 128). Averaging these estimates yielded an abundance of 1030 (CV: 16.0; 95% lognormal CI: 754–1406) for WH during the 2011 ice-free season.

4. Discussion

4.1. Distribution

Because the aerial survey was systematic and comprehensive, our data provide unique insights into the distribution and densities of bears across the entirety of WH. Residents of communities along the Nunavut coastline of WH report that encounters with polar bears have been increasing since the 1970s (Tyrrell, 2006), resulting in a perception among local communities that abundance has increased and that a significant proportion of bears are now summering outside the core MR study area (Dowsley and Taylor, 2006; NWMB, 2007). However, aerial survey data did not indicate a large-scale range shift; only about 6% of sightings during the 2011 survey occurred in Nunavut. This finding is consistent with previous research and suggests that the vast majority of individuals within WH still summer in Manitoba.

Similar to previous studies (e.g., Stirling et al., 1977; Derocher and Stirling, 1990; Lunn et al., 1997; Towns et al., 2010), we found marked differences in polar bear distribution comparing 2 broad geographic regions in Manitoba and Ontario (previously delineated by Stirling et al. (2004); Fig. 3). In Area 1 (including the core study area of the MR work), the highest densities of bears occurred along the coastline, but we also encountered a significant number of individuals >10 km inland, mostly within Wapusk National Park (Fig. 3). In contrast, virtually all polar bears in Area 2 (i.e., southeastern WH) were highly concentrated in a relatively narrow strip along the coast. These differences in distribution have been well-documented previously and attributed to several factors, including variation in the availability of suitable inland habitats for activities such as denning, avoidance of conspecifics, and thermoregulation (Stirling et al., 1977; Derocher and Stirling, 1990; Lunn et al., 1997; Clark and Stirling, 1998; Richardson et al., 2005).

Because nearly half of the sightings in Manitoba–Ontario occurred in southeastern WH, outside the core MR study area, we reviewed multiple lines of evidence to examine the hypothesis that the high proportion of bears encountered there was an anomaly reflecting temporary immigration of bears from the adjacent Southern Hudson Bay (SH) population. There is not strong support for this hypothesis. First, historical data indicate that there is little overlap during the ice-free season and high fidelity to on-land areas (e.g., Lunn et al., 1997; Stirling et al., 2004). Second, although they represent a small ($n = 7$) and sex-biased (i.e., all females) sample, bears outfitted with satellite collars in SH during 2011 did not exhibit unusual movements during the ice-free season and were well within SH's bounds during the late summer and fall (M. Obbard and K. Middel, Ontario Ministry of Natural Resources,

Table 1
Summary of most supported models (ΔAIC < 2) for distance sampling analyses of the WH polar bear aerial survey, conducted during August, 2011. In the column *Model*, the first term signifies the key function and subsequent terms represent covariates (Struc = habitat structure within a 30 m radius of the polar bear; Vis = visibility).

Dataset	Model	ΔAIC	Parameters	Global density[a] (bears per km^2)	Coefficient of variation (%)
All inland sightings	Half-normal/Struc + Vis	0.000	3	0.011	17.6
	Hazard/Struc + Vis	0.106	4	0.013	20.7
Sightings excluding coastal zone	Half-normal/Struc + Vis	0.000	3	0.007	20.3
	Hazard/Vis	0.331	3	0.008	23.3
	Hazard/Struc + Vis	1.030	4	0.008	24.2
	HN/Vis	1.059	2	0.007	18.8
	HN/Struc	1.630	2	0.007	20.0

[a] Global density estimates refer to density within the region estimated by distance sampling. For example, datasets excluding sightings in the coastal strip do not incorporate those bears in the global density estimate.

unpublished data). Third, an aerial survey of SH was conducted in Ontario, where most bears in that population summer (Obbard et al., 2007), during September, 2011, and in Quebec and offshore islands the following year (Obbard et al., 2013). The abundance estimate of SH (951, 95% CI: ~662–1366) derived from this aerial survey is consistent with other recent abundance estimates (900–1000; Obbard et al., 2007), suggesting that a large influx of bears from Southern Hudson Bay is unlikely to have significantly contributed to the high densities of bears observed in WH. Finally, the high number of bears sighted along the Area 2 coastline is consistent with long-term data from annual coastal surveys that show a trend of increasing use of this region (Stirling et al., 2004; Manitoba Conservation, unpublished data; Fig. 4).

4.2. Abundance estimation

4.2.1. Aerial survey-based estimation

We generated an aerial survey estimate of abundance for WH using a combination of sampling and analytical techniques. While our results provide an estimate of current polar bear abundance, this figure alone does not indicate population status or trend. Multiple surveys repeated at regular intervals would be required to assess trend.

Abundance estimates in which bears along the shore were estimated from perpendicular transects extending through the coastal zone (i.e., distance sampling) were generally consistent with estimates in which the coastal zone abundance was based on separate contour transects (i.e., sight–resight). To incorporate uncertainty in model selection and estimated detection functions as well as variability between techniques, we used model-averaging in the analyses. This procedure slightly inflated precision. However, we believe that it resulted in an estimate that better reflected true abundance (Anderson et al., 2000).

We sampled from both a helicopter and a fixed wing aircraft during the aerial survey due to logistical constraints. Insufficient detections from the fixed wing compelled us to pool data from the 2 platforms in our analyses. Our preliminary analyses including and excluding the fixed wing data from modeling and our experiences with helicopter and fixed wing surveys elsewhere suggest that pooling data from the platforms had a negligible effect on our results. The consistency in the number and distribution of sightings in Nunavut between this study and previous, helicopter-based research (e.g., Peacock and Taylor, 2007) also supports this assertion. Moreover, distance sampling models are robust to pooling of data with different detection functions (Buckland et al., 2001).

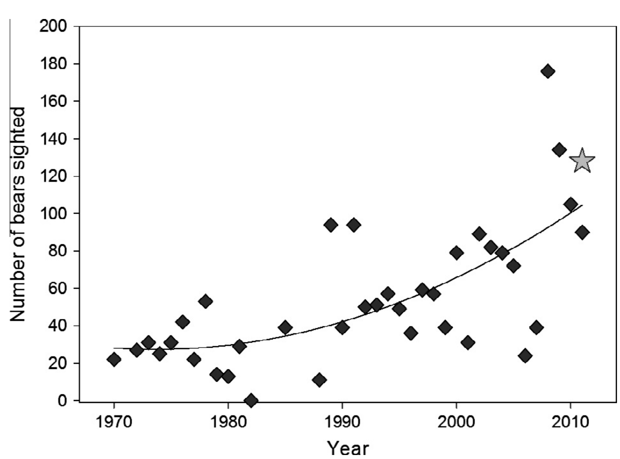

Fig. 4. Polar bear counts from annual coastal surveys conducted between August 15 and September 15 from 1970 to 2011 in Western Hudson Bay in the region extending from the Nelson River to the Manitoba–Ontario border (i.e., Area 2; Stirling et al., 2004, Manitoba Conservation unpublished data). The number of bears observed during this survey, including those sighted along the coast and on small islands during the coastal contour transects, is denoted by a gray star.

4.2.2. Methodological assumptions

Like all statistical methods, the ability of distance sampling to generate a reliable (unbiased) abundance estimate is contingent on meeting a set of assumptions. We attempted to minimize potential biases in the aerial survey through study design. Specifically, we surveyed with systematically spaced transects oriented against the coastal density gradient to ensure random sampling with respect to the distribution of bears. We also examined left-truncated data to account for blind spots and evaluated detection on the transect line with double-observer models, which we estimated at >97%. This result suggests that we detected virtually all animals on the transect line.

Detection of bears at their initial location (i.e., before responding to approaching observers) is another core distance sampling assumption (Buckland et al., 2001). Because polar bears in WH have been subject to an annual capture program over the past several decades, we hypothesized that they may have moved in response to an approaching aircraft. However, >75% of bears sighted within 500 m of the aircraft along perpendicular transects were stationary when first detected, and sighting distance histograms (Fig. 2) did not suggest significant responsive movement (sightings peaked in the distance bins closest to the transect). Additionally, the survey was flown at speeds much faster than a polar bear can travel, so the impact of movements prior to detection was likely minimal (Buckland et al., 2001).

Finally, accurate measurement of distances to sightings from the transect path is critical (Buckland et al., 2001). We used methods involving GPS and GIS technology adapted from Marques et al. (2006) that we previously implemented in large-scale polar bear aerial surveys in Foxe Basin (Stapleton et al., 2012). We are confident that our measures of perpendicular distance between the aircraft flight path and polar bears were accurate. Because our study met and evaluated fundamental distance sampling assumptions through proper study design and analysis, the aerial survey additionally fulfilled the implicit assumption that polar bear distances from the transects (i.e., observed plus unobserved bears) followed a uniform statistical distribution (Fewster et al., 2008).

Abundance estimates derived from mark–recapture (sight–resight) models will be negatively biased if heterogeneity in detection probabilities is not sufficiently modeled (Otis et al., 1978; Pollock et al., 1990). Here, sight–resight results may have been particularly susceptible to underestimation since observations by front and rear observers were nearly instantaneous and from very similar vantage points. In other words, sightings were not entirely independent (e.g., both observers may have been more likely to miss difficult-to-spot bears), potentially yielding an overestimate of detection. However, we adopted a conservative strip width and included multiple covariates to explain variability in detection. The habitat along the coast and on small islands also generally presented excellent sighting conditions, reducing the likelihood that a significant source of heterogeneity was not included in modeling.

4.2.3. Other potential biases

Several other factors may affect the accuracy of an aerial survey in WH. Available evidence suggests that our study area encompassed nearly all bears located within the bounds of the WH population during August, 2011. However, 2 groups were sighted beyond the inland extent of the study area, indicating that our delineation was not fully comprehensive. Polar bears located far from the coast during the ice-free season have been occasionally reported in the region, including a bear sighted in northeastern Saskatchewan, more than 400 km from the Hudson Bay coastline, during 1999 (Goodyear, 2003). While it is impossible to quantify the extent of these occurrences, we believe such far inland bears are rare. We also cannot discount the presence of some bears in far offshore waters during the survey period. Although we extended perpendicular transects over tidal flats and surveyed during ferry flights between small islands, safety concerns and logistical efficiency precluded systematically and intensively surveying offshore waters. Telemetry data indicate that bears predictably come ashore as sea ice melts and breaks up, rather than remaining in offshore, ice-free waters (Stirling et al., 1999; Parks et al., 2006; Cherry et al., 2013). Arrival on land occurs 3–4 weeks after ice breakup, defined as the date at which total ice cover decreases to 50% (Stirling et al., 1999) or 30% (Cherry et al., 2013). Polar bears in WH remain onshore throughout the ice-free season (Stirling et al., 1977) and their movements are markedly reduced (Parks et al., 2006). In 2011, Hudson Bay was completely ice-free several weeks prior to the commencement of the aerial survey (Canadian Ice Service regional charts, available: http://ice-glaces.ec.gc.ca/). In Manitoba, our sampling itinerary began at the Nunavut border and continued southward, such that southeastern WH, where sea ice tends to persist longest, was surveyed about 4 weeks after the last remnant ice floes had melted. Thus, any bears swimming in WH's offshore waters likely represent a negligible portion of the total population.

Polar bears that are entirely hidden from observation are not incorporated in an aerial survey abundance estimate. Such availability bias could arise from 2 sources. Whereas much of the WH study area consists of open coastal plains or tundra, dense vegetation and small trees encountered in some inland regions may completely obscure some polar bears from view. While we are unable to quantify such availability bias, our impression in the field was that although trees and brush impeded detection (e.g., habitat structure was an important covariate in modeling detection functions), it is likely that few, if any, bears were completely concealed by vegetation.

Second, polar bears in WH, particularly pregnant females, may use dens during the ice-free season, entering them as early as August (Stirling et al., 1977; Clark et al., 1997; Clark and Stirling, 1998; Lunn et al., 2004; Richardson et al., 2005). We cannot correct for bears that were underground during the survey, but several pieces of evidence suggest that this was rare. We observed numerous dens, some signs of recent digging, and sighted bears of various sex and age-classes in known denning areas (i.e., the high density stratum). However, we did not document any bears in dens or near mouths of dens, suggesting that overall denning activity was low during the survey. Additionally, more than 50% of bears classified as adult females in Manitoba and Ontario were solitary. These presumably pregnant bears (i.e., the reproductive class most likely to enter dens in late summer and fall) were proportionately more abundant than females that had cubs the previous year (with coy) or the year before (with yearlings). These findings suggest that few bears were missed in dens. Nevertheless, any availability bias arising from bears being obscured in dens or by vegetation would cause our estimate to be negatively biased.

4.2.4. Comparison with mark–recapture estimation

Our 2011 aerial survey results are consistent with a 2004 estimate of abundance based on MR (935; 95% CI: 794–1076; Regehr et al., 2007). However, previous analyses based on vital rates estimated from capture-based studies suggested that abundance would continue to decline beyond 2004 (Regehr et al., 2007; Obbard et al., 2010). Thus, we expected that our abundance estimate would be substantially less than the 2004 estimate. A review of how MR has been implemented in WH is informative for evaluating potential differences between aerial survey and MR-derived estimates of abundance.

Equal probability of detection is a key assumption of capture-based methods. Unmodeled heterogeneity in capture probabilities produces a negatively biased abundance estimate and may impact survival estimates (Pollock et al., 1990). Thus, obtaining a random sample of individuals that represents the entire population of interest (or completely modeling unequal capture probabilities to eliminate capture heterogeneity) is necessary to generate reliable results.

In WH, sampling effort for MR historically concentrated around Churchill and in Wapusk National Park (i.e., the high density stratum, Fig. 1; e.g., Regehr et al., 2007), with limited and less frequent sampling elsewhere, such as southeastern WH (e.g., Area 2, Fig. 3; Lunn et al., 1997). Despite this geographically limited sampling, MR analyses have been considered to reflect abundance and trends for the entire WH population (Regehr et al., 2007; Obbard et al., 2010), generally under the assumption that adequate 'mixing' ensures random sampling.

However, several lines of evidence suggest that this sampling strategy may have resulted in biased parameter estimates. Multiple studies have reported that polar bears in WH show a high degree of geographic fidelity within and between ice-free periods (Derocher and Stirling, 1990; Stirling et al., 2004; Parks et al., 2006). Such site fidelity suggests that sampling a limited portion of WH may yield an estimate that includes only those bears that used the sampled area, not the entire population.

Additionally, the results of the aerial survey demonstrate that a significant proportion of bears are found outside the core MR study area in late summer, when most capture work historically has occurred (e.g., Regehr et al., 2007). Very low densities of polar bears in the Nunavut portion of WH during the early ice-free season suggest that any bias arising from limited sampling in this region is likely minimal. Conversely, high densities of bears along the coast in southeastern WH represent a large and seemingly increasing proportion of the population (Fig. 4); failure to adequately sample this region could negatively bias abundance estimates and obscure population trends. Lunn et al. (1997) reported that MR estimates of population size did not differ based on the inclusion or exclusion of capture data from southeastern WH. However, sampling was limited and inconsistent in this region compared to the extensive, long-term sampling within the core study area. In contrast, Regehr et al. (2007) noted disparities in comparing abundance estimates derived from 2 MR datasets and attributed this finding to undersampling of subadults that tended to occupy areas closer to Churchill; the dataset that yielded a lower abundance estimate included less sampling around Churchill. Combined, these observations suggest that spatially limited sampling (i.e., concentrated within the densest region) may have resulted in an underestimate of abundance of WH.

The aerial survey represents the first systematic and geographically comprehensive survey of polar bears in WH. Thus, the results better represent the entire population than MR estimates based on sampling within a core study site. As such, WH appears to have more polar bears than previously thought. Our estimate, however, does not necessarily negate the declining trends in abundance, survival, reproductive output, and body condition reported from WH (Stirling et al., 1999; Regehr et al., 2007). Because the aerial survey reflects a larger effective area (the entirety of WH) than the MR studies (a smaller proportion of the population), results from the 2 methods cannot be directly compared to assess population trend. It would be erroneous to suggest that our estimate indicates that the population is not declining. Indeed, the aerial survey indicated that reproductive performance in WH during 2011 was relatively poor, consistent with findings of capture-based studies (Regehr et al., 2007). Mean litter sizes and the proportions of cubs-of-the-year and yearlings recorded in WH were low relative to adjacent populations (Table 2), suggesting that WH is currently less

Table 2
Polar bear litter sizes and number of dependent offspring observed (as proportion of total observations) during recent ice-free season studies in central and eastern Canada. Data are presented as mean (standard error).

Population	Litter size		Proportion of total observations		Source
	Cubs of the year	Yearlings	Cubs of the year	Yearlings	
Western Hudson Bay (2011)	1.43 (0.08)	1.22 (0.10)	0.07	0.03	This study
Southern Hudson Bay (2011)	1.56 (0.06)	1.54 (0.08)	0.16	0.12	Obbard et al. (2013)
Baffin Bay (2011)	1.57 (0.06)	1.51 (0.09)	0.19	0.10	Government of Nunavut (unpublished data)
Foxe Basin (2009–2010)	1.54 (0.04)	1.48 (0.05)	0.13	0.10	Stapleton et al. (2012)
Davis Strait (2005–2007)	1.49 (0.14)	1.22 (0.28)	0.08	0.09	Peacock et al. (2013)

productive than other populations in the Hudson Bay complex and nearby regions (Peacock et al., 2010). Nevertheless, the apparent increased use of southeastern WH, coupled with the lack of sampling there, could result in an inaccurate assessment of trends in abundance, survival, and other measures of population status. The differences in sampling frames and associated uncertainties must be clearly communicated to decision-makers, and southeastern WH should be fully integrated in future studies to evaluate demography and status of polar bears across the population. There are several fundamental questions about how this region functions within the broader Hudson Bay polar bear complex, including the suitability of current population delineation, the discreteness of bears that summer in southeastern WH from bears that summer elsewhere in the population, and the susceptibility of these bears to harvest by communities in Nunavut.

5. Conclusions

Recent changes in regional sea ice (Gough et al., 2004; Gagnon and Gough, 2005; Scott and Marshall, 2010) and reported deleterious impacts on body condition and vital rates (e.g., Stirling et al., 1999; Regehr et al., 2007) have placed Hudson Bay at the forefront of polar bear conservation and management. Indeed, polar bears in Western Hudson Bay are often cited as the most visible and dramatic example of the early impacts of climate change. The aerial survey results should not necessarily alter that impression, nor do they provide a more optimistic outlook for polar bears in the Hudson Bay region. However, our findings do highlight the need to identify the limitations of both aerial survey and MR sampling programs and to reconcile potentially conflicting results in order to correctly assess population status and quantify the impacts of climate change. Our results further suggest that the systematic and comprehensive sampling of aerial surveys can effectively complement capture-based initiatives, providing a sound means to track abundance and distribution. Their application may become particularly important in WH and similar populations subject to changing environmental conditions, given the increasing need for rapid dissemination of information, the strong objections by Inuit to physical capture, and the possible effects of capture on bears in a declining state of health.

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