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Apparent Collapse of the Peary Caribou (*Rangifer tarandus pearyi*) Population on Axel Heiberg Island, Nunavut, Canada

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ABSTRACT. In spring 2019, we conducted a comprehensive abundance and distribution survey for Peary caribou (*Rangifer tarandus pearyi*) and muskox (*Ovibos moschatus*) on Axel Heiberg Island, Nunavut, Canada. Although much of Axel Heiberg Island is rugged and extensively glaciated, areas east of the Princess Margaret mountain range have high productivity given the latitude and have supported relatively large numbers of Peary caribou and muskoxen. This region of the island has been previously identified as a potential High Arctic refugium. The last island-wide survey, in 2007, estimated 4237 muskoxen (95% confidence interval [CI] [3371:5325]) and 2291 Peary caribou (95% CI [1636:3208]); based on our 2019 results, it appears that muskox numbers have been stable on Axel Heiberg Island since then. Using distance sampling and density surface models, we estimated 3772 muskoxen (95% CI [3001:4742]) on Axel Heiberg Island during our 2019 survey. In contrast, Peary caribou, which is listed as an endangered species under the Canadian *Species at Risk Act*, appear to have declined dramatically from the 2007 estimate. During the 2019 survey, we observed only six Peary caribou and could not generate an island-wide estimate. Abrupt declines in numbers are characteristic of the species and are usually related to poor winter conditions such as dense snowpack or extreme weather events that result in widespread ground-fast icing. However, the limited monitoring information available at the northern extent of Peary caribou range presents major challenges to our understanding of the mechanisms leading to this near total absence of approximately 20% of range-wide Peary caribou numbers.

Key words: Peary caribou; muskox; density surface model; *Rangifer tarandus pearyi*; *Ovibos moschatus*; Axel Heiberg Island

RÉSUMÉ. Au printemps de 2019, nous avons réalisé un levé exhaustif de l'abondance et de la distribution du caribou de Peary (*Rangifer tarandus pearyi*) et du bœuf musqué (*Ovibos moschatus*) sur l'île Axel Heiberg, au Nunavut, Canada. Même si une grande partie de l'île Axel Heiberg est accidentée et considérablement englacée, des aires à l'est des monts Princess Margaret affichent une forte productivité en raison de la latitude et comptent des nombres relativement grands de caribous de Peary et de bœufs musqués. Cette région de l'île a déjà été reconnue comme refuge potentiel dans l'Extrême-Arctique. Le dernier levé effectué pour l'ensemble de l'île, en 2007, a permis d'estimer 4 237 bœufs musqués (intervalle de confiance de 95 % [IC] [3371:5325]) et 2 291 caribous de Peary (IC de 95 % [1636:3208]). D'après nos résultats de 2019, il semblerait que les nombres de bœufs musqués de l'île Axel Heiberg sont restés stables. À l'aide d'échantillonnage à distance et de modèles de densité surfacique, nous avons estimé 3 772 bœufs musqués (CI de 95 % [3001:4742]) sur l'île Axel Heiberg dans le cadre de notre levé de 2019. En revanche, le nombre de caribous de Peary, considérés comme une espèce en voie de disparition en vertu de la *Loi sur les espèces en péril* du Canada, semble avoir chuté énormément depuis l'estimation de 2007. Pendant le levé de 2019, nous n'avons observé que six caribous de Peary et n'avons pas réussi à produire d'estimation pour l'ensemble de l'île. La chute abrupte du nombre de caribous est caractéristique de cette espèce et est généralement attribuable à de mauvaises conditions hivernales, comme un enneigement dense ou des événements climatiques extrêmes se traduisant par de la glace généralisée fixée sur le sol. Cependant, les données de surveillance limitées pour l'extrémité nord de l'aire de répartition du caribou de Peary entravent considérablement notre compréhension des mécanismes menant à cette absence quasi totale d'environ 20 % des nombres de caribous de Peary à l'échelle de l'aire de répartition.

Mots clés : caribou de Peary; bœuf musqué; modèle de densité surfacique; *Rangifer tarandus pearyi*; *Ovibos moschatus*; île Axel Heiberg

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INTRODUCTION

Canada's High Arctic islands are home to two large-bodied terrestrial herbivores: the Peary caribou (*Rangifer tarandus pearyi*) and the muskox (*Ovibos moschatus*). In these remote regions, animals live in darkness with temperatures well below freezing for large parts of the year. Peary caribou are members of the deer family and the smallest of the North

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American *Rangifer*. They do not form large aggregations like barren-ground caribou (*R. t. groenlandicus*), but rather are dispersed across the Canadian Arctic Archipelago at low densities (COSEWIC, 2015). The much larger-bodied and shaggy-haired muskox is related to sheep and goats and is the only living member of the genus *Ovibos* (Tener, 1963). These two species have developed broadly different physical adaptations and life history strategies for the same harsh environmental conditions (Klein, 1992), and the extent of interspecific competition between these two ungulates is a long-standing question (Tener, 1963; Larter et al., 2002). Both caribou and muskox play ecological roles in nutrient cycling and altering vegetation communities (van der Wal, 2006; Mosbacher et al., 2019), provide food sources for predators and scavengers (Anderson et al., 2019), and are harvested for subsistence by High Arctic communities (Anderson, 2015).

Because of the difficult environmental conditions, limited transportation infrastructure, and sheer cost of research in the far North, regular monitoring of these species at the northern extents of their ranges is difficult, but important, given the growing impetus to understand climate change impacts to Arctic ecosystems (Gilg et al., 2012; Berger et al., 2018). Under these conditions, sporadic monitoring of Peary caribou and muskox populations in the Canadian Arctic Archipelago has occurred since the 1960s (Tener, 1963), with variable survey frequency across islands in the archipelago. Some areas, such as Bathurst and Banks Islands, have benefitted from more dedicated research programs, but many islands in the archipelago have been surveyed only a few times over the past 60 years (Johnson et al., 2016). For example, before this survey, Axel Heiberg Island had only been comprehensively surveyed for Peary caribou and muskox once, in 2007 (Jenkins et al., 2011). These monitoring difficulties create considerable uncertainty in our ability to assess the status and trends of both Peary caribou and muskox populations in the Canadian High Arctic.

Since 2011, Peary caribou has been listed as an endangered species under the Canadian *Species at Risk Act* (SARA), meaning the species is considered to be facing immediate extinction if actions toward protection and recovery are not taken. However, in 2015 the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) reassessed the species to a lower classification of threatened, citing increasing trends in Peary caribou numbers in two of four subpopulations, but this status change has not yet been reflected under SARA (COSEWIC, 2015). In Canada the muskox has not been assessed by COSEWIC and globally has been listed as least concern by the IUCN (Gunn and Forchhammer, 2008). A recent comprehensive consideration of global muskox populations suggests that populations remain stable across most of the species' range, though some populations are declining (Cuyler et al., 2020). With the sparse human population and minimal development across the Canadian High Arctic at present, the levels of direct anthropogenic disturbance to Peary caribou and muskoxen have been limited, with the preeminent threat to these species being climate change. The possible negative consequences for caribou and muskoxen in the High Arctic from climate change are similar but not identical. For both species, the potential increased frequency of extreme weather events that lead to ground-fast ice is a major concern (Berger et al., 2018; Mallory and Boyce, 2018). Rain-on-snow or thaw-freeze events that result in extensive icing can have severe consequences for herbivores and have led to die-offs of both Peary caribou and muskox (Miller and Gunn, 2003a; Rennert et al., 2009). Many Peary caribou rely on sea ice for movements between island habitats, and lengthening ice-free seasons in the Canadian Arctic are anticipated to continue to reduce seasonal habitat connectivity, with probable negative demographic consequences for the species (Mallory and Boyce, 2019). Occasional use of sea ice for movement by muskoxen must occur, however, at present there is no evidence to suggest that muskoxen use sea ice at a similar scale to Peary caribou across the archipelago.

This 2019 survey was undertaken as part of the Government of Nunavut's objective to update abundance estimates for Peary caribou across the species' range. Limited observations of caribou on Axel Heiberg Island during a wolf predation project from 2014 – 18 (Anderson et al., 2019) provided additional impetus given Axel Heiberg Island's infrequent survey history and once relatively large caribou population. The previous and only comprehensive survey of the island in 2007 estimated 2291 Peary caribou (95% CI [1636:3208]) and 4237 muskoxen (95% CI [3371:5325]). At the time of contemporary range-wide estimates, Axel Heiberg Island had proportionally large populations of both Peary caribou and muskoxen. Based on a 2011 report, Axel Heiberg Island's population represented approximately 57% of Peary caribou in Nunavut (Jenkins et al., 2011). COSEWIC's 2015 assessment estimated 13 200 Peary caribou across the Canadian Arctic, of which the Axel Heiberg 2007 estimate would have made up 17%. Cuyler et al. (2020) reviewed circumpolar muskoxen estimates and based on recent surveys the Axel Heiberg muskox population represented 7% of muskox in the Canadian Arctic Archipelago (13% including Nunavut islands only).

MATERIALS AND METHODS

Study Area

Axel Heiberg Island (43 178 km^2) is the second-most northern island in Canada (Fig. 1). Much of it is mountainous and glaciated; aside from seasonal researchers, the island is uninhabited. The Princess Margaret Mountain Range dominates a large central swath of Axel Heiberg Island, and glaciers and ice caps cover approximately 27% of the island (Thomson et al., 2011). Like most of the High Arctic, climate conditions challenge plant growth and barren and sparsely vegetated landscapes occur across Axel Heiberg

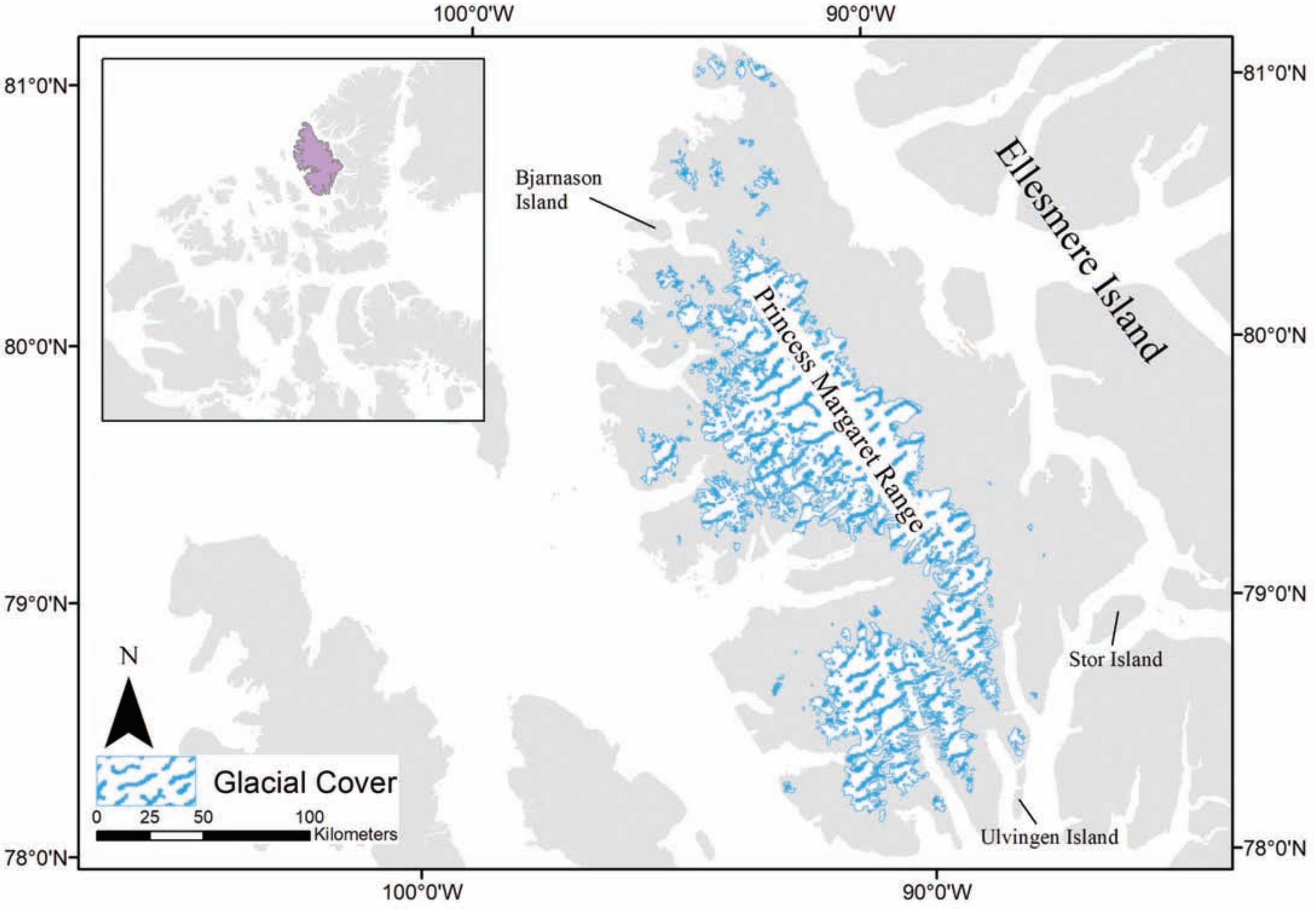

FIG. 1. Location of Axel Heiberg Island within the Nunavut Territory of Canada.

Island. However, some regions of greater plant diversity and higher productivity can be found, such as the lower-lying coastal areas east of the Princess Margaret Range (Edlund and Alt, 1989). The eastern portion of the island adjacent to the Fosheim Peninsula has been noted as a potential refugium for muskox and Peary caribou due to physiographic characteristics that give the area its varied topography, more amenable climate, and higher plant productivity and diversity (Thomas et al., 1981). In addition to Axel Heiberg Island, our study area also covered several small islands, including Stor Island, Ulvingen Island, and Bjarnason Island. Based on our survey and analysis design, the total study area covered by our survey is 31 736 km^2.

Aerial Survey

We conducted the aerial survey using a distance sampling line-transect method (Buckland et al., 2001) from 25 March 2019 to 6 April 2019. We used a systematic line-transect design with random start location to establish east-west transects 5 km apart and parallel to lines of latitude. Our survey followed the transects of the previous aerial survey of Axel Heiberg Island conducted in 2007 (Jenkins et al., 2011). We did not survey the extensively glaciated and mountainous central portion of the island (approximately 11 000 km^2, blue and white areas in Fig. 2) because of the low probability of caribou or muskox presence. We considered stratifying the survey area based on observations from the 2007 survey, however ultimately decided against it. Due to the substantial time period that elapsed between surveys, and because the 2019 survey was conducted earlier in the year than the 2007 survey, we were uncertain whether the distribution of individuals would be similar between surveys and elected to use a consistent survey effort across the study area.

Transects were flown in an AS350 B2 helicopter with a survey crew consisting of the pilot, a front left observer and two rear observers. Flight altitude and speed were maintained at near 121 m aboveground and between 150 to 180 km/h, respectively. We used a double observer distance sampling method that considered the entire survey crew as a single observer during analysis. When groups of animals were observed from the transect line, we took a waypoint on-transect before flying to the observed animal location to count and identify the composition of the group. We took a second waypoint at the position where the group was first observed. We took photographs of all wildlife observations to improve counts and composition and to reduce the time spent flying in close proximity to the animals. To ensure accurate measurements from transect lines to clusters, we measured the perpendicular distance from the transect line to each cluster (location of group when it was first observed) using ArcMap 10.6.1 following completion of the survey (Esri, 2017).

For each observed group of animals, we also recorded the following covariates at cluster locations: slope index (categorical from 1 to 3), elevation index (categorical from 1 to 3), snow patchiness (continuous from 0 to 100), percent snow cover, and percent cloud cover. We recorded aircraft speed at the time the group was first spotted.

Density and Abundance Estimation

Distance sampling techniques are well established for estimating the density and abundance of wildlife populations (Thomas et al., 2010), and numerous survey designs and analyses have been developed to expand upon the core distance sampling concepts and methods (e.g., Buckland et al., 2001, 2004). Fundamentally, distance sampling methods use measured distances from point or line transects to observations of objects of interest (in our case groups of Peary caribou and muskox) to estimate density or abundance of those objects across a survey area (Buckland et al., 2001).

We estimated the density and abundance of muskox across the study area via three methods: conventional distance sampling (CDS), multiple covariate distance sampling (MCDS), and density surface models (DSMs) (Buckland et al., 2001, 2004; Miller et al., 2013). CDS estimates are generated from models in which the probability of detection depends only on distance from the transect (Buckland et al., 2001). With MCDS, we can model the probability of detection using distance and other covariates. These covariates can be related to either the observed cluster (e.g., number of animals), the environment (e.g., topography), or the observer (Buckland et al., 2004). For our DSMs, we used a two-stage approach: in the first stage we fit a detection function to the distance sampling data, and in the second stage we used generalized additive models (GAMs) to fit a spatial model to the detection-corrected count data (Miller et al., 2013). By fitting detection functions with covariates in addition to distance, we not only improve the precision of abundance estimates, but also investigate relationships between wildlife distribution, abundance, and environmental covariates (Buckland et al., 2004; Miller et al., 2013). The DSM approach for line transects requires that counts be summarized by segments, within which wildlife densities and chosen environmental covariates should not change markedly (Miller et al., 2013). To fit these criteria, we divided transects into approximately 2 km segments (mean: 2.017 km, SD: 69.6 m), which is similar to the right-truncation distance of our detection functions (see supplementary Appendix 1).

Conventional and Multiple Covariate Distance Sampling: We compared candidate detection functions using Akaike's Information Criterion (AIC), and considered models within 2 AIC to be competitive (Burnham and Anderson, 2002). The AIC values are useful for model comparison, but do not test overall goodness-of-fit and so we also evaluated models with goodness-of-fit tests available through the dsm, Distance, and mrds packages in R (Laake et al., 2018; Miller et al., 2019, 2020; R Core Team, 2019). We used all candidate models to produce abundance estimates and confidence intervals and calculated model-averaged estimates from competitive (within 2 ΔAIC) models using the AICcmodavg package in R (Mazerolle, 2020).

Density Surface Modelling: After comparing candidate detection functions, we proceeded to step two of the DSM approach by fitting GAMs to the detection-corrected count data. We used two spatial covariates to model animal densities: a continuous elevation surface derived from the NRCan Canadian Digital Elevation Model (NRCan, 2016) and a vegetation factor that indicated whether a grid cell was predominantly vegetated or barren. This categorical factor was derived from the North American Land Change Monitoring System Land Cover Map of North America (Latifovic et al., 2017) by combining all vegetated classes on Axel Heiberg Island. One factor level represented the combined vegetation class and the other level represented the remaining barren land-cover class.

We tested and compared several candidate models for the second stage of the DSM analysis. We varied models by detection function, response distributions (quasi-Poisson, negative binomial, or Tweedie), and spatial covariates. The validity of candidate models was evaluated using model diagnostic tools from the mgcv and dsm R packages (Wood, 2011, 2017; Miller et al., 2020), and we tested models for residual autocorrelation. For all valid candidate models, we produced abundance estimates and confidence intervals. We identified the best performing models based on the deviance they explained and AIC scores. Additional details of our analysis methods can be found in Appendix 1.

RESULTS

Aerial Survey

Over the two-week duration of the survey, we flew roughly 12 363 km, of which approximately 6169 km were on transect. The additional distances flown were for ferry flights to and from transects and fuel caches. Over the course of the survey period, we had four weather days where we could not fly: 28 and 30 March, 1 and 3 April. During the survey we saw 2629 muskoxen in 204 groups on transect. The average group size was 13 (± 11 SD), with a maximum group size of 66 individuals. We saw a total of six Peary caribou in four groups (two lone individuals and two pairs). The highest densities of muskoxen were in the lower-lying regions east of the Princess Margaret range

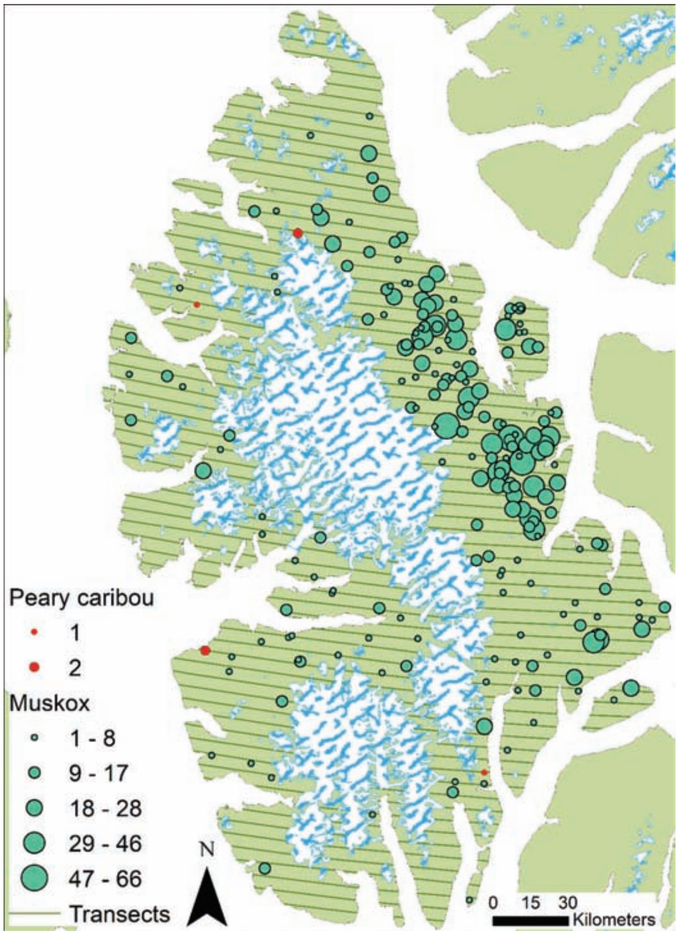

FIG. 2. Summary of Peary caribou (*Rangifer tarandus pearyi*) and muskox (*Ovibos moschatus*) aerial abundance survey of Axel Heiberg Island. Graduated circles indicate numbers of individuals within observed groups of caribou and muskoxen. The blue and white areas show glaciated regions.

(Fig. 2). There were too few Peary caribou observations to establish any distributional patterns.

Muskox Density and Abundance Estimation

Conventional and Multiple Covariate Distance Sampling: Three detection functions (2, 5, 6) were within 2 ΔAIC of each other. Model performance and abundance estimates for all detection functions can be found in Appendix 1, Table A1. For our final estimate from the CDS methods, we produced a model-averaged abundance estimate from the three competitive detection functions of 4315 (SE = 739, 95% CI = [2866:5764]).

Density Surface Modeling: We tested DSMs using detection functions 2 and 5 from the first stage of the analysis (see Appendix 1 for rationale). The range of abundance estimates produced by the DSMs was relatively small, with a mean of 3907 ± 156 SD, and confidence limits for all estimates overlapped (Appendix 1, Table A2). Our most-supported model in terms of AIC score was DSM 6, which included detection function 2, a bivariate smooth of location, a smooth of elevation, and a vegetation binary parametric factor (Appendix 1, Table A2).

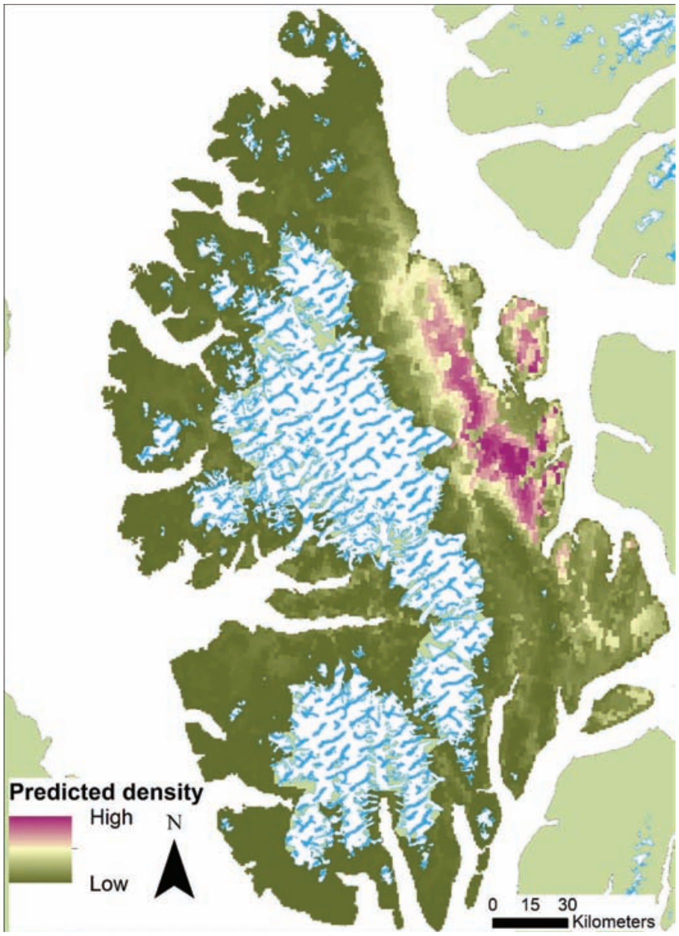

FIG. 3. Predicted muskox (*Ovibos moschatus*) densities on Axel Heiberg Island derived from our most supported density surface model. Predicted abundances per grid cell range from 0 to 4.68 muskoxen/grid cell. The mean predicted density across the study area was approximately 0.12 muskoxen/km^2. The blue and white areas show glaciated regions.

DSM 6 estimated 3772 muskoxen (95% CI [3001:4742]) with a CV of 12%. From DSM 6, we found, unsurprisingly, that vegetation had a positive effect on muskox counts (β = 0.99, SE = 0.22). Appendix 1, Figure A1 plots the smooth of elevation from DSM 6, suggesting that muskox abundance increases from sea level to about 300 m of elevation and declines thereafter. The low number of observations at higher elevations causes the uncertainty in predicted values to become very large above approximately 1000 m above sea level. The predicted spatial distribution of muskox densities from DSM 6 is shown in Figure 3. The mean predicted density across the study area was approximately 0.12 muskoxen/km^2.

DISCUSSION

Muskox Abundance Trends

The results of our survey and analysis suggest that muskox numbers on Axel Heiberg Island have been stable since the last survey in 2007. The 2007 survey saw approximately 50% more muskox groups (301 in 2007 vs. 204 in 2019), although average groups sizes were larger in 2019 (8 in 2007 vs. 13 in 2019) (Jenkins et al., 2011). This difference could have been related to the timing of the survey, as muskox groups are typically larger in the winter and the 2019 survey was conducted about one month earlier in the year (late March) than the 2007 survey effort (late April) (Heard, 1992). In this area, this month's difference between surveys represents the transition from late winter to early spring. The distributions of muskoxen across the island were similar between both surveys, with most animals observed to the east of the Princess Margaret Range (Fig. 2). Muskox abundance estimates on Axel Heiberg Island before 2007 are limited. Tener (1963) estimated 1000 muskox on the island based on a survey with less than 3% coverage, and a 1973 reconnaissance survey counted 866 muskox on eastern Axel Heiberg Island (Ferguson, 1995). Jenkins et al. (2011) cautiously suggested that muskoxen numbers likely increased between 1961 and 2007, although the limited data make any assessment of trend difficult.

Our DSM muskox abundance estimate of 3772 (95% CI [3001:4742]) was lower than the model-averaged MCDS estimate of 4315 (95% CI = [2866:5764]), although confidence limits overlapped. Both methods provided comparable estimates, but the greater precision provided by the DSM is valuable, particularly in a management context. During the survey and through our analysis, we found that muskox densities were greater in vegetated areas and at moderate elevations. Use of more elevated areas in late winter is fairly common for muskoxen, where lower snow depths on windswept hills and ridges usually offer easier access to forage compared to low-lying areas with greater snow accumulation (Thing et al., 1987; Schaefer and Messier, 1995). Across their global range, muskoxen are found to use a variety of habitat types, from boreal forest to polar desert (Cuyler et al., 2020). However, at the northern reaches of their range, muskoxen are typically concentrated in patches of higher-quality vegetated habitat within larger matrices of lower-quality barren habitats with limited vegetation (Parker and Ross, 1976; Thomas et al., 1981; Pearce, 1991). The results from our DSM reflect this type of distribution, with a patch of high muskox density on eastern Axel Heiberg Island, and low densities across the rest of the island. Muskoxen densities on Axel Heiberg Island have previously been reported to be the highest in the Canadian Arctic Archipelago (Jenkins et al., 2011), and the island appears to remain a very productive and important area for the species at the northern extent of its range.

Peary Caribou Abundance Trends

As with muskox, it is impossible to adequately assess trends in Peary caribou abundance on Axel Heiberg Island given the infrequency of abundance information. Regardless, considering the relatively large number of caribou on the island in 2007, the near absence of Peary caribou during this survey is alarming and immediately calls to mind the possibility of a die-off. However, granted that we know very little about this High Arctic system, we should also consider some potential mitigating factors and alternatives to a catastrophic die-off. First, during the survey we did not observe any Peary caribou carcasses. That said, the ground was snow covered and, depending on when a potential die-off occurred, carcasses might not have been obvious. Another important consideration is that Peary caribou are well-known to move between islands for both seasonal migrations and desperation movements to escape ground-fast ice or poor forage conditions (Miller et al., 1977). Of course, given that 12 years passed between surveys, there are numerous possible scenarios for Peary caribou moving away from Axel Heiberg Island during the intervening period. A large-scale synchronized exodus of animals is unlikely given the island's geography and Peary caribou behaviour, and it would be more likely that some number of caribou might have emigrated over several years. For example, during periods of poor forage conditions, potentially related to icing events, smaller groups of caribou might have made dispersal movements off the island. However, even if some caribou were able to move away from poor forage conditions, there is little evidence to suggest that a substantial proportion of caribou would have successfully escaped a weather-related die-off. Data from a die-off on Bathurst Island suggest that the proportion of caribou that manage to emigrate compared to the number that perish is small. From 1994 to 1997, there was an approximate 97% decline in Peary caribou abundance on Bathurst Island and neighbouring islands resulting from severe snow and ice conditions. Based on carcass counts, it was estimated that emigration could have accounted for at maximum 15% of the decline in Peary caribou numbers (Miller and Gunn, 2003a).

We also have no reported evidence of large numbers of Peary caribou appearing on nearby islands, though the minimal human presence in the surrounding region limits our ability to detect such events. A survey of central Ellesmere Island in 2017, observed only 14 Peary caribou (Fredlund et al., 2019). This survey included coverage of the Fosheim and Raanes Peninsulas, which are directly adjacent to the highest reported densities of Peary caribou on Axel Heiberg Island from the 2007 survey and so would seem to be likely destinations for emigrants. From 2014 to 2018, Anderson et al. (2019) conducted a research program to investigate interactions between Arctic wolves (*Canis lupus arctos*), Peary caribou, and muskox on eastern Axel Heiberg Island and central Ellesmere Island. Over the course of their research program, they reported seeing very few Peary caribou across their study area. In 2014, Anderson et al. (2019) conducted reconnaissance flights looking for Peary caribou on the eastern slopes of Axel Heiberg Island and did not observe many animals where densities had been relatively high in 2007.

The apparently stable number of muskoxen on the island is worth noting in the context of a potential die-off in response to severe weather and ground-fast ice. These weather events can also be catastrophic for muskox, with severe weather-driven die-offs of muskoxen reported on Banks Island, Melville Island, and the Bathurst Island Complex, among others areas (Parker et al., 1975; Miller and Gunn, 2003a; Rennert et al., 2009). There has been some speculation that muskoxen might be more resistant to severe weather events because they are able to subsist on lower quality forage than caribou, which typically require more digestible winter forage (Klein, 1992). Additionally, given their much larger size, muskoxen are in some circumstances better adapted to breaking through ice layers and may use their massive boss to break through ice-layered snow to access the vegetation below. Despite the muskox's possible resistance to severe weather events and adaptation to icing, weather-related die-offs that have been reported typically affect both species if they are present (e.g., Parker et al., 1975; Miller and Gunn, 2003a). For environmental conditions to be so poor as to almost completely remove Peary caribou from an area but have only a limited effect on sympatric muskoxen seems questionable, although we must consider that we do not know the status of the muskox population on Axel Heiberg Island between 2007 and 2019. It is possible that they also suffered some level of decline, though not as severe.

Another possible contributor to the decline is predation by Arctic wolves. Research from 2014 to 2018 by Anderson et al. (2019) found consistently high wolf densities of approximately seven adult wolves/1000 km^2 in the summer on the Fosheim Peninsula and eastern Axel Heiberg Island. This density is within the range that has been suggested to limit caribou populations (Bergerud, 1988), although the authors were unable to assess whether this threshold is applicable to Peary caribou given the species' very low occurrence across their study area. During calving, caribou typically attempt to avoid high predator densities through "spacing away" (migration) or "spacing out" (dispersion to lower densities, often in habitats avoided by wolves and alternative prey) strategies (Bergerud, 1988). The extent to which Peary caribou employ "spacing away" or "spacing out" antipredator strategies is not well understood but has important implications for their ecological relationships to wolves and muskox. Understanding interactions between wolves and these prey species is vital in the context of potential apparent competition in areas where Peary caribou are sympatric with relatively dense muskox populations such as those observed on eastern Axel Heiberg Island in 2007 (Jenkins et al., 2011; Anderson et al., 2019).

Although our discussion above is largely speculative, we hope that it provides useful context for management and conservation decision-making, along with strategic research that could help us better understand what might have led to the sharp change in Peary caribou numbers on Axel Heiberg Island. Despite the possible alternative mechanisms we discussed above and given what we know about Peary caribou population dynamics the most probable cause of this decline remains extreme weather events. Reality likely lies in some combination of factors, with the primary mechanism being a climate-driven die-off, and contributions from movement off of the island and predation by wolves.

Abrupt fluctuations are pervasive in Peary caribou population trends (Miller and Gunn, 2003b). Over the past 50 years of monitoring, rapid increases and severe decreases in abundance within the same local populations have been reported across a number of islands in the archipelago, including Banks Island (Davison et al., 2014), Melville and Prince Patrick Islands (Davison and Williams, 2012), and the Bathurst Island Complex (Miller and Barry, 2009). During this time population trends have varied markedly across the archipelago. Peary caribou numbers were historically highest in the southern portion of their range, with relatively large populations on Banks Island and Prince of Wales Island, but declined to low densities throughout the 1980s (Johnson et al., 2016). In recent years Peary caribou populations on Banks Island have begun to show some signs of recovery, but remain much lower than their peak numbers (Davison et al., 2014). In contrast, Peary caribou numbers on the Prince of Wales/Somerset/Boothia Complex have shown no signs of recovery since their collapse in the early 1980s. On the Bathurst Island Complex, recovery from crashes in the 1970s had occurred by the mid 1990s, at which point the population crashed again, and only began to recover by 2013 (Anderson, 2014). At the eastern extent of Peary caribou range, including Ellesmere Island and Axel Heiberg Island, the limited survey information that exists has mainly reported low densities of Peary caribou (Jenkins et al., 2011; Fredlund et al., 2019). In this context, it is certainly possible that the high densities of animals reported in 2007 were atypical, and densities on Axel Heiberg Island might usually be lower. Unfortunately, the monitoring history for the species is too inconsistent to give us more than a partial understanding of Peary caribou population dynamics across most of their range, particularly at the northern extent. Though sharp fluctuations in abundance related to climate conditions are undoubtedly characteristic of the species, it is difficult to gauge whether the modern fluctuations are consistent in severity and frequency with historical contexts (Gunn et al., 1981). Given the observed increases in rain-on-snow events across the Canadian Arctic Archipelago (Langlois et al., 2017), which are one of the main drivers in Peary caribou population fluctuations, we would hypothesize that Peary caribou population dynamics probably have changed from those in recent history and are likely to continue to do so (Mallory and Boyce, 2018).

Management Implications and Future Directions

In a more accessible area, this level of population decline could warrant a prompt implementation of harvest restrictions or other management actions. Considering that Axel Heiberg Island is exceptionally remote, difficult to access, and usually visited only by researchers, we would deem harvest restrictions for the island's Peary caribou or muskox populations a low priority. Of course, should these factors change, there may be a need to review management options. Harvest management aside, because of the significant proportion of the total range-wide Peary caribou abundance that had previously been reported on Axel Heiberg Island, our survey results provide important information for Peary caribou recovery planning under SARA. We caution that although it is tempting to view our results as the apparent loss of nearly 20% of the Peary caribou population (COSEWIC, 2015; Johnson et al., 2016), we simply do not know enough about the behaviour and movement patterns of the species at the northern extent of their range to be confident that a meaningful proportion of these caribou haven't moved elsewhere. Further, it is possible that the previous (and only) comprehensive survey of Peary caribou on Axel Heiberg Island occurred when the local population of animals was at an unusually high abundance and might not have represented the island's typical caribou population or relative contribution to total Peary caribou numbers. The irregularity of surveys in the Canadian High Arctic results in a temporally disjointed picture of Peary caribou distribution and abundance across their range that challenges our ability to track and understand of population dynamics of the species. In Nunavut since 2015, surveys of Prince of Wales Island, Somerset Island, Devon Island, southern and central Ellesmere Island, and now Axel Heiberg Island have consistently found very low Peary caribou densities, often too low to generate useful abundance estimates (Anderson, 2016a, b; Anderson and Kingsley, 2017; Fredlund et al., 2019). Recognizing the numerous logistical and financial obstacles associated with Peary caribou monitoring, research and management agencies should consider survey designs that prioritize covering larger areas with lower effort. This approach could help to obtain a more temporally coherent picture of Peary caribou distribution and provide information that allows for more targeted effort to estimate abundance through stratified survey designs.

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