Spatial and temporal changes in seasonal range attributes in a declining barren-ground caribou herd

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Abstract: From 1996 to 2015 the Bathurst caribou herd has declined from approximately 349,000 to 20,000 animals. Aboriginal traditional knowledge (TK) has recently observed the later arrival of the herd below the treeline, an attribute of the autumn range. Science also predicts that seasonal range attributes (e.g., area, location) likely vary with population size, and perhaps climate. We used Aboriginal TK and science to identify several seasonal range attributes that were examined for changes through time (decreasing population abundance). Attributes of seasonal ranges for female Bathurst caribou were calculated using satellite radio-collar data from January 1996 through October 2013. Climate data from CircumArctic Rangifer Monitoring and Assessment Network were analyzed for trends from 1979 to 2009. Analyses showed a significant decrease in the area of post-calving and autumn ranges, but no changes in winter and spring ranges. Results supported Aboriginal TK that female caribou have shifted the autumn range farther from the treeline and moved into the forest later in the year. Analysis of climate variables found no trends at the spatio-temporal scale of the post-calving to autumn ranges. Working hypotheses to explain these patterns, which are not mutually exclusive, include reduced predation risk, increased use of core areas at lower population density, and greater utilization of areas of taiga where arboreal and ground lichen availability and accessibility are relatively higher than in the forest. This analysis demonstrates how including Aboriginal TK can lead to stronger connections and results, with potential to provide new and different insights for further investigations.

Key words: Aboriginal traditional knowledge; Bathurst caribou herd; climate; density dependence; predation risk; seasonal range attributes.

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Introduction

Barren-ground caribou are an important social and economic resource for people in the Northwest Territories and Nunavut. For many Aboriginal communities, the Bathurst herd is heavily relied on for food, and closely tied to a traditional lifestyle of hunting with strong cultural and spiritual values. Aboriginal traditional knowledge (TK) and science have recorded that barren-ground caribou display large fluctuations in abundance and distribution over decades (Ferguson *et al.*, 1998; Zalatan *et al.*, 2006; Adamczewski *et al.*, 2009; Festa-Bianchet *et al.*, 2011). From 1996 to 2015 the Bathurst caribou herd declined from approximately 349,000 to 20,000 animals.

Some studies have reported that fluctuations in the abundance of barren-ground caribou populations appear to be linked to changes in climatic patterns and winter range quality (Ferguson and Messier 2000; Weladji and Holand 2003; Gunn et al., 2009; Vors & Boyce, 2009). Long-term trends in weather patterns can influence seasonal range conditions for caribou by altering food availability and quality, and other environmental stressors such as the level of insect harassment (Russell et al., 1993; Weladji et al., 2003; Bergerud et al., 2008; Gunn et al., 2009; Witter et al., 2012). Although weather acts in a density independent manner on caribou populations, by modifying environmental conditions and caribou behaviour and distribution, climate may explain some variation in seasonal range attributes (Bergerud et al., 2008; Sharma et al., 2009).

In addition to changes in abundance, there is a large amount of spatial and temporal variability in the distribution of the Bathurst herd, which typically winters south of the treeline and calves in the barren-ground tundra near the Arctic coast. Relationships have been reported between the declines and increases in barren-ground caribou population sizes and the contraction and expansion of their ranges (Messier *et al.*, 1988; Bergerud 1996; Bergerud *et al.*, 2008). During the recent decline of the Bathurst herd, Aboriginal TK has also observed changes in the migratory movements and use of ranges, and later arrival of animals below the treeline (Jacobson *et al.*, 2011).

In this study we characterize seasonal range use of the Bathurst herd by measuring variation in several attributes such as the size, fidelity, and location of ranges, and the timing of autumn to winter range movements from 1996 to 2013; a period with a 90% decline in abundance. Further, we examine trends in summer weather variables in an attempt to explain the observed patterns in seasonal movements and distributions.

Material and Methods

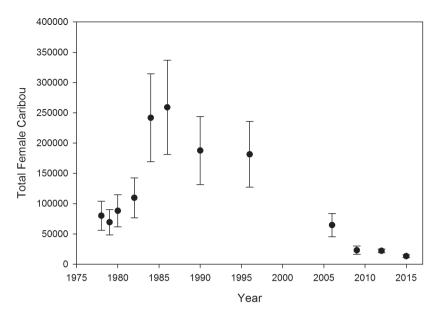
Temporal trends in Bathurst caribou population abundance and seasonal range attributes

Recently the Bathurst caribou herd has declined from an estimated 259,000 female caribou (472,000 total population) in 1986 to 182,000 females (349,000 total) in 1996 and then to 13,265 females (19,769 total) in 2015 (Gunn *et al.*, 1997; Boulanger and Gunn, 2007; Boulanger *et al.*, 2016; Figure 1).

Variation in seasonal range attributes was calculated from female Bathurst caribou fitted with Argos and Global Positioning System (GPS; hereafter satellite) radio-collars during January 1996 through October 2013 (courtesy of the Department of Environment and Natural Resources, Government of Northwest Territories). While radio-collared animals are all female and represent a low proportion of the herd, their movements have historically corresponded with estimates of caribou abundance from aerial surveys (Boulanger et al., 2004; Virgl et al., 2011). The Bathurst herd occupies an annual range spanning the barren-grounds and boreal forest in northcentral Canada (Figure 2). Seasonal ranges for the Bathurst caribou herd were defined using the following temporal boundaries (Johnson et al., 2005):

- Spring: 1 May 14 June
- Post-calving: 15 June– 31 August
- Autumn: 1 September 31 October
- Winter: 1 November 30 April

Seasonal ranges were delineated from satellite radio-collar data with a 95% kernel density (i.e., probability) estimate. From 1996 to 2013, Argos locations were acquired every 5 to 7 days, and from 2008 to 2013, GPS locations were acquired at hourly and daily intervals, depending



Note: Sources of values are as follows: 1977 to 1984 (Case *et al.*, 1996), 1986 to 2006 (Boulanger and Gunn 2007), 2009 (Adamczewski *et al.*, 2009), 2012 (Boulanger *et al.*, 2014), 2015 (Boulanger *et al.*, 2016); values from 1997 to 1980 based on a visual census, whereas values after 1980 based on a photograph method.

Figure 1. Temporal trend in number of females from the Bathurst caribou herd, 1976 to 2015.

on season. All location data from all years were pooled for each season and the multi-annual 95% kernel for each season was taken to represent the seasonal range.

For each of the four seasons, kernel density analyses were completed independently for each calendar year; for winter ranges, the data represent the pair of years comprising a given winter (e.g., winter 2004/2005 includes data from 1 November 2004 to 30 April 2005). Each 95% kernel for each season in each year was edited to remove small outlier polygons, leaving a single polygon for each season in each year. The following attributes were calculated in a geographic information system (GIS):

- Seasonal range polygon areas;
- Seasonal range polygon centroids (the central geographic latitude and longitude coordinates of the polygon);

- Area of overlap between each seasonal range polygon and the polygon for the same season in the previous year;
- The date after 1 September of each year of the first observation of each radio-collared caribou below the treeline;
- Distance from each autumn range polygon centroid to the nearest point on the treeline; and,
- Distance from each autumn range polygon centroid to the subsequent winter range polygon centroid.

Although the treeline may represent a transition zone between boreal and tundra environments, we used the treeline isocline of Timoney et al (1992), which represented a 50:50 ratio or forest to tundra units as a reference point to calculate variables.

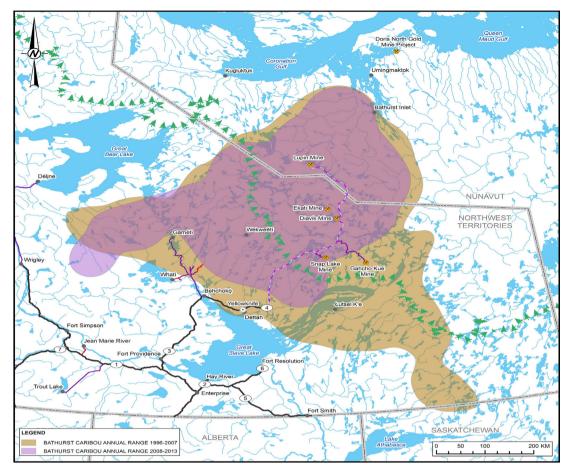


Figure 2. Annual range of Bathurst radio-collared females, 1996 to 2007 and 2008 to 2013, in northcentral Canada.

The calculation of year-to-year overlap of a given seasonal range (i.e., range fidelity) followed Faille *et al.* (2010): proportional overlap=Area₁₂/(Area₁+Area₂-Area₁₂). Where Area₁ is the range size in year 1, Area₂ is the range size in year 2, and Area₁₂ is the common area of the ranges for the two years. The proportional overlap ratio is > 1.00 when there is more area shared between the two annual ranges than the sum of the areas that are unique to either year.

To determine if there were trends in autumn migration patterns, three attributes were assessed: the distance between the autumn range centroid and the treeline; the mean date of arrival of collared caribou below the treeline on or after 1 September (restricted to animals that were observed below the treeline during winter); and the distance between autumn and subsequent winter range centroids for each year.

Trends through time in seasonal range size attributes were analyzed using ordinary least squares regression in NCSS (Hintze, 2009). For all statistical tests, a *P*-value > 0.05 was judged to be not significant.

Temporal trends in summer range weather

A retrospective set of environmental variables derived from the National Aeronautics and Space Administration's (NASA's) Modern Era Table 1. Number of active radio-collars on Bathurst herd caribou at the start of each season in each year based on telemetry location data. Also shown are annual

Range (m) Range (m) 83,873 84,952 90,914 132,045 109,355 106,273 117,992 106,556 117,992 106,556 117,992 106,556 111,704 73,182 92,412 97,560 111,704 73,182 83,315 73,429 100,038 81,996 74,768 57,204 100,927 124,654 99,811 97,918 94,176 78,586 51,830 68,966 51,830 56,831 75,853 56,831 75,853 56,831 74,350 36,124	Year	Year Spring Po	Post-calving	Autumn	Winter	Spring Bando (km²)	Post-calving	Autumn Bando (km ²)	Winter Bando (km²)
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Radio-collars were first deployed in March 1996, so there are fewer location data for the winter and annual ranges.

Retrospective-Analysis for Research and Applications (MERRA) (Russell *et al.*, 2013) for the Bathurst caribou summer range was acquired from CircumArctic Rangifer Monitoring and Assessment Network (CARMA). This data set includes a range of years from 1979 to 2009 and a number of climatic variables derived from NASA's Earth Observation satellites. The dataset provided by CARMA include a daily median value for each variable at the scale of the seasonal range. More recent data are not included as they were not available from CAR-MA at the time the study was completed.

Mean daily temperature (°C), total daily precipitation (mm), total seasonal precipitation (mm) and a Keetch Byram drought index (KBDI; Keetch and Bryam, 1968) were obtained from CARMA (Russell *et al.*, 2013) and analyzed for inter-annual patterns. These variables were assessed for the period of 15 June to 31 October, representing the post-calving to autumn range. All environmental variables were analyzed using general linear models in R (RDCT, 2014).

An information theoretic approach (Burnham & Anderson, 2002) was used to evaluate relative support for temporal patterns in the weather variables. The approach included evaluation of three candidate models for each climate variable. Models were scored using Akaike's Information Criteria (AIC). For each climate variable, the three models evaluated included year as a continuous variable to identify a temporal trend among years, year as a categorical variable to test for annual differences (i.e., variation among years but without a trend), and a null model that included only a y-intercept term, which predicts no change over time. The candidate set for total seasonal precipitation only included temporal trend and null models since annual values contain no within-year variation to estimate "year" effects.

Results

Temporal trends in seasonal ranges attributes

From 1996 to 2013 during a decline phase in the Bathurst herd, seasonal range sizes of radio-collared cows varied from 62,470 km² to 241,268 km² for spring, from 44,350 km² to 152,946 km² for post-calving, from 36,125 km² to 229,727 km² for autumn, and from 53,458 km² to 148,152 km² for winter (Table 1). The mean area and coefficient of variation (%CV) for each seasonal range were: spring $= 131,084 \text{ km}^2$ (40); post-calving = 93,676km² (28); autumn = 91,054 km² (48); winter = $79,565 \text{ km}^2$ (38). Based on the pooled location data, spring range size did not change significantly from 1996 to 2013 (Figure 3a, t = 0.56, P = 0.58). Post-calving range size decreased by 3,047 km² / year from 1996 to 2013 (Figure 3b, t = -3.09, *P* < 0.01). Autumn range size decreased 5,055 km² / year from 1996 to 2013 (Figure 3c, t = -3.12, P < 0.01). Winter range size did not change significantly from 1996/1997 to 2012/2013 (Figure 3d, t = -0.52, P = 0.61). Post-calving and autumn ranges of the Bathurst caribou herd contracted from 1996 to 2013.

There were no significant trends observed in range fidelity for any particular season from 1996 to 2013: spring range overlap (t = 1.08, P = 0.30); post-calving range overlap (t = 0.25, P = 0.80); autumn range overlap (t = -0.66, P= 0.52); and winter range overlap (t = 1.20, P= 0.25).

From 1996 to 2013, there was a significant increase in the distance between the centroid of the autumn range and the nearest location of the treeline (Figure 4a, t = 2.96, P < 0.01). The autumn ranges moved an average of 5.5 km farther from the treeline each year. For animals that overwintered below the treeline, the date of arrival at the treeline changed significantly (Figure 4b, t = 10.37, P < 0.001). Arrival below the treeline was delayed by an additional 3.7 days per year and since 2009 the mean date for

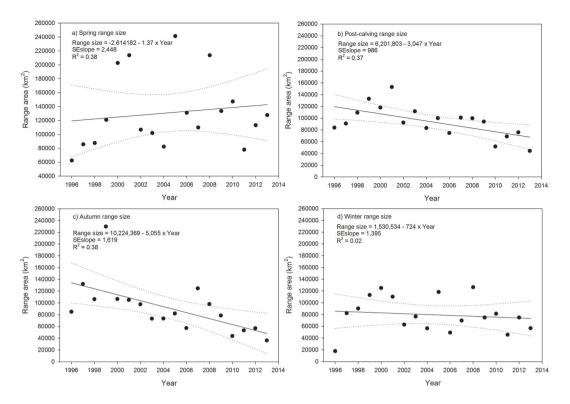


Figure 3. Trends (red lines) and 95% confidence intervals (blue lines) in 95% kernel range sizes (km²) of the Bathurst caribou herd for (a) spring, (b) post-calving, (c) autumn and (d) winter.

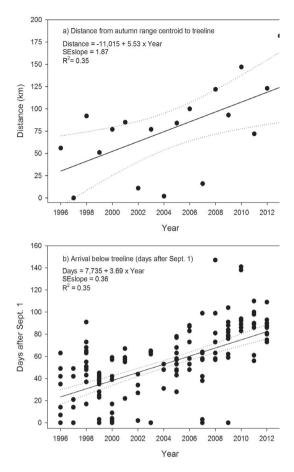
the arrival at the treeline implies that the rut for those animals occurred above the treeline. While animals were distributed farther north during autumn and moved below the treeline later in the year, there was no trend in the distance between autumn range centroids and the corresponding winter range centroids (t = 0.26, P = 0.80), as seasonal range centroids had tended to move northward over time in both seasons (Figures 5, 6).

Trends in summer range weather

For the CARMA climate variables analyzed, there was no support for temporal trends occurring at the broad spatio-temporal scales of the Bathurst post-calving to autumn (summer) range. The KBDI drought index data were best explained by a model of annual variation (ANOVA, F = 23.67, P < 0.01). The null model (y-intercept only) was the most parsimonious explanation for patterns of mean daily temperature (t = 33.97, P < 0.01), total daily precipitation (t = 33.80, P < 0.01), and total seasonal precipitation (t = 28.34, P < 0.01). Thus, there was no evidence of linear trends during the post-calving to autumn range for any of the weather variables considered.

Discussion

Using radio-collar data from female caribou comprising 17 winter seasons and 18 spring to autumn seasons, we were able to support several of the previous observations reported by Aboriginal TK and science. Our study found statistically significant decreases in the area



Note: circles denote values for each individual that spent at least part of each winter below the treeline.

Figure 4. Trend (red line) and 95% confidence interval (blue lines) in (a) distance (km) from the annual autumn range centroid to the treeline for the Bathurst caribou herd and (b) number of days after 1 September of each year that individual females from the Bathurst caribou herd arrived below the treeline.

of the post-calving and autumn ranges from 1996 to 2013; the data do not support significant changes in winter and spring range sizes. Female caribou also shifted their distribution farther from the treeline during autumn and moved into the forest later in the winter. We did not observe changes in the degree of interannual overlap for any given seasonal range

(range fidelity), which indicates that caribou were generally using similar broad-scale core areas from year-to-year, independent of changes in both population abundance and range size. The distance between centroids of the autumn range and subsequent winter range also did not statistically vary over the study period, despite females occupying an area farther from the treeline during the autumn period. While our results are derived from a low number of collared females relative to population size, their distribution over time generally corresponds to movements of the herd (Gunn et al., 2002). Had males been collared we would expect larger post-calving and autumn ranges because these are the seasons when males exhibit much less aggregation with females. Nonetheless, we would expect male-biased variation to be systematic through time and have little influence on the observed patterns and conclusions.

There are a number of working hypotheses, which are not mutually exclusive, that may explain the patterns observed in our study, by Aboriginal TK, and other investigations of caribou seasonal range attributes. Smaller postcalving to autumn ranges may be the result of density-dependent resource selection where the availability of preferred habitat increases with a reduction in the number of conspecifics (McLoughlin et al., 2006). During the decline phase of the Bathurst herd, an increasing proportion of female caribou likely had the ability to use the most suitable areas of habitat resources, which is predicted and measured as a decrease in range size. There are several limiting factors that can operate consecutively and/ or synergistically across different spatial and temporal scales, and varying population abundance to drive caribou habitat selection and demographic patterns (see reviews by Bergerud, 1996; Vors & Boyce, 2009; Tyler, 2010). Our analysis of weather variables detected no broadscale trends in temperature, drought index and precipitation; indices of forage condition or climate did not correspond to changes in caribou abundance or seasonal ranges. However, wolf predation and availability of quality food are expected to be key factors influencing caribou habitat selection, demography and correspondent variation in seasonal range attributes.

Similar to our results, Klaczek et al. (2015) also found: 1) the area of the Bathurst herd summer range decreased consistently from 1996 to 2012; and 2) a northward trend in the use of the summer and autumn ranges towards the calving ground (Figure 5). Furthermore, this change in caribou distribution was associated with an increase in the duration and distance of active wolf den sites from caribou (Klaczek et al., 2015). As the abundance of the herd and wolves declined, female caribou appeared to respond by spacing away farther and for a longer period of time from their primary predator on the tundra. Although wolf numbers and active dens decreased with caribou density, strong fidelity for quality den sites resulted in a lack of a behavioural response by wolves to the spatial and temporal changes in the movement and occurrence of caribou within the post-calving to autumn range (Klaczeck et al., 2015). Significant patterns in seasonal range attributes found in our study may also be the result of an adaptive response by caribou to avoid risky habitat in the late fall to winter period. The increase in distance between the autumn range and treeline, and later arrival on the winter range may decrease encounter rates with predators (and people that hunt caribou) in the forest. Remaining on the tundra longer could decrease predation risk from wolves inhabiting areas of forest farther below the treeline (Bergerud, 1996; Coulton et al., 2016).

The inability to detect a change in the distance between centroids of the autumn range and subsequent winter range, even though animals were farther from the treeline each autumn, is consistent with a recent study on winter range selection in the Bathurst herd.

Coulton et al. (2016) found that female caribou preferred to distribute their home ranges in the upper area of the winter range and above the northern extent of trees. During the recent decline, the distribution of caribou shifted so that the distance to the treeline increased in the autumn and decreased in the winter, resulting in no statistical change between centroids. As mentioned above, selection for the treeline may reduce predation risk, but could also be related to abundance and accessibility of ground and arboreal lichen. Wildfire is known by Aboriginal TK and science to influence caribou distribution (Thomas et al., 1998; Kendrick et al., 2005; Parlee et al., 2005; Joly et al., 2007; Jacobson, 2011; Anderson & Johnson, 2014). Coulton et al., (2016) analyzed fire frequency in the Bathurst winter range and found that forested areas approaching the treeline isocline have not been burned in the last 40 years. Shorter trees and lower tree density may reduce the likelihood and intensity of wildfire, which consumes arboreal lichens, a preferred forage of wintering Bathurst caribou (Barrier & Johnson, 2012). Thus, the parts of the forest approaching the geographic extent of trees may have an abundance of older arboreal lichen stores that are available to caribou for longer periods of time than more southerly areas that are burned at a higher frequency. Shorter trees and low tree density may also result in shallower and wind-swept snow, which may improve access to ground forage, mobility between foraging and resting areas, or vigilance and escape from predators (Bergerud, 1996; Bergerud et al., 2008). At low population size lichen resource patches near the treeline may sustain caribou; however, with increasing animal numbers these patches are expected to become limiting and range expansion should include more of the boreal forest to the south (Bergerud, 1996).

We have no strong supporting evidence to explain the failure to detect significant trends in the area of winter and spring ranges over

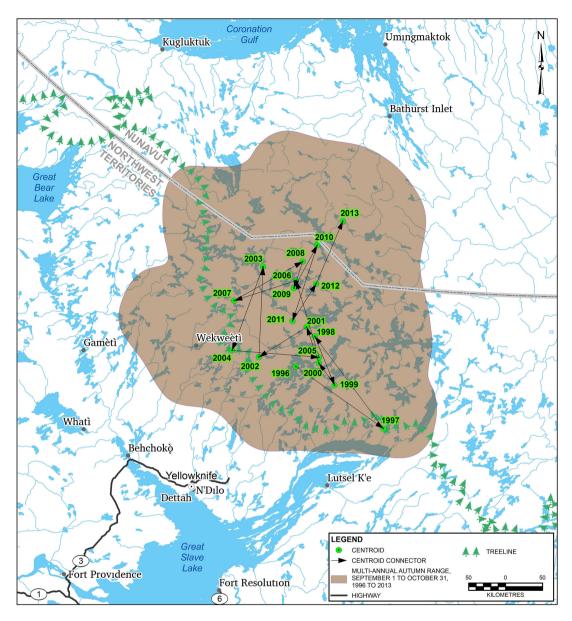


Figure 5. Movement of annual centroids of the autumn seasonal range of the Bathurst caribou herd.

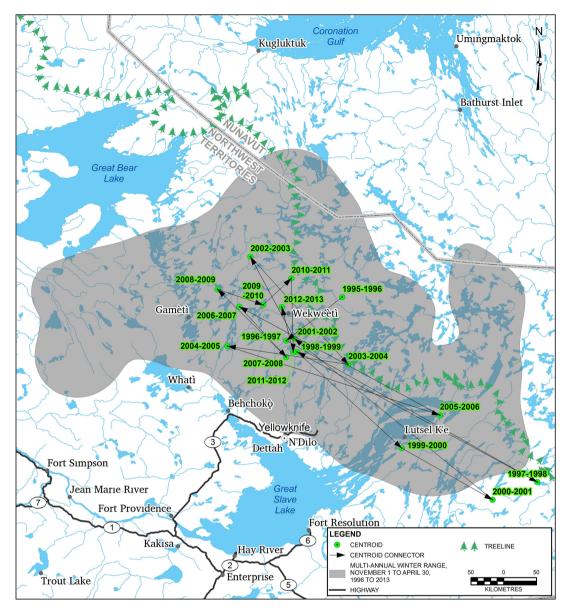


Figure 6. Movement of annual centroids of the winter seasonal range of the Bathurst caribou herd.

the study period. Why should post-calving and autumn ranges contract with decreasing caribou abundance but not the other seasonal ranges examined? Factors could be linked to study design and/or ecological processes. One explanation may be related to the type of collars and frequency of locations collected over the years. Briefly, for this study, Argos satellite radio-collars were in service from 1996 to 2013 and recorded locations approximately every five to seven days on seasonal ranges, with an error radius of 150 to 1,000 m. From 2008 to 2013, GPS satellite radio-collars were also deployed, which recorded locations about once per day with an error radius of 8 to 10 m, and more frequently (every 3 hours) during July and August (post-calving range) beginning in 2009. Detecting trends in the size of post-calving and autumn ranges may be less sensitive to radio-collar location frequency and error than winter and spring ranges. However, we believe that caribou life history and ecology likely explain more than radio-collar data with respect to the lack of covariation between population size and the area of winter and spring ranges. Even though female caribou have shown increased selection for habitat near the treeline, they remain widely distributed across the winter range from year-to-year (Figures 2 and 6). Wildfire and snow conditions on the winter range can alter forage availability and predation risk quickly and over large areas, with the effects from fire lasting for multiple decades (see Barrier & Johnson, 2012). Perhaps contraction of the winter range is constrained by these environmental selection pressures that operate over large spatial and temporal scales, particularly fire.

We had combined northern migration and calving ground ranges into one (spring) seasonal range to apply previously fitted resource selection functions (Johnson *et al.*, 2005) for a different study. The annual location and size of the Bathurst herd calving grounds are the

most predictable and smallest of the seasonal ranges (Gunn et al., 2002, 2013). Spring or northern migration routes are also largely influenced by the location of animals on the winter range, which as discussed above is expected to be highly variable within and among years (see also Gunn et al., 2013). Not observing a statistical change in spring range size may be a consequence of combining these two different but highly correlated life history events; future analyses of seasonal range attributes should separate northern migration from calving ground distributions. Still, variation in calving ground size may be also constrained by a set of interacting environmental and social factors, such as climate, forage availability and phenology, and time and synchrony of parturition. Thus, similar to the winter range, spring migration distribution and calving ground area can vary markedly from year-to-year, but not necessarily as a function of herd abundance.

Migratory behaviour in barren-ground caribou is an important life history strategy, likely to access the best quality food and space away from predators (Bergerud, 1996; Gunn et al., 2009; Avgar et al., 2014). Aboriginal TK and science understand that the availability of large amounts of space (habitat) is critical for resilience in caribou populations (Parlee et al., 2005; Gunn et al., 2009). Currently, space is not a limiting factor for the Bathurst herd during either extremes of the population cycle. Mineral development was occurring during the recent population decline; however, about 2% of habitat has been physically removed and 8% has been degraded (i.e., affected by modelled zones of influence or avoidance; Boulanger et al., 2012) by active mining in the post-calving to autumn ranges. There is no development on the calving grounds. Aboriginal TK and science indicate that caribou may be particularly sensitive to human developments during the calving and post-calving periods (Kendrick et al., 2005; Festa-Bianchet et al., 2011). There is much

concern for the population as it is continuing to decline, with both low adult female survival and low calf productivity (Boulanger et al., 2016). However, the variation in seasonal range attributes detected in this study demonstrates the adaptive capacity of caribou to an environment that is highly unpredictable. The northern shift in distribution and contraction of the post-calving and autumn ranges is predicted to result in a reduction in caribou encounter rates with mines, and/or in interactions that occur later during the autumn when cows and calves may be more resilient to disturbance. These changes in seasonal range attributes should have implications for environmental assessments, monitoring and mitigation programs, and land use and range management plans.

We believe that there is still enough space available for the Bathurst herd to be resilient to fluctuations in forage availability and quality, natural predators, insects and climate. Conversely, the effectiveness of spacing away to minimize encounter rates with hunters has likely decreased since the modernization of hunting technologies, which is largely unrelated to the amount of space available to caribou. The use of snowmobiles, all-terrain vehicles, aircraft, winter roads and rapid communications are expected to have altered hunting effort and harvest levels, but the relationship between these two variables is largely unknown (Gunn et al., 2011). Threats to caribou abundance and distribution can occur when hunting technologies adversely alter the relationship between harvest rate and animal abundance (Festa-Bianchet et al., 2011). Analyses of the recent rapid declines in the Bathurst herd have implicated overharvesting as a possible key factor (Adamczewski et al., 2009; Boulanger et al., 2011). Understanding the complex ecological relationships that influence caribou and the people that depend on them will require collaboration across cultural, geographic and disciplinary boundaries (Gunn et al., 2009). Involving and integrating Aboriginal communities and local knowledge in land use plans and research programs can lead to developing stronger connections and results, with the potential to provide new and different insights for further studies directed at the conservation of caribou.

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