Habitat indicators for migratory tundra caribou under a changing climate: calving ground and summer range

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Abstract: Fluctuations in migratory tundra caribou (*Rangifer tarandus*) abundance in the Arctic North America have long concerned the indigenous people, many of whom identify themselves as “caribou people”. A complex of factors (e.g., habitat, harvest, predators, diseases/parasites, extreme weather events, climate change, and pollution) interact to influence the abundance of caribou. To understand the interactions of those factors with caribou abundance especially in the face of a changing climate, we need to quantify these factors. In this study, we defined and developed habitat indicators for the calving ground and summer range of Bathurst caribou herd using field measurements, satellite earth observations, and climate records. On the calving ground, Bathurst caribou eat primarily lichens and switch to foliage of vascular plants as the plants green-up. We found increases in the availability of green foliage, an increase in forage quality associated with an earlier growing season, but a general decrease in lichen cover area in recent decades. On the summer range, climate warming increased forage availability, but also increased insect harassment and decreased forage quality. Further analyses that directly link habitat indicators with caribou body and health conditions as well as population changes are needed to assess the overall impact of climate change on caribou abundance as mediated through habitat.

Key words: Habitat indicator, migratory tundra caribou, remote sensing, climate change, Bathurst caribou herd, forage availability, forage quality, insect harassment

1 Introduction

Caribou (*Rangifer tarandus*) are the most important terrestrial subsistence resource for many indigenous people in Arctic North America (Klein 1989). Despite trends towards more cash economies (e.g., commercial harvesting, oil and mineral extraction, and tourism), subsistence-harvesting remains a central feature in aboriginal people's cultures and relationship with the land.

There are many factors, such as habitat harvest, predators, diseases/parasites, extreme weather events, and climate, whose interactions could affect the abundance of migratory tundra caribou (Klein et al. 2005). Although climate change is occurring in the Arctic at double the rate of the global average and is predicted to continue at an even faster rate (Kattsov et al. 2005), the overall impact of climate change on the populations of North America's barren-ground caribou herds is less clear. Indeed, the Intergovernmental Panel on Climate Change's 3rd Assessment Report stated that "the overall impact of climatic warming on the population dynamics of reindeer and caribou is controversial" (IPCC 2001). One view is that there may be declines in caribou and muskoxen, particularly if the climate becomes more variable (Brotton and Wall 1997, Gunn and Skogland 1997). An alternative view is that because caribou are generalist feeders and appear to be highly resilient, they should be able to tolerate climate change (Callaghan et al. 1998).

To understand the relative importance of trends in environmental factors on caribou abundance and to quantify their integrated impacts under a changing climate, we need to first develop comprehensive datasets for these factors and relate them to indicators of caribou productivity. As a first step, we will develop habitat indicators for the Bathurst caribou herd. The Bathurst herd is a major Canadian migratory tundra caribou herd and its abundance has been monitored since 1970 (http://www.enr.gov.nt.ca/_live/pages/wpPages/caribou_information.aspx). Every spring cows and juveniles from the Bathurst herd migrate from the forested winter ranges in Northwest Territories and northern Saskatchewan northwest to the calving grounds on the tundra in Nunavut. After calving, the cows and calves disperse southward across their tundra summer range. Annual fidelity to calving and summer ranges is relatively high (Fig. 1). Ten northern communities (i.e., Behchokö, Cambridge Bay, Dettah, Gamètì, Kugluktuk, Lutsel K'e, N'Dilo, Wekweètì, Whatì, and Yellowknife) are within or near the herd's ranges and harvest the herd. The objectives of this study are: (1) to define a comprehensive set of habitat indicators: calving ground forage availability and forage quality; summer range forage availability, forage quality, and insect harassment severity; winter range forage availability, forage quality, and forage accessibility; and pre-calving migration snow condition; (2) to develop historical datasets of these habitat indicators for the Bathurst caribou herd using field measurements, satellite remote sensing imagery, and climate records; and (3) to analyze the relationships between climate variables and these habitat indicators for the Bathurst caribou herd.

To maintain comprehensiveness while being as succinct as possible, we report the results of this study in two parts. In this paper, we report results for calving ground and summer range, while results for winter and pre-calving migration ranges will be reported in a companion paper (Chen et al. 2009a).

2 Definition, calculation method, and data sources

2.1. Calving ground forage availability indicator

We had access to a dataset giving daily or 5-day locations for caribou cows fitted with satellite-collars. The movements of the satellite collared cows during 1996-2003 reveal that the peak calving was June 2-12. On the calving ground, caribou mainly forage on lichens, switching to foliage of vascular plants as buds unfurl and green-up is underway (Griffith et al. 2001). In years when green-up is late, lichens remain important in the caribou diet. Therefore, we evaluate both the green foliage and lichen components of the calving ground forage availability indicator for three specific periods: pre-calving period (May 20-30), peak calving period (June 1-10), and post-calving period (June 11-30).

Annual estimates of green foliage biomass during pre-calving, peak calving, and post-calving periods can be derived from remote sensing data, but not lichen biomass. At present, we are only able to estimate areas with lichen dominant cover every few years using Landsat time series. The estimates of green foliage biomass of vascular plants on the calving ground are calculated using the following up-scaling approach.

(a) Relationships between field measured foliage biomass and Landsat-based biomass indices were assessed to select the best fitting linear relationship. Possible Landsat-based biomass indices (Tucker 1979; Huete 1988; Lloyd 1990; Goward et al. 1991; Myneni et al. 1997; Brown et al. 2000) include the Normalized Differential Vegetation Index NDVI = $(\rho_{\mathrm{NIR}}-\rho_{\mathrm{red}})/(\rho_{\mathrm{NIR}}+\rho_{\mathrm{red}})$, the Short Wave Vegetation Index

SWVI = $\rho_{\mathrm{MIR}}/\rho_{\mathrm{NIR}}$, the Simple Ratio SR = $\rho_{\mathrm{NIR}}/\rho_{\mathrm{red}}$, the Reduced Simple Ratio RSR = $\rho_{\mathrm{NIR}}/\rho_{\mathrm{red}}\times(\rho_{\mathrm{MIR,max}}-\rho_{\mathrm{MIR}})/(\rho_{\mathrm{MIR,max}}-\rho_{\mathrm{MIR,min}})$, and the Soil Adjusted Vegetation Index SAVI = $(\rho_{\mathrm{NIR}}-\rho_{\mathrm{red}})(1+\mathrm{L})/(\rho_{\mathrm{NIR}}+\rho_{\mathrm{red}}+L)$, where ρ_{red}, ρ_{NIR}, ρ_{MIR} are, respectively, the reflectance values of Landsat TM/ETM spectral channels 3 (red; 630–690 µm), 4 (Near Infrared; 750–900 µm), and 5 (mid-Infrared; 1550–1750 µm), and L is a constant, set to 1 in this study. The best relationship is then selected on the basis of values of R^2, standard error, F, and P, as well as linearity. A linear relationship is preferable because a non-linear relationship is often associated with the saturation problem in remote sensing indices, and more prone to error when applying to areas outside the field measurements.

(b) A 30-m ground resolution baseline map of foliage biomass over the summer range of the Bathurst caribou herd is then developed by applying the best relationship to a Landsat mosaic. As most Landsat scenes used in the study were acquired under different atmospheric conditions and at different times, radiometric normalization is needed to generate a consistent mosaic. Normalization was achieved in a recursive manner, in which a normalized scene becomes the reference for the subsequent overlapping scene entering into the mosaic. In order to minimize error propagation across the mosaic (Guindon, 1997), the centre scene was chosen as the initial reference for the mosaic. Radiometric normalization equations were developed based on inter-scene overlap using a Scattergram Controlled Regression method (Elvidge et al. 1995; Yuan and Elvidge 1996).

(c) At 30-m ground spatial resolution, the Landsat imagery can only provide cloud-free coverage over the entire summer range once every several years, and usually these cloud-free images are acquired at different periods during the growing season.

Consequently, Landsat imagery cannot directly provide the mean foliage biomass during June 11 and September 30. On the other hand, coarse-resolution satellite remote sensing data (e.g., Advanced Very High Resolution Radiometer or AVHRR at 1-km ground resolution) can provide largely cloud-free coverage over the entire Bathurst caribou habitat through a 10-day composite (Latifovic et al. 2005). To take advantage of the well calibrated historical AVHRR 10-day composite data, we develop the relationship between foliage biomass and AVHRR-based vegetation index at 1 km spatial resolution. Here the value of foliage biomass is calculated by aggregating the 30-m pixel value from the Landsat-based baseline map to the 1-km ground resolution, and we use the same vegetation index that gives the best relationship between foliage biomass and Landsat-based indices. (d) Applying the relationship between foliage biomass and an AVHRR-based vegetation index to the well calibrated historical AVHRR 10-day composite data, we calculate foliage biomass for each 1-km×1-km pixel every 10 days over the summer range from 1985 to 2006. Despite of the fact that 10-day composite uses only the maximum vegetation index value in a 10-day period, some pixels may still have abnormally low vegetation index value because of sub-pixel contamination by clouds. We replace abnormally low vegetation index values by the average of values in two adjacent 10-day periods. The values of foliage biomass during May 21-30, June 1-10, and June 11-30 on the calving ground of the Bathurst caribou herd are then calculated using the corrected 10-day AVHRR-based foliage biomass data.

Remote sensing change detection can be used to derive the changes in land cover area that has dominant lichen cover from time series of Landsat imagery (Koeln and Bissonnette 2000; Olthof and Fraser 2007). Estimation of lichen biomass using this approach, however, can result in substantial error for the following reasons. First, for the same land cover category of dominant lichen cover, the actual lichen percent cover can be 5% or 95%. Secondly, the conversion of lichen percent cover into lichen biomass, without any knowledge of the mean height of lichen concerned, may also introduce significant error because some lichen species may have a height of 10 cm whereas others less than 1 mm (Chen et al. 2009c). Furthermore, because of limited spatial coverage and cloud contamination, we generally only have a whole coverage over the calving ground every few years, and therefore cannot estimate lichen biomass annually as required by equation (2). Considering all these factors, we will not attempt to develop estimates of lichen biomass annually. Instead, we will use the Landsat time series circa 1990 and 2000 to provide compare the extent of lichen dominated areas, and assign an estimation of lichen biomass to be used in equation 2, on the basis of field measurements and the Landsat-based dominant lichen land cover area. We determine the dominant lichen cover area in the calving ground circa 1990 and circa 2000, using Landsat TM/ETM+ images and the method described by Olthof and Fraser (2007) and Fraser et al. (2009). Temporal signature extension is used to generate hard classifications with 6 aggregated classes and post-classification comparison is the performed.

2.2 Calving ground forage quality indicator

The green foliage of vascular plants can provide carbohydrate, protein, and other nutrients, and thus constitute a more favorable diet than lichens that provide only easily digested carbohydrates. The measurements by Griffith et al. (2001) on the calving ground of the Bathurst caribou herd during 1998 and 1999 show that the nitrogen concentration of green foliage range typically 1.3-4.2%, while that of lichen range 0.3-0.5%. Therefore, an increase in green foliage biomass during the pre-calving, peak calving, and post-calving periods means improvement in calving ground forage quality.

2.3 Summer range forage availability indicator

Summer is when caribou allocate their body reserves and nutrient intake to their survival and the growth and survival of their young (Russell et al. 1993). For the Bathurst caribou herd, we defined summer foraging from the end of calving until early September, prior to fall migration. We used the locations of satellite collared cows to map the summer range (Environment and Natural Resources, Government of Northwest Territories, unpublished data). As we have foliage biomass estimates every 10 days during the summer months from satellite imagery, we select the average value of vascular foliage biomass from June 11 to September 30 as a forage availability indicator on the summer range for the Bathurst caribou herd $I_{fa,sr}$.

The mean foliage biomass during June 11-September 30 over the summer range of the Bathurst caribou herd is calculated using the 10-day AVHRR-based foliage biomass data, developed using the same up-scaling procedure as described in 2.1.

2.4 Summer range forage quality indicator

Even small variations in forage quality in the summer range can strongly influence caribou body growth and development through a multiplier effect (White 1983). Leaf N concentration and forage digestibility are two commonly used measures of forage quality (Griffith et al. 2001; Finstad 2008; McArt et al. 2009). Without adequate measures of forage digestibility and because forage digestibility is positively correlated with leaf N concentration when the latter is < 3% (Finstad 2008; McArt et al. 2009), we use only leaf N concentration in defining the forage quality indicator in the summer range.

Measurements on reindeer ranges of the Seward Peninsula, Alaska, show seasonal patterns in leaf N concentration (Finstad 2008): peaking at or near the beginning of the growing season with leaf N concentration between 2 and 6%, rapidly decreasing toward the middle of the growing season when vascular plant foliage biomass peaks, stabilizing around 1-3%, and then decreasing further near the end of growing season (Fig. 2). The review by Johnstone et al (2002) showed a similar pattern of N concentration in key caribou forage groups across North America. Nitrogen concentrations in deciduous shrubs and forbs showed a pattern of peak nitrogen at the start of the growing season and a subsequent decline to low levels at the end of the growing season. In cottongrass flowers, N concentrations also declined through the growing season, although less dramatically than in deciduous shrubs or forbs. Among graminoids, N concentrations peak approximately 15-30 days after the start of the growing season (usually June 1 – June 15), and then declined over the rest of the summer. Nitrogen concentrations in evergreen shrubs showed no clear seasonal pattern (Johnstone et al. 2002). The decrease in leaf N concentration near the end of growing season was due to N resorption before senescence (van Heerwaarden et al. 2003). The decrease in leaf N concentration from the beginning to the middle of growing season was N dilution caused by the increase in foliage biomass significantly exceeding the supply from root N uptake and transfer of N resorbed in the previous year from storage organs to leaves. Because it is relatively less variable and is positively correlated with leaf N concentration at senescence, the leaf N concentration at peak foliage biomass is a good representation of forage quality during the entire growing season and was thus selected as the forage quality indicator in the summer range.

We quantify the summer range forage quality indicator using the peak foliage biomass obtained from the 10-day AVHRR-based foliage biomass data and the N allocated to foliage biomass. The N allocated to foliage is determined using a fully coupled carbon-nitrogen cycle model (Chen et al. 2000), calibrated with two growing seasons' leaf N concentration measurements on reindeer ranges of the Seward Peninsula (Finstad 2008), and our measurements of C/N ratio during 2004-2008 over Canada's arctic tundra ecosystems (unpublished data). The processes considered in the N cycle include N mineralization, N deposition, N fixation, N resorption, and N partition. The measurements of C/N ratio in 2004-08 over Canada's Arctic tundra ecosystems were used to set the value of leaf N concentration during 2004-06 at the level 1.6%.

To better account for the effect of changes in soil temperature on N mineralization, we use a modified Arrhenius-type equation for the abiotic decomposition factor Λ (Lloyd and Taylor 1994):

$$\Lambda = e^{\left(\frac{308.56}{T_s(0)+46.02} - \frac{308.56}{T_s+46.02}\right)} \tag{1}$$

where T_s is soil temperature at 5 cm depth, and $T_S(0)$ is the long-term mean soil temperature at 5 cm depth. In this study, we estimated the soil temperature using a northern ecosystem soil temperature model (Zhang et al. 2003), which considers the effects of climate, vegetation, organic layer, snow, and geothermal flux. Using acetylene reduction techniques, Steward and Coxson of University of Northern British Columbia (unpublished data) measured N fixation rates across ecosystems at Darling Lake (65^{o}52N, 111^{o}34W) over the growing seasons in 2007 and 2008. These measurement sites are within the summer range of the Bathurst caribou habitat. The landscape average value of N fixation rates was found to be 0.115 g N m^{-2} $year^{-1}$, quantified along 10 1-km transects, which include all 4 types of ecosystems on the landscape: xerophytic herb tundra, heath-mat/heath-lichen tundra, birch hummock, and wet sedge/dry sedge meadow. In this study, we followed the same equations for N fixation as described in Chen et al. (2000) and used the mean value to constrain the annual N fixation rates over the Bathurst caribou summer range in recent years. We also use the same equations for N deposition, which are based on the spatial distribution of ground measurements of N deposition (Ro et al. 1995) as described in Chen et al. (2000).

Nitrogen resorption from senescing leaves represents a large fraction of available N (van Heerwaarden et al. 2003; Yuan et al. 2005; Finstad 2008). van Heerwaarden et al. (2003) investigated six sub-arctic bog species in northern Sweden and found a general trend of decreased N re-sorption ratio occurred in response to increased N supply. Because of the similarities between this study and that of Finstad (2008): both investigate non-manipulative, ambient changes in leaf N concentration, and study areas are used as reindeer/caribou summer range, we use the two full growing seasons' measurements of leaf N concentration by Finstad (2008) to quantify N resorption ratio, $R_{N,resorp}$ (%), given by (Fig. 3):

$$R_{N,resorp} = 109.3 - 29.9 N_{pb,sr}, \text{ with } R^2 = 0.73, F = 10.7, P = 0.03, \tag{2}$$

where $N_{pb,sr}$ is the leaf N concentration at peak foliage biomass in the summer range (in units of %), given by the value at the middle of summer shown in Fig. 2.

For arctic ecosystems, up to 75% of the total available N is concentrated in leaves (Chapin et al. 1987). The percentage decreases as leaf N concentration increases. As a result, we estimated the N partition ratio to leaves, $R_{N,partition}$ (%) so follows:

$$R_{N,partition} = 40 + \frac{0.35}{N_{pb,sr}}. \tag{3}$$

Because the index of insect abundance is based on wind speed and temperature, its calculation is straightforward following its definition.

2.5 Summer range insect harassment indicator

Caribou respond to oestrid flies (nasal bot flies, *Cephenemyia trompe* and warble flies, *Hypoderma tarandi*) by aggregating together or panic-stricken running. Time spent foraging is reduced and there is a metabolic cost to the subsequent parasitic larval infestation (White et al. 1975; Walsh et al. 1992, Pollard et al. 1996). We have no direct measures of insect harassment for the Bathurst herd, instead we use an index developed by Russell et al (1993) of insect abundance based on wind speed (m s^{-1}) and temperature (^{o}C). The model was derived by quantifying overt reactions of caribou to different levels of oestrid harassment. A separate index was derived for mosquitoes by sampling mosquitoes (*Culicidae*) at different wind speeds and temperatures. These indices ranged from 0 to 1, with 1 being the highest.

2.6 Data sources

Foliage biomass was measured at 27 tundra sites during July 18-27, 2005 in and around the Bathurst caribou habitat. At each site, we sampled five 1-m × 1-m plots (i.e., four plots in four directions at 30 m apart and a random plot) (Chen et al. 2009b). At each plot, all plants were harvested, sorted into dead and live, different species, leaves, stem, and roots, and then oven-dried and weighed.

To develop a Landsat-based baseline foliage biomass map over the calving ground and the summer range and of the Bathurst caribou herd, we used 32 cloud-free circa 2000 Landsat scenes.

The 1-km AVHRR data used in this study for quantifying foliage biomass every 10-day during 1985-2006 were processed with an improved methodology for georeferencing and compositing (Latifovic et al. 2005), correction for viewing and illumination conditions (Latifovic et al. 2003), cloud screening (Khlopenkov and Trishchenko, 2006), and atmospheric correction. Atmospheric correction was performed using the simplified method for atmospheric correction. Inputs included water vapour and pressure taken from the North America Reanalysis Project (http://www.emc.ncep.noaa.gov/mmb/rreanl), ozone from the Total Ozone Mapping Spectrometer (http://toms.gsfc.nasa.gov/ozone/ozone_v8.html), and stratospheric aerosol optical depth at 550 nm from the Goddard Institute for Space Studies (http://data.giss.nasa.gov/modelforce/strataer).

The growing season start date, end date, and length on the calving ground and the summer range during 1985 and 2006 was determined using the AVHRR-derived foliage biomass, with the start date set to be the day when foliage biomass first becomes > 0 and ends as foliage biomass is reduced to 0. We acknowledge that the existence of snow and evergreen shrub may result in errors in the estimates of start date, end date, and length of growing season. For example, the existence of snow in the spring could result in the estimated start date to be later than the actual date, whereas the existence of evergreen shrub would caused an error in the opposite direction. The opposite effects of snow and evergreen shrub on the estimates of start and end dates of growing season suggest that they can be partially cancelled by each other, and so their overall impact on growing season estimates may be small. Nevertheless, further investigations are needed to quantify the actual magnitudes of their effects.

For estimating dominant lichen cover area on the calving ground in 2000, a total of 6 Landsat-7/ETM+ scenes during 1999 and 2002 were used. An additional 5 nearly clear-sky circa 1990 Landsat-5 TM scenes were used to detect change in dominant lichen cover area on the calving ground between 1990 and 2000. Most of these images were acquired in July and August supplemented by some June or September scenes. The same mosaic procedure was applied to create the winter range Landsat imagery coverage.

Climate data for investigating relationships with habitat indicators were from the Canadian Daily Climate Database (ftp://arcdm20.tor.ec.gc.ca/pub/dist/CDCD). For the summer range and calving ground of the Bathurst caribou herd, station T23026HN

(Lupin at 65°46'N, 111°15'W) has the longest climate record: daily maximum air temperature, daily minimum air temperature, and daily mean air temperature since January 1, 1982. We used the temperature data from this station to represent conditions on the summer range and the calving ground.

3 Results

3.1 Calving ground forage availability indicator and relationship with climate

Among Landsat-based vegetation indices investigated, the Simple Ratio (SR) was found to fit the foliage biomass measurements best over the Bathurst caribou habitat, with $R^2 = 0.86$, standard error = 26.2 g m^{-2}, and $P = 2.6\times10^{-12}$ for a sample size $n = 27$ (Fig. 4). In comparison, the NDVI relationship has $R^2 = 0.74$ and standard error = 36.4 g m^{-2}, the SWVI relationship has $R^2 = 0.66$ and standard error = 41.3 g m^{-2}, the RSR relationship has $R^2 = 0.69$ and standard error = 39.7 g m^{-2}, and the SAVI relationship has $R^2 = 0.71$ and standard error = 38.1 g m^{-2}.

Applying this SR relationship to the Landsat mosaic, we developed the circa 2000 mid-summer baseline foliage biomass map at 30-m resolution over the Bathurst caribou habitat (Fig. 5). Since this SR relationship was developed using only measurements at non-treed sites, foliage biomass for treed forest areas was not estimated. We masked out the treed forest areas using land cover map developed using same Landsat-7/ETM+ mosaic. From this map, we found that the foliage biomass over this calving ground was significantly lower than that in the summer range.

By aggregating the 30-m foliage biomass pixel values to 1-km resolution, we had more than 300,000 data pairs of 1-km foliage biomass and AVHRR-based Simple Ratio (SR = $\rho_{\mathrm{NIR}}/\rho_{\mathrm{red}}$, where ρ_{red} and ρ_{NIR} are reflectance values of AVHRR spectral channels 1 (red; 580–680 μm) and 2 (Near Infrared; 725–1100 μm). We randomly selected 833 data pairs in the summer range and the calving ground, and developed the relationship between foliage biomass at 1-km resolution and AVHRR-based SR, with $y = 25.482x - 36.402$, $R^2 = 0.68$, standard error = 10.8 g m^{-2}, $F = 1730$, and $P = 2.5\times10^{-205}$. As shown in Fig. 6, the AVHRR-based SR relationship remained linear and statistically significant. The slopes and intercept of the Landsat-based and AVHRR-based SR-foliage biomass relationships are quite different because of differences on spectral band centers, band widths, and spatial resolutions. Directly applying Landsat-based relationships to AVHRR or other coarse resolution remote sensing data is thus not proper. Instead, one should follow a proper up-scaling approach corresponding to the size of field measurement site and spatial resolutions of remote sensing data.

Applying this AVHRR-based relationship and correction procedure for the contamination by clouds, we calculated the values of pre-calving (May 21-31), peak calving (June 1-10), and post-calving (June 11-30) foliage biomass on the calving ground of the Bathurst caribou herd during 1985-2006 (Fig. 7). Fig. 7 shows that during the pre-calving period of May 21-31, there was essentially no green foliage biomass on the calving ground. Out of the 22 years investigated during 1985-2006, only 5 years had green foliage biomass larger than zero in the peak calving period. One of the 5 years was 1998, in which the green foliage biomass during June 1-10 was estimated to be 10 g m^{-2} during the perk calving period, while in the follow year 1999 the green foliage biomass was 0 g m^{-2}. This finding is consistent with the field survey results by Griffith et al. (2001) in 1998 and 1999. The green foliage availability was further improved during the post-calving period of June 11-30, with green foliage biomass ranging from 2-37 g m^{-2} during 1985-2006. There were no temporal trends for the pre-calving and the peak calving foliage biomass. For the post-calving foliage biomass, there was a 55% increase, from 9.1 g m^{-2} in 1985 to 16.4 g m^{-2} in 2006. The temporal trend was, however, not statistically significant because of substantial inter-annual variations in the foliage biomass, with $R^2 = 0.07$, $F = 1.5$, $P = 0.24$, and $n = 22$.

Although the temporal trend of a caribou habitat indicator can be informative, it is not a causal-effect relationship. When there are large inter-annual variations, the slope or even the direction of the trend may change substantially dependent on the starting and end dates and durations. A more useful way to understand the change of a habitat indicator is to relate it to key driving factors. In the Arctic, climate change has been recognized as the most dominant factor influencing the changes in ecosystems, given that land use change over Canada’s North has been found to be minimal (Chen et al. 2009d). Therefore, we further investigated the relationships between habitat indicator and climate variables. As shown in Fig. 8, the relationship between the calving ground green foliage biomass and the start date of growing season in the calving ground of the Bathurst caribou herd is statistically significant for both the peak calving and post-calving periods. The later the start date, the lower the biomass. This result indicates an effect of climate change on calving ground green foliage biomass.

In addition to vascular green foliage, caribou use lichen on the calving ground (Griffith et al 2001). As shown in Fig. 9, the area with dominant lichen cover decreased significantly from 1990 to 2000 on the calving ground, from 44% to 22% of the total calving ground area. Kennedy et al. (2001), using repeated ground observations, found that lichen cover decreased from 17% to 6% within cottongrass tussocks ecosystems, and 10% to 6% in Dryas-vetch-Arctic willow ecosystems in northern Yukon during 1985 and 2000. Similar results have been reported over Alaska by other remote sensing studies (Jandt et al. 2008). A meta-analysis of lichen responses to warming experiments across the Arctic (i.e., the International Tundra Experiment ITEX) showed that lichen biomass decreased as vascular plant biomass increased following warming and across the Arctic by warming (Cornelissen et al. 2001). These results suggest a possible declining trend of lichen cover on the tundra under a warming climate.

3.2 Calving ground forage quality indicator and relationship with climate

Given that green foliage has a much higher N concentration than lichens, the increases in green foliage biomass during the peak calving and the post-calving periods on the calving ground in earlier spring years under a warming climate would mean also an increase in forage quality on the calving ground. However, since there were no significant temporal trends in the pre-calving, peak calving, and post-calving foliage biomass during 1985-2006, there was no significant temporal trend for the calving ground forage quality during the same period.

3.3 Summer range forage availability indicator

Applying the AVHRR-based relationship and the correction procedure for eliminating contamination by clouds, we calculated the mean June 11-September 30 foliage biomass in the summer range of the Bathurst caribou herd (Fig. 10). Between 1985 and 2006, a significant positive trend was observed in the summer range forage availability indicator. In addition to the trend, we also noticed that there were large inter-annual variations, with the standard deviation divided by corresponding mean value during 1985-2006 equaling 30%.

Although there was no ground measurement of inter-annual changes in foliage biomass within the Bathurst caribou summer range that would allow us to directly validate these results, foliage biomass was repeatedly measured in a moist acidic tussock tundra experimental site near Toolik Lake North Slope, Alaska (Shaver and Chapin III 1991; Mack et al. 2004). While the focus of their experiments was on ecosystem responses to various manipulative treatments, the information on the control plots is comparable to this study. The control plots at the site were set up in 1981 and foliage biomass of each vascular plant species was measured on July 31 in 1982, July 30 in 1993, July 26 in 1984, July 21 in 1989, July 31 in 1995, and July 30 in 2000. The plot foliage biomass was then calculated by summing the foliage biomass of all vascular plant species and averaged to obtain the foliage biomass at the site. From 1989 to 2000, the foliage biomass at the Toolik site increased from 121 to 203 g m^{-2} or by 68%, compared with the 33% increase of the Bathurst caribou summer range forage availability during the same period as determined from this study. As for the inter-annual variations, we calculated the standard deviation divided by corresponding mean value during 1982-2000 at the site =

20%, also comparable with that of mean June 11-September 30 foliage biomass in the Bathurst caribou summer range.

The relationship between the summer range forage availability indicator and the growing season length in the summer range of the Bathurst caribou herd, is statistically significant ($R^2 = 0.34$, $F = 10.1$, and $P = 4.6\times10^{-3}$), for 1985-2006 (Fig. 11).

3.4 Summer range forage quality indicator

The components of the N cycle in the summer range of the Bathurst caribou herd is shown in Fig. 12. As expected, N mineralization was the largest contributor to the total available N, followed by N resorbed, while N fixation and N deposition were relatively small. Overall, the available N showed a significant increase trend from 1985-2006. Using these N cycle estimates and the annual peak foliage biomass, we calculated the values of the leaf N concentration at peak foliage biomass in the summer range, $N_{pb,sr}$. Fig. 13 shows a decline but not significant trend in $N_{pb,sr}$ during 1985 and 2006. The standard deviation in $N_{pb,sr}$ was 0.33% with a mean value of 1.67% during 1985 and 2006, which gives an average inter-annual variation of 20%. As a comparison, the measurements of leaf N concentration on ranges of the Seward Peninsula, Alaska, during two full growing seasons in 1996 and 1997 gave an inter-annual variation in mid-summer leaf N concentration at 9% for sedges, 25% for forbs, and 8% for willows (Fig. 2).

Because $N_{pb,sr}$ is not a direct observation, we tested its sensitivity to uncertainties in N cycling processes. Besides the baseline Arrhenius method, we used two alternative methods to calculate N mineralization, the largest component in N cycle. The "$Q_{10} = 2$"

method calculates N mineralization using power function with Q_{10} = 2 while keeping other processes at the baseline conditions (Lloyd and Taylor 1994). The same can be said for the "Q_{10} = 3" method except we used Q_{10} = 3. As shown in Fig. 15, most of the inter-annual variations in $N_{pb,sr}$ were related from large variations in the peak foliage biomass and its associated diluting effect. The differences in $N_{pb,sr}$ caused by different estimation methods were much smaller.

Some arctic plants are reported to be capable of direct up-take of organic N (Atkin et al. 1993), which is difficult to quantify and so not included in this study. Yet, the fact that arctic tundra ecosystems are highly N limited (Chapin et al. 1993) suggests that the amount of N uptake is likely to be very small and thus inadequate to make up the gap between N demand and supply.

In contrast to the temporal trend in $N_{pb,sr}$, we found $N_{pb,sr}$ was negatively correlated with growing season length during 1985-2006, with $R^2 = 0.16$, $F = 3.6$, $P = 0.07$, and $n = 22$ (Fig. 14). Other studies indicated similar results. For example, Körner (2003) reported a negative relationship between growing season length and leaf N concentration for plants from tropical to arctic. In addition to the effect of increasing temperature, the increase in atmospheric CO_2 concentration may also result in decrease in summer range forage quality. For example, experiments conducted on reindeer forage species in Finland have shown that elevated CO_2 reduces the N concentration of leaves of dark-leaved willow (*S. myrsinifolia* Salib.) and silver birch (*B. pendula* Roth.) (Veteli et al. 2002, Rey and Jarves 1988, Riikonen et al. 2005). These changes are most probably due to the dilution effect caused by carbon accumulation, as is the case for the increasing temperature. Whatever the cause, leaf N concentration can vary between ranges with significant consequences for the availability of digestible N (McArt et al. 2009).

3.5 Summer range insect harassment indicator

Applying the insect harassment index of Russell et al (1993) for oestrids to the Bathurst herd summer range, we calculated insect harassment indicator on the summer range during 1957 and 2006. The late 1970's and early 1980's marked the beginning of a global temperature increase (Jones and Moberg, 2003). On basis of this, the period of 1957 to 2005 was divided into 1957-1981 and 1982-2005. The results show that the number of "high" osterid ratings was significantly greater in the 1982-2005 grouping than during the earlier time period ($\chi^2 = 18.7$, $df = 1$, $p < 0.01$), suggesting a possible increase in insect harassment severity under a warming climate. Details of the insect harassment indicator will be reported in another paper.

4 Conclusions

As change comes to the north from trends in climate, expanded industrial development and other human presence, and with shifts in harvesting technology, tracking trends in habitat quality and quantity is essential to monitor how caribou are coping with change and how they may respond under future global change scenarios. In this study we have focused on the habitat indicators for the Bathurst herd, which has been declining since the mid 1980's. To monitor habitats over the large home range of this herd, we selected habitat indictors that can be derived from remote sensing products and climate records.

We defined indicators for habitat quantity and quality to reveal trends in calving ground and summer range forage availability and forage quality for the Bathurst herd of migratory tundra caribou. We also found relationships between the indicators and climatic variables. The trends since the mid-1980s for calving and summer ranges reveal an increase in green forage biomass. Start date of green-up influenced the green biomass – a late start-up decreased the amount. The indicators for both the calving and summer ranges were annually variable which reduces their sensibility to detect trends over shorter time periods. However, for the calving range, we detected a decrease in the extent of lichen habitats; on the summer ranges, the trend was a decrease in forage quality (leaf N concentration at peak foliage biomass).

The habitat indicators that we selected were based on our understanding of caribou nutritional ecology. Weather and climate effects on habitat (forage quality and quantity) interact with predation and harvesting to drive the population dynamics of the large migratory caribou herds. The link between habitat and caribou abundance is through caribou nutritional responses to their forage (White et al., 1981; Russell et al., 1993; Parker et al., 2009). The late spring and summer period is a dynamic time in the arctic: 1) when 100% snow cover to peak biomass can occur in a month, 2) when cows enter calving season in the lowest condition (Gerhart et al., 1996; Adamczewski et al. 1987), 3) when energetic demands for cows double within 10 days of the calf's birth (White and Luick 1984; Parker et al. 1990; Chan-McLeod et al. 1994), 3) when insect harassment can reduce foraging time and result in days to weeks of negative energy balance (White et al., 1975; Dau and Cameron 1986; Russell et al., 1993) and 4) when muscle mass and fat reserves need to be replenished in preparation for the autumn breeding and long winter season (Gerhart et al. 1996; Adamczewski et al. 1987; Barboza and Parker 2008) . Consequently, lactating females have complex reproductive strategies to ensure primarily that they can survive the winter, and secondarily, that the calf is of sufficient mass and condition in late summer-early winter to survive the winter (Griffith et al., 2002). The weaning strategy in arctic caribou is thus critical to the productivity of the herd (Russell et al., 1996). In a synthesis and modeling paper, Parker et al. (2009) argue that these life history strategies detailed above are consequences of seasonal and ecological components of nutrition. Consequently, caribou have evolved mechanisms to cope with annual variability in habitats and each herd has nutritional bottlenecks that have to be overcome to remain productive, even to the extent that breeding pauses are common (Cameron 1994).

For the Bathurst herd, one such nutritional bottleneck is forage on the calving grounds. The location of the calving grounds means that the pregnant cow’s arrival in late May and early June, coincides with snowmelt and flushing of fresh green vegetation. This is particularly important seven to 10 days after calving when maximum milk production is achieved and thus when energy and protein demands are high (White and Luick 1984; Parker et al., 1990). Just prior to snowmelt pregnant cows will forage on anything that is available to fill the rumen. For the Bathurst herd, lichens comprise the primary food source during the pre-calving, post-calving and immediate post-calving periods (Griffith et al 2001). By contrast, cows in the Porcupine Herd forage on moss and any available emerging *Eriophorum* flowers in the pre-calving and calving period before switching to deciduous shrubs immediately after calving (Russell et al 1993; Griffith et al., 2002). In the George River herd, cows feed primarily on standing dead graminoids and evergreen shrubs from the calving to immediate post-calving periods (Manseau et al 1996). Moss, evergreen shrubs and standing dead graminoids are less digestible than lichen and provide lower metabolizable energy (Person et al., 1980; Staaland et al., 1988) that also could affect protein allocation to reproduction (Chan-McLeod et al. 1994; Barboza and Parker 2008).

In our study, we have shown that the extent of vegetation communities dominated by lichens has declined on the Bathurst calving grounds between 1990 and 2000. Griffith et al (2001) documented in the late 1990's that cows were still feeding primarily on lichens prior to green-up although given the low biomass values, calculated food intake (White and Trudell 1980) was considerably lower than the Porcupine and George River herds. The low biomass lichen habitats may cause a significant energy deficit in the calving and immediate post-calving period.

Bathurst cows quickly leave the calving ground within 10 days after the peak of calving and move south to habitats with higher biomass of green vegetation. Replenishing muscle and producing milk for their calves becomes a priority for lactating females. It is at this time fresh green vegetation, that is digestible and high in nitrogen, needs to be readily available. One of our indicators during this period was the green foliage biomass during pre-calving (May 21-31), peak calving (June 1-10), and post-calving (June 11-30). We did not detect significant temporal trends possibly because inter-annual variations in green foliage biomass values during pre-calving, peak calving, and post-calving periods are large. It is interesting to note that consistence between our data and results by Griffith et al (2001) on the calving grounds: a year of high (1998) and low (1999) green foliage biomass. For the Porcupine Caribou herd, Griffith et al (2002) found a significant positive relationship between the amount of green forage after calving (NDVI during June 21-30) and early calf survival.

Since the mid 1980's, habitat quality during calving has been declining for the Bathurst herd (based on the decline in lichen dominated communities and the dependence on lichens during this period), while after calving the trend toward higher N-concentration in the forage may have enhanced the survival of newborns. The effect of those two opposing trends will depend on the cow's condition as they arrive on the calving grounds; this is a critical factor for neonatal survival (Adams 2005). Bathurst cows may wean calves early if their condition is low and the lichens on the calving grounds are insufficient to sustain adequate milk production until forage high in available nitrogen becomes available.

During 1985 to 2006 the trend for summer habitat is toward increased green biomass but decreased N-concentration. Total food intake (g day^{-1}) is primarily governed by biomass of preferred plant species (White and Trudell 1980) while metabolizable energy and protein intake also incorporates forage quality measures (digestibility, N-concentration, for example) that can have a multiplicative effect on energy retention (White 1983). At its peak, biomass is likely unlimited as regards to food intake. The trend towards declining forage quality (our N-concentration indicator) has negative impacts on the herd during the 1986 to 2006 period. Not only will cows reduce milk production as a trade-off with depositing protein (Chan-McLeod et al., 1994), but under extreme conditions cows will even wean calves during the summer which results in the calf dying

(Russell and White 2000). If they wean during late summer and early fall, calves may survive on their own (Russell et al 1991).

Clearly the overall impact of trends in our calving and summer indicators cannot be resolved by looking at the indicators alone; further analysis directly linking both calving ground and summer (this study) and winter and pre-calving migration (Chen et al., 2009a) habitat indicators with caribou biological conditions such as growth rate, weaning strategy, calf survival, pregnancy rates, overwinter survival and population change are needed. The approach we have described in this paper resulted from cooperation through remote sensing experts, wildlife biologists and university staff that was under the auspices of the CircumArctic Rangifer Monitoring and Assessment network (CARMA). CARMA is a collaboration among communities, scientists, governments to exchange information on wild Rangifer populations across the circumpolar north

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References

Adamczewski JZ, Gates CC, Hudson RJ, Price MA (1987) Seasonal changes in body composition of mature female caribou and calves (*Rangifer tarandus groenlandicus*) on an arctic island with limited winter resources. Can J Zoology 65:1149-1157

Adams LG (2005) Effects of maternal characteristics and climatic variation on birth masses of Alaskan caribou. J Mammalogy 86:506–513

Atkin OK, Villar R, Cummins WR (1993) The ability of several high arctic plant species to utilize nitrate nitrogen under field conditions. Oecologia 96:239-245

Barboza PS, Parker KL (2008) Allocating protein to reproduction in arctic reindeer and caribou. Physiological and Biochemical Zoology 81:835–855

Brotton J, Wall G (1997) Climate change and the Bathurst caribou herd in the Northwest Territories, Canada. Climatic Change 35:35-52

Brown L, Chen JM, Leblanc SG, Cihlar J (2000) A shortwave infrared modification to the simple ratio for LAI retrieval in boreal forests: An image and model analysis. Remote Sens Environ 71:16–25

Callaghan TV, Körner C, Lee SE, Cornelison JHC (1998) Part 1: scenarios for ecosystem responses to global change. In: Heal, OW, Callaghan TV, Cornelissen JHC, Körner C, Lee SE (eds.) Global Change in Europe's Cold Regions. European Commission Ecosystems Research Report, 27, L-2985, Luxembourg, pp 11–63

Cameron RD (1994) Reproductive pauses by female caribou. J Mammalogy 75:10–13

Chan-McLeod ACA, White RG, Holleman DF (1994) Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. Can J Zool 72:938-947

Chapin III FS, Bloom AJ, Field CB, Waring RH (1987) Plant-responses to multiple environmental-factors. Bioscience 37:49-57

Chapin III FS, Moilanen L, Kielland K (1993) Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. Nature 361:150-153

Chen W, Chen JM, Cihlar J (2000) An integrated terrestrial carbon-budget model based on changes in disturbance, climate, and atmospheric chemistry. Ecol Model 135:55-79

Chen W, Russell DE, Gunn A, Croft B, Chen WR, Fernandes R, Zhao H, Li JH, Zhang Y, Koehler K, Olthof I, Fraser RH, Leblanc SG, Henry GR, White RG, Finstad GL (2009a) Habitat indicators for migratory tundra caribou under a changing climate: winter and pre-calving migration ranges. Climatic Change (submited)

Chen W, Blain D, Li J, Keohler K, Fraser R, Zhang Y, Leblanc S, Olthof I, Wang J, McGovern M (2009b) Biomass measurements and relationships with Landsat-7/ETM+ and JERS-1/SAR data over Canada’s western sub-arctic and low arctic. Int J Remote Sens 30(9):2355-2376

Chen W, Li J, Zhang Y, Zhou F, Koehler K, Leblanc S, Fraser R, Olthof I, Zhang Y, Wang J (2009c) Relating biomass and leaf area index to non-destructive measurements for monitoring changes in arctic vegetation. Arctic 62(3):281–294

Chen W, Blain D, Li J, Keohler K, Fraser R, Zhang Y, Leblanc S, Olthof I, Wang J, McGovern M (2009d) Estimating carbon release caused by land use changes over Canada’s north during 1985–1990 and 1990–2000 using satellite Earth observation. J Geophys Res 114, G01017, doi:10.1029/2007JG000631

Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH, Henry GHR, Shaver GR, Phoenix GK, Gwynn-Jones D, Jonasson S, Chapin III FS, Molau U, Lee JA, Melillo JM, Sveinbjornsson B, Aerts R (2001) Global change and Arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? J Ecol 89:984–994

Dau JR, Cameron RD (1986) Effects of a road system on caribou distribution during calving. Rangifer (Special Issue) 1:95-101

Elvidge CD, Yuan D, Weerackoon RD, Lunetta RS (1995) Relative radiometric normalization of Landsat Multi-spectral Scanner (MSS) data using an automatic scattergram-controlled regression. Photogr Engineer Remote Sens 61:1255-1260

Finstad GL (2008) Applied range ecology of reindeer (*Rangifer tarandus tarandus*) on the Seward Peninsula, Alaska. Dissertation, University of Alaska, Fairbanks

Fraser RH, Olthof I, Pouliot D (2009) Monitoring land cover change and ecological integrity in Canada’s national parks. Remote Sens Environ (in press)

Gerhart KL, White RG, Cameron RD, Russell DE (1996) Body composition and nutrient reserves of arctic caribou. Can J Zool 74:136-146

Goward S, Markham B, Dye D, Dulaney W, Yang J (1991) Normalized difference vegetation index measurements from the Advanced Very High Resolution Radiometer. Remote Sens Environ 35:257-277

Griffith B, Douglas D, Walsh N, Young D, McCabe T, Russell DE, White RG., Cameron R, Whitten K (2002) The Porcupine caribou herd. In: Douglas D, Reynolds P, Rhode E (eds) Arctic Refuge coastal plain terrestrial wildlife research summaries. U.S. Geological Survey, Biological Science Report BSR-2002-0001

Griffith B, Gunn A, Russell DE, Johnstone J, Kielland K, Wolfe S, Douglas DC (2001) Bathurst caribou calving ground studies: Influence of nutrition and human activity on calving ground location. Final report submitted to West Kitikmeot Slave Study Society. Yellowknife, NWT, pp 90

Guindon B (1997) Assessing the radiometric fidelity of high-resolution satellite image mosaics. J Photogram Remote Sens 52:229-243

Gunn A and Skogland T (1997) Responses of caribou and reindeer to global warming. Ecological Studies 124:189–200

Huete AR (1988) A soil adjusted vegetation indices index (SAVI). Remote Sens Environ 25:295-309

IPCC (2001) Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change, McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS (eds), Cambridge University Press, Cambridge

Jandt, R Joly K, Meyers CR, Racine C (2008) Slow Recovery of Lichen on Burned Caribou Winter Range in Alaska Tundra: Potential Influences of Climate Warming and Other Disturbance Factors. Arctic, Antarctic, and Alpine Research 40:89–95

Johnstone J, Russell DE, Griffith B (2002) Variation in forage quality in the range of the Porcupine Caribou Herd. Rangifer 22 (1):83-91

Jones PD, Moberg A (2003) Hemispheric and large scale surface air temperature variations: an extensive revision and update to 2001. J Clim 16:206-223

Kattsov VM, Källén E, et al. (2005) Future Climate Change: Modeling and Scenarios for the Arctic. In: Symon C, Arris L, Heal B (eds.) (2005) Arctic Climate Impact Assessment, Cambridge Univ. Press, Cambridge, pp 99-150

Kennedy CE, Smith CA, Cooley DA (2001) Observations of change in the cover of polar grass, *Arctagrostis latifolia*, and arctic lupin, *Lupinus arcticus*, in upland tundra on Herschel Island, Yukon Territory. Can Field-Naturalist 115:323-328

Khlopenkov K, Trishchenko A (2006) SPARC: New cloud, clear-snow/ice and cloud shadow detection scheme for historical AVHHR 1-km observations over Canada. J Atmos Oceanic Technol 24:322-343

Klein DR (1989) Subsistence hunting. In: Hudson RJ, Drew KR, Baskin LM (eds) Wildlife Production Systems: Economic Utilisation of Wild Ungulates, Cambridge University Press, Cambridge, pp 96–111

Klein DR, Baskin LM, Bogoslovskaya LS, Danell K, Gunn A, Irons DB, Kofinas GP, Kovacs KM, Magomedova M, Meehan RH, Russell DE, Valkenburg P (2005) Management and Conservation of Wildlife in a Changing Arctic Environment. In: Symon C, Arris L, Heal B (eds) Arctic Climate Impact Assessment, Cambridge University Press, Cambridge, pp 597-648

Koeln G, Bissonnette J (2000) Cross-correlation analysis: mapping landcover change with a historic landcover database and a recent, single-date multispectral image. Proc. 2000 ASPRS Annual Convention, Washington DC, pp 8

Körner C (2003) Alpine Plant Life. Springer, Heidelberg

Latifovic R, Cihlar J, Chen J (2003) Comparison of BRDF models for the normalization of satellite optical data to a standard sun-target-sensor geometry. IEEE Transact Geosci Remote Sens 41:1889-1898

Latifovic R, Trishchenfo, AP, Chen J, Park WB, Kholpenkov KV, Fernandes R, Pouliot D, Uugurennu C, Luo Y, Wang S, Davidson A, Cihlar J (2005) Generating historical AVHRR 1 km baseline satellite data records over Canada suitable for climate change studies. Can J Remote Sens 31:324-346

Lloyd D (1990) A phenological classification of terrestrial vegetation cover using shortwave vegetation index imagery, Int J Remote Sens 11:2269- 2279

Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration, Functional Ecol 8:315-323

Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR, Chapin III FS (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. Nature 431:440-443

Manseau M, Huot J, Crête M (1996) Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. J Ecol 84: 503-513

McArt SH, Spalinger DE, Collins WB, Schoen ER, Stevenson T, Bucho M (2009) Summer dietary nitrogen availability as a bottom-up constraint on moose in south-central Alaska. Ecology 90: 1400-1411

Miller FL, Gunn A (2003) Catastrophic Die-off of Peary Caribou on the Western Queen Elizabeth Islands, Canadian High Arctic. Arctic 56:381-390

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981to 1991. Nature 386:695-702

Olthof I, Fraser R (2007) Mapping northern land cover fractions using Landsat ETM+. Remote Sens Environ 107:496-509

Parker KL, Barboza PS, Gillingham MP (2009) Nutrition integrates environmental responses of ungulates. Functional Ecol 23:57-69

Parker KL, White RG, Gillingham MP, Holleman DF (1990) Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. Can J Zool 68:106-114

Person SJ, Pegau RE, White RG, Luick JR (1980) In vitro and nylon bag digestibilities of reindeer and caribou forages. J Wildl Manage 44:613-622.

Pollard RH, Ballard WB, Noel LE, Cronin MA (1996) Parasitic insect abundance and microclimate of gravel pads and tundra within the Prudhoe Bay Oil Field, Alaska, in relation to use by caribou, Rangifer tarandus granti. Can Field-Naturalist 110:649-658

Rey A, Jarves PG (1988) Long-term photosynthetic acclimation to increased atmospheric CO_2 concentration in young birch. Tree Physiol 18:441-450

Riikonen J, Holopainen T, Oksanen E, Vapaavuori E (2005) Leaf photosynthetic characteristic of silver birch during three years of exposure to elevated CO_2 and O_3 in the field. Tree Physiol 25:621-632

Ro C, Vet R, Ord D, Holloway A (1995) Canadian Air and Precipitation Monitoring Network (CAPMoN) Annual Summary Reports (1983-1994), National Atmospheric Chemistry Data Base (NAtChem), Atmospheric Environment Service, Environment Canada

Russell DE, Fancy SG, Whitten KR, White RG (1991) Overwinter survival of orphan caribou, *Rangifer tarandus*, calves. Can Field-Naturalist 105:103-105

Russell DE, Kofinas G, Griffith B (2002) Barren-Ground Caribou Calving Ground Workshop Report of Proceedings. Canadian Wildlife Service, Technical Report Series Number 390

Russell DE, Martel AM, Nixon WAC (1993) Range ecology of the Porcupine Caribou Herd in Canada. Rangifer Special Issue 8:1–168

Russell DE, van de Wetering D, White RG, Gerhart KL (1996) Oil and the Porcupine Caribou Herd-Can we quantify the impacts? Rangifer Special Issue 9:255-257

Russell DE, White RG (2000) Surviving in the north - a conceptual model of reproductive strategies in arctic caribou. Proc 8th North American Caribou Workshop, 23-25 April 1998. Whitehorse, YT, Canada. Rangifer, Special Issue 12:67

Shaver GR, Chapin III FS (1991) Production: biomass relationships and element cycling in contrasting arctic vegetation types. Ecol Monogr 61:1-31

Staaland H, Øritsland NA, White RG (1988) Digestion of energy and nutrients in Svalbard reindeer. Rangifer 8:2-10

Tucker CJ (1979) Red and Photographic Infrared Linear Combinations for Monitoring Vegetation. Remote Sens Environ 8:127-150

van Heerwaarden LM, Toet S, Aerts R (2003) Nitrogen and phosphorus resorption efficiency and proficiency in six sub-arctic bog species after 4 years of nitrogen fertilization. J Ecol 91:1060-1070

Veteli TO, Kuokkanen K, Julkunen-Tiitto R, Rioninen H, Tahvavainen J (2002) Effects of elevated CO_2 and temperature on plant growth and herbivore defensive chemistry. Glob Change Biol 10:1240-1252

Walsh NE, Fancy SG, McCabe TR, Pank LF (1992) Habitat use by the Porcupine caribou herd during predicted insect harassment. J Wildl Manage 56:465-473

White RG (1983) Foraging patterns and their multiplier effects of productivity of northern ungulates. 0ikos 4:377-384

White RG, Bunnell FL, Gaare E, Skogland T, Hubert B (1981) Ungulates on arctic ranges. In: Bliss LC, Heal OW Moore JJ (Ed.) Tundra Ecosystems: A Comparative

Analysis. IBP Vol. 25. Cambridge Univ. Press, Cambridge. pp 397-483.

White RG, Luick JR (1984) Plasticity and constraints in the lactational strategy of reindeer and caribou. In: Peaker M, Vernon RG, Knight CH (Ed.) Physiological Strategies in Lactation. Symp Zool Soc London No. 51, Academic Press. pp. 215-232

White RG, Thomson BR, Skogland T, Person SJ, Russell DE, Holleman DF, Luick JR (1975) Ecology of caribou at Prudhoe Bay, Alaska. In: Brown J (Ed.) Ecological Investigations of the Tundra Biome in the Prudhoe Bay Region, Alaska. Biol. Papers, Univ. Alaska, Spec. Report No. 2. pp 151-201

White RG, Trudell J (1980) Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. Arctic and Alpine Research 12:511-529

Yuan D, Elvidge CD (1996) Comparison of relative radiometric normalization techniques. J Photogr Remote Sens 51:117-126

Yuan ZY, Li LH, Huang JH, Han XG, Wan SQ (2005) Effect of Nitrogen Supply on the Nitrogen Use Efficiency of an Annual Herb, *Helianthus annuus* L. J Integrative Plant Biol 47:539-548

Zhang Y, Chen W, Cihlar J (2003) A process-based model for quantifying the impact of climate change on permafrost thaw. J Geophys Res 110:D03112, doi:10.1029/2004JD00491

Figure list

Fig. 1 Bathurst caribou habitat as defined by the cumulative range and the calving ground, on basis of satellite collared cows during 1996-2003. The green tree line separates the summer range from the winter range. Locations of field measurements of foliage biomass were also plotted, as well as an inserted map showing the distribution of major caribou and wild reindeer herds around the Arctic (CARMA website at http://www.carmanetwork.com)

Fig. 2 Leaf N concentration measurements over on the Davis, Gray, Olanna, and Noyakuk reindeer ranges of the Seward Peninsula, Alaska, in 1996 and 1997. Data are from (Finstad 2008)

Fig. 3 Leaf N re-sorption ratio, plotted against the leaf N concentration at peak foliage biomass (i.e., values at mid-summer), on basis of measurements over on the Davis, Gray, Olanna, and Noyakuk reindeer ranges of the Seward Peninsula, Alaska, during 1996 and 1997, with $R^2 = 0.73$, $F = 10.7$, $P = 0.03$, and $n = 6$. Data are from Finstad (2008)

Fig. 4 Relationship between measured foliage biomass and Landsat-based Simple Ratio (SR = band/band 3) in the Bathurst caribou habitat, with $y = 33.335x - 84.155$, $R^2 = 0.86$, standard error = 26.3 g m^{-2}, $F = 158$, $P = 2.6\times10^{-12}$, and $n = 27$. The measurements were made at 27 non-treed sites in and around the Bathurst caribou habitat during July 18-27, 2005. Landsat-7/ETM+ images were acquired in summers circa 2000

Fig. 5 Circa 2000 mid-summer baseline foliage biomass map at 30-m spatial resolution over the Bathurst caribou habitat, derived from Landsat-7/ETM+ mosaic and field measurements. Foliage biomass was estimated only for non-forested tundra ecosystems. Forested areas were masked out using land cover map developed using the same Landsat-7/ETM+ mosaic

Fig. 6 Relationship between foliage biomass at 1-km resolution aggregated from the Landsat-based baseline foliage biomass map and AVHRR-based Simple Ratio (SR = band 2/band 1) over the Bathurst caribou habitat, with $y = 25.482x - 36.402$, $R^2 = 0.68$, standard error = 10.8 g m^{-2}, $F = 1730$, $P = 2.5\times10^{-205}$, and $n = 833$

Fig. 7 Green foliage biomass during pre-calving (May 21-31), peak calving (June 1-10), and post-calving (June 11-30) on the calving ground of the Bathurst caribou herd during 1985 and 2006. The straight lines represent temporal trends: for the pre-calving foliage biomass $R^2 = 0.00$, $F = 0.05$, $P = 0.82$, and $n = 22$; for the peak calving foliage biomass

$R^2 = 0.00$, $F = 0.00$, $P = 0.98$, and $n = 22$; and for the post-calving foliage biomass $R^2 = 0.07$, $F = 1.5$, $P = 0.24$, and $n = 22$

Fig. 8 Relationship between green foliage biomass during June 1-10 and June 11-30 on the calving ground of the Bathurst caribou herd and the growing season start date from 1985 to 2006, with $y = -0.9798x + 152.87$, $R^2 = 0.9038$, $F = 28$, $P = 0.013$, and $n = 5$ for peak calving period in years with the growing season start date being earlier than June 5; $y = -1.0745x + 185.41$, $R^2 = 0.80$, $F = 81.9$, $P = 1.7\times10^{-8}$, and $n = 22$ for the post-calving period during 1985-2006.

Fig. 9 Calving ground land cover change from 1990 to 2000 derived from Landsat images, including 5 aggregated classes: lichen dominant, shrub/grass, barren/rock/bare soil, woodland/forest, and water

Fig. 10 The summer forage availability indicator, defined as the average foliage biomass from June 11 to September 30 in the summer range, for the Bathurst caribou herd during 1985 to 2006. The straight line represents temporal trend with $R^2 = 0.29$, $F = 8.3$, $P = 0.009$, and $n = 22$

Fig. 11 Relationship between summer range forage availability indicator of the Bathurst caribou herd and growing season length during 1985-2006, with $y = 0.3558x - 6.5495$, $R^2 = 0.34$, $F = 10.1$, $P = 4.6\times10^{-3}$, and $n = 22$

Fig. 12 Simulated N cycle components in the summer range of the Bathurst caribou herd during 1985 and 2006. Total available N = N mineralization + N resorbed in the previous year + N fixation + N deposition. The straight line represents temporal trend for the total available N, with $R^2 = 0.41$, $F = 13.8$, $P = 0.001$, and $n = 22$

Fig. 13 Leaf N concentrations at peak foliage biomass, the summer range forage quality indicator for the Bathurst caribou herd from 1985-2006. The Arrhenius method is the baseline method. Two alternative methods were used for sensitivity analyses: the "Q_{10} = 2 (or 3)" method calculates N mineralization using power function with Q_{10} = 2 (or 3) while keeping other processes at baseline conditions. Peak foliage biomass was also plotted for comparison. The straight line represents the temporal trend of leaf N concentrations at peak foliage biomass calculate using the Arrhenius method, with $R^2 = 0.08$, $F = 1.7$, $P = 0.2$, and $n = 22$

Fig. 14 Relationship between summer range forage quality indicator of the Bathurst caribou herd and growing season length during 1985-2006, with $y = 46.05x^{-0.7076}$, $R^2 = 0.16$, $F = 3.6$, $P = 0.07$, and $n = 22$