The influence of fire history on selection of foraging sites by barren-ground caribou

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Abstract: We used an information-theoretic model comparison approach to investigate the influence of forest stand attributes resulting from wildfire on the occupancy of winter habitats by barren-ground caribou (Rangifer tarandus groenlandicus) in the Northwest Territories, Canada. We used field data describing forest stand and understory attributes to develop multinomial regression models. These analyses identified a combination of ground cover type and tree volume (i.e., stand basal area) as best able to describe the observed selection of feeding sites. An observed increase in the percent ground cover of lichen had a positive influence on site selection, while an increase in the percent rock cover and basal area of conifer trees had a negative influence on selection of feeding sites by caribou. The most parsimonious regression model predicted site use with an accuracy of 87%. Lastly, we used published equations to determine the biomass of fruticose lichens on experimental and control sites classified as unburned. Our data indicated that fruticose lichen biomass on the winter range of the Bathurst herd of barren-ground caribou was high compared to winter habitats of caribou in Alaska and the Yukon Territory, and falls in the general range of lichen values reported for winter habitats of the more easterly Beverly herd, as well as portions of Saskatchewan, Manitoba, and Ungava. Overall, the analyses of feeding-site selection suggest that Bathurst caribou forage in areas with a high percentage cover and biomass of lichen, and that future increased incidence and severity of forest fires could cause a temporary decrease in the quality of winter habitat available to the Bathurst herd.

Keywords: barren-ground caribou, climate change, fire, habitat selection, lichen, winter range ecology.

Résumé : Nous avons utilisé une approche de comparaison de modèles basée sur la théorie de l'information pour examiner l'influence des caractéristiques attribuables aux feux dans un peuplement forestier sur l'occupation des habitats d'hiver par le caribou de la toundra (Rangifer tarandus groenlandicus) dans les Territoires du Nord-Ouest, Canada. Nous avons utilisé des données de terrain sur les caractéristiques du peuplement et du sous-étage forestiers pour développer des modèles de régression multinomiale. Ces analyses nous ont permis de déterminer la combinaison de type de couverture de sol et de volume d'arbres (c'est-à-dire la surface terrière du peuplement) permettant le mieux de décrire la sélection observée pour les sites alimentation. Une augmentation du pourcentage de couverture de lichens au sol avait une influence positive sur la sélection, tandis qu'une augmentation du pourcentage de couverture de roches et de la surface terrière résineuse avaient une influence négative sur la sélection de sites d'alimentation par le caribou. Le modèle de régression le plus parcimonieux prédisait l'utilisation d'un site dans 87 % des cas. Finalement, nous avons utilisé des équations connues pour déterminer la biomasse de lichens fruticuleux dans des sites expérimentaux et contrôle classés comme non brûlés. Nos données ont indiqué que la biomasse de lichens fruticuleux dans l'aire d'hivernage du caribou de Bathurst était élevée en comparaison aux aires d'hivernages du caribou en Alaska et au Yukon; cette biomasse est comparable aux valeurs rapportées pour le troupeau de Beverley plus à l'est, ainsi que pour certaines parties de la Saskatchewan, du Manitoba et de l'Ungava. Dans l'ensemble, les analyses de la sélection des sites d'alimentation suggèrent que le caribou de Bathurst s'alimente dans des secteurs ayant un pourcentage élevé de couverture de lichens ainsi qu'une biomasse élevée de lichens et qu'une augmentation future de l'incidence et de la sévérité des incendies de forêt pourrait causer une diminution temporaire de la qualité de l'habitat d'hiver disponible pour le troupeau de Bathurst.

Mots-clés : caribou de la toundra, changement climatique, écologie de l'aire d'hivernage, feu, lichen, sélection d'habitats.


Introduction

At least 34 of 58 major Rangifer herds throughout Russia, Alaska, and Canada are currently declining in numbers (Vors & Boyce, 2009). In particular, populations of barren-ground caribou in the Canadian Central Arctic have markedly decreased since the late twentieth century. For example, the Bathurst barren-ground herd, which was estimated at 472 000 ± 72 900 (95% confidence interval [CI]) caribou in 1986, declined slowly through the 1990s and then more rapidly during the late 2000s (Gunn, Adamczewski & Nishi, 2008; Adamczewski et al., 2009). The June 2009 photo survey of the Bathurst herd provided an estimate of 31 897 ± 5345 caribou, representing a decline of 75% in 3 y (128 000 ± 27 300 caribou in 2006; Adamczewski et al., 2009). Although conditions for individual herds of caribou and reindeer are undoubtedly unique, a changing climate may be driving these declines at a large spatial scale (Brotton & Wall, 1997; Gunn, 2003; Vors & Boyce, 2009).
Northern landscapes are changing at an unprecedented rate (Johnson et al., 2005; Joly, Jandt & Klein, 2009; Vors & Boyce, 2009). Scenarios depicting future climates for northern latitudes predict that warmer annual temperatures and drier summer weather may lead to an increased frequency and severity of forest fires (Rupp et al., 2006), as well as deeper and denser snowpacks, with an increase in severe winter-weather events (Vors & Boyce, 2009). Lichen-rich habitats, vital to caribou during winter, have decreased largely due to increases in forest fires, which are shown to correlate with an increase in mean summer temperature (1959–2006; Vors et al., 2009). Also, warmer winter temperatures have caused denser and harder snowpacks. Such unfavourable snow and ice conditions decrease the accessibility of terrestrial lichen for caribou (Bergerud, 1974; Thomas, Kiliaan & Trottier, 1998). Of greater concern, warmer winters can result in an increase in the frequency of freezing-rain events that lock lichen pastures under impenetrable layers of ice (Kohler & Aanes, 2004). In addition, climate-induced increases in the abundance of vascular plants will likely result in declining macrolichen biomass in subarctic ecosystems (Cornelissen et al., 2001). Such conditions both increase the energy required to search for food resources (Fancy & White, 1985; Brotton & Wall, 1997) and decrease the nutrient gains obtained from foraging for lichens. Moreover, these losses could be additive with poorer summer-range condition and increasing human disturbance across seasonal ranges (Harrington & Veitch, 1991; Dyer et al., 2001; Mahoney & Schaefer, 2002; Frid, 2003; Nelemann et al., 2003; Johnson et al., 2005).

The influence of forage type and site conditions on the selection of winter feeding sites by barren-ground caribou has been relatively well studied. Most literature suggests that caribou prefer mature forested habitat with abundant mat-forming lichens (Scotter, 1964; Kelsall, 1968; Klein, 1982). These authors believe that fire has a negative effect on caribou habitat, due to the slow recovery time of terricolous (ground-dwelling) lichens that form the majority of a caribou’s diet during winter (60–80%; Scotter, 1964; Kelsall, 1968; Klein, 1982; Fleischman, 1990; Joly et al., 2003). Although researchers have noted that caribou sometimes forage in recently burned habitats (Johnson & Rowe, 1975; Joly et al., 2003), they are mostly observed to avoid these areas in favour of older, lichen-rich communities (> 55 y; Klein, 1982; Thomas, Barry & Alaie, 1996; Joly et al., 2003; Joly, Jandt & Klein, 2009). Lichen species preferred by caribou (e.g., Cladina rangiferina, Cladina mitis) are associated with late-successional seral stages in boreal forests (Maikawa & Kershaw, 1976) and in the short term are lost following fire (Klein, 1982; Thomas, Barry & Alaie, 1996; Joly et al., 2003; Payette et al., 2004; Joly, Bente & Dau, 2007; Joly, Jandt & Klein, 2009).

In addition to a high biomass of terricolous lichens, mature stands of winter range generally yield more favourable snow conditions compared to younger stands (Thomas, Kiliaan & Trottier, 1998), allowing caribou to access lichen mats while expending less energy (Pruitt, 1959; Skogland, 1978; Fancy & White, 1985). When snow is particularly deep or hard, the amount of energy required to excavate a feeding crater increases substantially, decreasing the nutritional gain from ingesting lichens (Fancy & White, 1985; Russell, Martell & Nixon, 1993; Brotton & Wall, 1997).

From a management perspective, it is crucial to have an understanding of what effect, if any, a change in the amount or connectivity of lichen-rich habitat may have on the current distribution and foraging ecology of caribou. In addition to the rapid decline in numbers of caribou, potential shifts in their geographical distribution threaten northern communities with strong cultural and subsistence ties to the land. A further reduction in the availability or quality of forage could cause herds to adopt an alternative winter range (Joly, Jandt & Klein, 2009; Joly, Chapin & Klein, 2010), distant from dependent human communities.

We assessed the influence of forest stand attributes on the occupancy of winter habitats by a population of barren-ground caribou. We predicted that caribou would avoid post-fire vegetation types yielding unfavourable snow conditions and would select older stands composed largely of herbaceous forage and terricolous lichens. We focused sampling and analysis on components of caribou habitat that were related to vegetation dynamics following wildfire. Between 2008 and 2009, we collected forest stand and understory data at habitats used by caribou and at paired control sites on the winter range of the Bathurst herd, located in the Northwest Territories, Canada. We used multinomial logistic regression and an information-theoretic model comparison (ITMC) approach to identify factors associated with the use of forest patches by caribou as foraging habitat. We present these findings in the context of other populations of migratory caribou experiencing changing fire dynamics and range quality.

**Methods**

**STUDY AREA**

We investigated winter range habitat for the Bathurst caribou herd across a broad area north and northwest of Yellowknife, Northwest Territories, Canada. Sample sites were dictated by locations of collared caribou monitored during February and March of 2008 and 2009. The historical boundaries of the winter range were approximately delineated by the territorial borders to the north and east and by Great Slave Lake and Great Bear Lake to the south and northwest, respectively; however, the distribution of Bathurst caribou has extended as far south as northern Saskatchewan (Figure 1; Gunn, Dragon & Boulanger, 2002).

The winter range of the Bathurst herd spans both Taiga Shield and Southern Arctic ecozones, which are divided by the northern treeline (Ecological Stratification Working Group, 1996). Above treeline, lichen barrens and graminoid-tundra and dwarf-shrub communities characterise most of the caribou summer range, as well as portions of the winter range. Below treeline, vegetation on the winter range is characterised by northern boreal forest ecosystems, where dominant tree and shrub species include black spruce...
winter to verify the presence of feeding craters and thus caribou. Likewise, control sites consisted of random plots of adjacent lichen-bearing and burned habitat near lakes that were within 17.5 km of the paired foraging site but showed no evidence of foraging by caribou during late winter. The acceptable radius for sampling random lichen-bearing and burned site types was defined by the average distance collared caribou moved in a week (Gunn, Dragon & Boulanger, 2002) during late winter (February–March). We assumed that sampling locations within this radius were accessible to the caribou that chose to occupy the paired foraging site instead. Field evidence suggested that caribou occupied less than 1% of burned sites that we investigated.

During February and March of 2008 and 2009, we used a small fixed-wing aircraft to locate areas on the Bathurst winter range where caribou foraged and areas where they did not (i.e., control and burned sites). The primary purpose of these investigations was to confirm caribou activity at foraging sites and the absence of caribou at burned and control sites (n = 75 total sites). Upon landing at 27 sites, we measured snow depth, density, and hardness using a ruler, cylinder of known volume, and a homemade ramsonde penetrometer (Skogland, 1978) at 3 randomly selected undisturbed and open locations.

During July and August of 2008 and 2009, we revisited all 75 sites and documented lichen diversity and abundance, as well as forest stand attributes that may have influenced the distribution of caribou relative to forage availability. Specifically, we measured percent ground cover of lichen; volume of terrestrial lichen; occurrence of bryophytes, shrubs, and graminoids; tree and shrub cover; canopy closure; and stand age. Each foraging and random site that we investigated was approximately 0.09 ha (30 m × 30 m), representing the minimum size of a foraging area noted during initial field investigations of the Bathurst winter range (February–March 2008).

At each site, we flagged seven 30-m transects occurring at 5-m intervals perpendicular to the baseline transect. We used a 50- × 50-cm point frame with 16 pins to determine the volume of terrestrial lichen taxa at 7 randomly selected quadrats at each study site. Quadrat sampling for volume required that observations were independent, the area sampled was known, and the organisms were relatively immobile (Higgins et al., 2005). In order to meet the assumption of independence, eliminate bias, and ensure a representative measurement, we used a systematic random sampling design to mark 1 location per transect for quadrat sampling. At each pin on the point frame, we recorded the species or genus and height of lichen or other ground cover. We later used equations developed by Moen, Danell, and Holt (2007) to estimate the biomass of fruticose lichens at experimental and control study sites classified as unburned. We categorised percent ground cover of vegetation into species and groups based on relevance to caribou foraging ecology and reliability of identification in the field (Hollemann & Luick, 1977; Thomas, Kroeger & Hervieux, 1984; Russell, Martell & Nixon, 1993; Thomas, Barry & Alaie, 1996). Specifically, we identified 5 taxa of lichen that were found in abundance on the winter range of barren-ground caribou: Cladina, Cladonia, Cetraria,
We classified Cladina stellaris, Cladina rangiferina, Stereocaulon species, and Cetraria nivalis as caribou forage lichens and all other taxa as non-forage lichens. We also considered graminoids, forbs, bryophytes, dwarf shrubs (<30 cm tall), litter, soil, and rock as independent groups of ground cover.

Within each site, we used a systematic random design to select two locations on transects 2 and 6 to measure crown closure and tree cover. We obtained crown closure with a spherical densiometer. We then used a metric clear-glass prism with a basal area factor of 4 to separately estimate the basal area of surrounding coniferous and deciduous trees. At the centre of each site, we used a fixed-area plot (5.64 m radius; 0.01 ha) to visually estimate percent cover of short and tall shrubs (<2 and >2 m, respectively). In order to estimate stand age, we extracted wood core samples from several of the largest trees of each species. Core samples were later analysed using dendrochronological techniques to determine the approximate stand age of each site.

**Model development and assessment**

We used multinomial logistic regression to contrast forest stand and understory attributes measured at sites used by caribou and paired control sites of similar vegetation classification, as well as burned habitats where caribou were absent (n = 75 total sites). Choosing from the predictor variables identified at study sites, we developed a set of 8 candidate models to assess the influence of percent cover of vegetation and associated forest stand attributes on feeding-site selection by caribou (Table I). These models represented ecologically plausible hypotheses that explained the distribution of barren-ground caribou across forested habitats relative to their foraging ecology. Weather and time constraints prevented us from completing an assessment of snow conditions at all study sites during the winter field seasons (n = 27 of 75 total sites). Also, we could not reliably age all stands (n = 41 of 75 total sites). Thus, snow and stand age data were not considered within the model comparison procedure. We assumed that lichen volume and cover served as a proxy measure for stand age (Russell, Martell & Nixon, 1993; Thomas, Barry & Alaie, 1996). However, insufficient weather station data prevented us from establishing an appropriate proxy for local snow conditions. We used tolerance scores to assess excessive collinearity (threshold of ≤ 0.2) among the variables in each model (Menard, 2001).

We used Akaike’s Information Criterion (AIC,) for small sample sizes (Anderson, Burnham & Thompson, 2000) to select the most parsimonious model from the candidate set. The “best” model had the lowest AIC, score. We also calculated AAIc values and Akaike weights (w), which represent the difference in AIC, values between each model and the model having the lowest AIC, and the approximate probability that a particular model was the best in the candidate set, respectively. One of the main criticisms of the ITMC method is that it allows for too many models to be tested (Guthery et al., 2005). We avoided this problem by limiting the number of competing hypotheses to 8.

We used the receiver operating characteristics (ROC) score to assess the ability of the model to differentiate between sites classified as used and random. The area under the ROC curve (AUC) is useful for determining predictive accuracy when true presence and absence data are available (Fielding & Bell, 1997). The AUC is the proportion of correctly and incorrectly classified cases when presence is predicted across the entire range of probability thresholds (0–1; Fielding & Bell, 1997). AUC values of 0.5 indicate that a model has no ability to discriminate beyond random assignment of cases, and a value of 1.0 indicates that a model is a perfect predictor. Values ranging between 0.7 and 0.9 suggest that the model possesses good discriminatory ability (Fielding & Bell, 1997). We used 95% confidence intervals (CI) to assess the relative strength of selection or avoidance for each covariate in the models. Covariates with confidence intervals that did not overlap 0 were considered significant predictors of the distribution of barren-ground caribou across forest patches. We used odds ratios to interpret the effect of each covariate on the differentiation of site types. In order to provide a relative measure of the importance of habitat features not included in the models, we used 95% confidence intervals to test for differences in mean stand age and snow conditions between used and control sites. All statistical analyses were completed using Stata (StataCorp LP, 2006).

**Table I. Candidate models for predicting feeding sites used by Bathurst caribou during late winter (2008–2009).**

<table>
<thead>
<tr>
<th>Model theme</th>
<th>Model parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lichen volume + forest understory</td>
<td>Volume of Cladina, Cladonia, Cetraria, and Stereocaulon species; percent cover of moss and linter</td>
</tr>
<tr>
<td>Percent lichen cover + forest understory + tree cover</td>
<td>Percent cover of lichen, moss, litter, and rock; basal area of conifers</td>
</tr>
<tr>
<td>Lichen volume + forest understory + tree cover</td>
<td>Total lichen volume; percent cover of shrubs, moss, litter, and rock; basal area of conifers</td>
</tr>
<tr>
<td>Lichen volume + forest understory (short shrubs only) + tree cover</td>
<td>Volume of Cladina mitis, Cladina rangiferina, Cetraria nivalis, and Stereocaulon species; percent cover of short shrubs, moss, linter, rock; basal area of conifers</td>
</tr>
<tr>
<td>Percent lichen cover + forest understory + forest canopy</td>
<td>Percent cover of lichen, shrubs, moss, litter, and rock; percent canopy closure</td>
</tr>
<tr>
<td>Lichen volume + forest understory + forest canopy</td>
<td>Total lichen volume; percent cover of shrubs, moss, litter, and rock; percent canopy closure</td>
</tr>
<tr>
<td>Percent lichen cover + forest understory + tree cover + forest canopy</td>
<td>Percent cover of lichen, moss, litter, and rock; basal area of conifers; percent canopy closure</td>
</tr>
<tr>
<td>Full model</td>
<td>Total lichen volume; percent cover of lichen, shrubs, moss, linter, and rock; basal area of conifers; percent canopy closure</td>
</tr>
</tbody>
</table>
**Results**

**Stnd attributes**

We sampled 75 sites over 2 winter and summer field seasons. Of these sites, 33 showed evidence of caribou foraging, 22 were randomly selected lichen-bearing habitats, and 20 were randomly selected burned habitats. During 2009, snow depth at used and random lichen-bearing habitats averaged 56.6 ± 4.6 cm (95% CI; n = 11) and 59.3 ± 3.6 cm (n = 11), respectively. Contrary to our hypothesis, snow hardness and snow density did not differ significantly between used (0.158 ± 0.016 g·cm⁻² and 0.222 ± 0.034 g·cm⁻³) and random (0.141 ± 0.016 g·cm⁻² and 0.218 ± 0.016 g·cm⁻³) sites. However, snow conditions at sites used by caribou varied between years. Average snow depth was 24.7% higher in 2009 than 2008 (56.6 ± 4.6 cm versus 45.4 ± 2.2 cm, respectively) (n = 22 in 2009; n = 5 in 2008), and both snow hardness and snow density were significantly lower in 2009 than in 2008.

Eleven distinct species of ground-dwelling fruticose lichens and 8 types of ground cover were regularly observed at the 3 site types. Arboreal lichens (*Bryoria* species) were also present in some areas, but they were not prevalent enough to be included in the analysis. Percent cover of lichens was greater at feeding sites than at random lichen-bearing and burned sites (Figure 2). *Cladina* species, such as *Cladina mitis* and *Cladina rangiferina*, were the most prevalent at used sites, averaging 27% and 18% of total lichen volume, respectively (Figures 3, 4). Unburned control sites had a greater percent cover of moss than feeding sites (Figure 5). Burned sites were characterised by a low volume and cover of ground lichens (Figure 2), as well as a comparatively high percentage of ground cover of litter (Figure 5).

Biomass of fruticose lichens did not differ significantly between used and unburned sites. The average biomass of fruticose lichens at feeding sites was 241 ± 34 g·m⁻² (2412 ± 338 kg·ha⁻¹), compared to 252 ± 37 g·m⁻² (2516 ± 370 kg·ha⁻¹) at unburned controls. We did not calculate the biomass of lichens observed at burned sites because this site type did not meet the assumption of a lichen-dominant habitat, which is required to compute reliable assessments of biomass (Moen, Danell & Holt, 2007). Instead, we relied on lichen volume as an indicator of lichen quantity in burned habitats. A comparison of all 3 site types showed that burned sites had the lowest amount of terrestrial lichen (3.5 ± 1.0 m³ versus 10.6 ± 2.0 m³ at used sites and 8.0 ± 2.2 m³ at unburned control sites; Figure 2), most of which were Cladonia species, a genus not highly sought after by caribou (exceptions include *Cladonia uncialis* and *Cladonia gracilis*; Russell, Martell & Nixon, 1993).

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![Figure 2](https://via.placeholder.com/150)  
**Figure 2.** Mean (95% CI) a) lichen cover and b) lichen volume at caribou feeding sites (n = 33) and random lichen-bearing (n = 22) and burned sites (n = 20) on the Bathurst winter range (2008–2009).

![Figure 3](https://via.placeholder.com/150)  
**Figure 3.** Mean (95% CI) volume of lichen taxa at caribou feeding sites (n = 33) and random lichen-bearing (n = 22) and burned sites (n = 20) on the Bathurst winter range (2008–2009).
Basal area of conifer trees was less at burned sites than at lichen-bearing control sites (4.7 ± 2.1% and 11.7 ± 3.9%, respectively). Shrub cover, canopy closure, and stand age did not differ significantly between the 3 site types. However, on average, total shrub cover was less at feeding sites than on paired unburned and burned sites (1.6 ± 1.8%, 5.7 ± 3.4%, and 6.5 ± 5.9%, respectively); this was a result of fewer short shrubs in areas used by caribou. Similarly, the mean value for canopy closure was lower at feeding sites than at unburned control sites, ranging from an average of 17.5 ± 5.6% at used sites to 27.4 ± 8.8% at random lichen-bearing sites. The trees at feeding sites (n = 13) were generally older than those at lichen-bearing control sites (n = 8). The average stand age of a feeding site was
143 ± 35 y, compared to 96 ± 19 y for random sites in comparable habitat types.

MODEL FIT

The most parsimonious multinomial logistic regression model used to describe selection of feeding sites by caribou contained predictors for basal area of conifers, percent ground cover of lichen, moss, litter, and rock (Table II). The second-ranked model differed by nearly 3 AICc points and included an additional variable for percent canopy closure. The best model had good discriminatory ability (AUC = 0.873). Variables that had a positive influence on feeding-site selection included percent ground cover of lichen, litter, and rock; basal area of conifers and percent ground cover of moss had a negative influence on feeding-site selection (Table III). Burned sites were more likely to have a lower basal area of conifers and percent ground cover of moss, with a higher percent ground cover of lichen, litter, and rock. However, only lichen cover made a statistically significant (β = 0.057 ± 0.055; 95% CI) contribution to the differentiation between feeding sites and unburned control sites; both lichen and rock cover had a significant (β = 0.152 ± 0.090 and β = −0.225 ± 0.218, respectively) effect in distinguishing feeding sites from burned sites (Table III).

Holding values for all other covariates in each best model at their respective means (i.e., basal area of conifers and percent ground cover of moss, litter, and rock), we calculated the probability of a caribou choosing a known feeding site over both lichen-bearing and burned sites as the percent ground cover of lichen increased (Figure 6). Relative to unburned areas, caribou were more likely to feed in a patch of forest when cover of lichen exceeded 43%. Similarly, these data suggest that caribou will occupy previously burned patches of forest when lichen cover is greater than 33%. Considering only the percent cover of lichen, caribou have a lower threshold for using burned sites compared to unburned sites where no signs of foraging were detected.

Discussion

Most continental populations of caribou forage primarily on terricolous lichens throughout winter, focusing on fruticose species such as Cladina rangiferina and Cladina mitis (Pegau, 1968; Russell, Martell & Nixon, 1993; Thomas, Barry & Alaie, 1996; Joly et al., 2007) and choosing mature forested habitats over recently burned areas of winter range (Klein, 1982; Thomas, Barry & Alaie, 1996; Joly et al., 2003; Joly, Bente & Dau, 2007). Our results agree with those findings. With few exceptions (Joly, Bente & Dau, 2007), however, most studies have failed to investigate habitat selection at a geographic scale that is representative of the movement patterns of caribou during the winter. Rather, studies of the foraging ecology of barren-ground caribou have focused on quantifying general winter range conditions (Russell, Martell & Nixon, 1993; Jandt et al., 2008) and feeding habits (Thomas & Hervieux, 1986; Russell, Martell & Nixon, 1993), examining patterns of habitat use (Carruthers et al., 1986), assessing feeding-site selection within a foraging patch (Saperstein, 1996), and comparing site conditions and caribou use at burned and unburned habitats across the seasonal range (Thomas, Barry & Alaie, 1996; Joly, Chapin & Klein, 2010). Here, we have expanded upon those studies by quantifying the influence of lichen cover and associated stand characteristics on the selection of feeding sites by Bathurst caribou with respect to paired random unburned and burned sites at a geographic scale that is equivalent to the weekly movement patterns of the herd.

Table II. Model-selection statistics for candidate models used to predict feeding-site selection by Bathurst caribou during late winter (2008–2009).

<table>
<thead>
<tr>
<th>Model</th>
<th>Rank</th>
<th>ΔAICc</th>
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<tbody>
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<td>Percent lichen cover + forest understory + tree cover</td>
<td>1</td>
<td>0.00</td>
<td>0.7720</td>
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<tr>
<td>Percent lichen cover + forest understory + tree cover + forest canopy</td>
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<td>2.97</td>
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<td>5.41</td>
<td>0.0516</td>
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<tr>
<td>Lichen volume + forest understory</td>
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<td>13.38</td>
<td>0.0010</td>
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<tr>
<td>Lichen volume + forest understory + tree cover</td>
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<td>0.0003</td>
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<tr>
<td>Lichen volume + forest understory + forest canopy</td>
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<td>17.49</td>
<td>0.0001</td>
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<tr>
<td>Lichen volume + forest understory (short shrubs only) + tree cover</td>
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<td>19.60</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Full model</td>
<td>8</td>
<td>53.25</td>
<td>&lt; 0.0001</td>
</tr>
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</table>
and greater lichen cover. However, terrain variability may also affect the foraging decisions of caribou at larger spatial scales. For example, the Beverly and Porcupine herds generally occupy areas that will later accumulate large amounts of snow early in the winter, before heavy snowfall impedes movement and foraging (Turney & Heard, 1991; Russell, Martell & Nixon, 1993; Thomas, 1998; Thomas, Kiliaan & Trottier, 1998).

Lichen abundance also plays an important role in feeding-site selection by caribou. It is very likely that our measures of lichen abundance at feeding sites underrepresented the ground cover and height of lichens available to caribou. In addition to cropping the lichen during feeding, caribou may have reduced the lichen mat through ancillary digging and pawing actions while cratering (Pegau, 1969); we rarely observed evidence of caribou trampling or cropping of the entire lichen thallus, however. This bias would force us to test a more conservative model that reduced the likelihood of differentiating foraging sites from random controls and burned sites.

**Influence of ecological factors on site selection**

Past research on the winter ecology of barren-ground caribou suggests that herds prefer areas with a high abundance of fruticose lichen, low snow depths, and access to small lakes (Klein, 1982; Carruthers *et al.*, 1986; Thomas, Barry & Alaie, 1996; Joly, Chapin & Klein, 2010). Although the role of fire is widely debated, most researchers agree that a lack of available forage caused by frequent fire activity can influence the distribution of caribou on forested winter range (Klein, 1982; Thomas, Barry & Alaie, 1996; Joly *et al.*, 2003; Payette *et al.*, 2004; Joly, Bente & Dau, 2007; Sharma, Couturier & Côté, 2009). Thomas, Barry, and Alaie (1996) conducted a 7-yr comprehensive study on the winter range of the more easterly Beverly herd and reported that lichens preferred by caribou required 80–150 y to reach maturity, and that an abundance of these lichens may be a primary reason that caribou favour stands that are 151–250 y of age. Within the context of such works, our results add to the understanding of feeding-site selection on a small spatial scale by illuminating differences between used and comparable random and burned habitats. Furthermore, we show that percent ground cover of lichen may be a primary factor driving the selection of feeding sites by barren-ground caribou in the central Canadian Arctic.

**Table III.** Selection coefficients for parameters in the best (Table II) multinomial logistic regression model used to predict feeding-site selection by Bathurst caribou during late winter (2008–2009).

<table>
<thead>
<tr>
<th>Feeding sites versus unburned control sites (n = 75)</th>
<th>Model parameters</th>
<th>β</th>
<th>SE</th>
<th>95% CI</th>
<th>Odds ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model parameters</td>
<td>Basal area of conifers</td>
<td>-0.071</td>
<td>0.054</td>
<td>-0.177 – 0.035</td>
<td>-7.1%</td>
</tr>
<tr>
<td></td>
<td>Lichen cover</td>
<td>0.057</td>
<td>0.028</td>
<td>0.002 – 0.112</td>
<td>+5.7%</td>
</tr>
<tr>
<td></td>
<td>Moss cover</td>
<td>-0.061</td>
<td>0.057</td>
<td>-0.173 – 0.051</td>
<td>-6.1%</td>
</tr>
<tr>
<td></td>
<td>Litter cover</td>
<td>0.018</td>
<td>0.043</td>
<td>-0.066 – 0.102</td>
<td>+1.8%</td>
</tr>
<tr>
<td></td>
<td>Rock cover</td>
<td>0.003</td>
<td>0.067</td>
<td>-0.128 – 0.134</td>
<td>+0.3%</td>
</tr>
<tr>
<td></td>
<td>Constant</td>
<td>-1.710</td>
<td>2.076</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Feeding sites versus burned control sites (n = 75)</th>
<th>Model parameters</th>
<th>β</th>
<th>SE</th>
<th>95% CI</th>
<th>Odds ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model parameters</td>
<td>Basal area of conifers</td>
<td>0.022</td>
<td>0.088</td>
<td>-0.151 – 0.195</td>
<td>+2.2%</td>
</tr>
<tr>
<td></td>
<td>Lichen cover</td>
<td>0.152</td>
<td>0.046</td>
<td>0.062 – 0.242</td>
<td>+15.2%</td>
</tr>
<tr>
<td></td>
<td>Moss cover</td>
<td>-0.031</td>
<td>0.064</td>
<td>-0.156 – 0.094</td>
<td>-3.1%</td>
</tr>
<tr>
<td></td>
<td>Litter cover</td>
<td>-0.091</td>
<td>0.053</td>
<td>-0.200 – 0.013</td>
<td>-9.1%</td>
</tr>
<tr>
<td></td>
<td>Rock cover</td>
<td>-0.225</td>
<td>0.111</td>
<td>-0.443 – -0.007</td>
<td>-22.5%</td>
</tr>
<tr>
<td></td>
<td>Constant</td>
<td>-2.054</td>
<td>2.434</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Figure 6.** Predicted probability of positive identification of forest stands, relative to the percent cover of lichens measured at 3 site types on the winter range of Bathurst caribou. Values for all other covariates in each best model (*i.e.*, basal area of conifers and percent ground cover of moss, litter, and rock) were held at their respective means.
Our model of feeding-site selection indicates that caribou chose to forage in areas that were characterised by a high percentage of ground cover of lichen and a low volume of conifer trees. Feeding sites were also older than random sites in comparable habitats (143 ± 35 y versus 96 ± 19 y, respectively). These findings are in accordance with studies of the winter foraging ecology of barren-ground caribou across North America. For example, Thomas, Barry, and Alaie (1996) reported that caribou favoured stands with a high abundance of terricolous lichens, particularly Cladina mitis and Cetraria nivalis, and generally occupied forests older than 150 y. Likewise, Saperstein (1996) found that Alaskan caribou (Rangifer tarandus granti) disproportionately cratered at sites yielding high lichen to moss ratios, and Sharma, Couturier, and Côté (2009) determined that caribou on the Quebec–Labrador peninsula preferred open forests containing terrestrial lichen in the understory.

**Importance of Lichen Biomass**

There is increasing evidence that abundant lichen forage is an important determinant of caribou distribution on winter range (Klein, 1982; Thomas, Barry & Alaie, 1996; Joly et al., 2003; 2007; Joly, Bente & Dau, 2007; Sharma, Couturier & Côté, 2009; Joly, Chapin & Klein, 2010). In the absence of sufficient lichen forage, caribou herds may experience altered distribution patterns (Joly et al., 2003; 2007; Joly, Bente & Dau, 2007; Joly, Chapin & Klein, 2010) and in some cases declining recruitment (Skogland, 1986). However, moderate lichen depletion has not been shown to affect caribou population dynamics in North America, except during unusually severe winters (Fleischman, 1990). Until recently, the Beverly caribou herd maintained a high reproductive rate and fair body condition (Thomas & Kiliaan, 1998) despite a high frequency of forest fires on their winter range (Scott, 1964; Miller, 1976; Thomas, 1991; Thomas & Kiliaan, 1998). However, the relationship between the reproductive productivity of individual caribou and lichen availability is complex. One must also consider the availability of alternative forage, distribution of lichen habitats (i.e., foraging efficiency), abundance of lichens on non-traditional ranges, severity of snow conditions, and physiological condition of individual caribou.

Although our data on lichen abundance fall short of a range-wide analysis, we were able to capture site conditions in traditional areas of the winter range used by Bathurst caribou. We employed equations developed by Moen, Danell, and Holt (2007) to determine the biomass of fruticose lichens (excluding Stereocaulon species) at experimental and control sites classified as unburned. Our data indicated that the biomass of fruticose lichens on the winter range of Bathurst caribou was high (2464 ± 248 kg ha⁻¹) compared to winter habitats of caribou in Alaska and the Yukon Territory (Fleischman, 1990; Russell, Martell & Nixon, 1993) and falls in the general range of lichen values reported for winter habitats of the more easterly Beverly herd, as well as portions of Saskatchewan, Manitoba, Ungava, and Scandinavia (Table IV; Scotter, 1970; Miller, 1976; Gaare & Skogland, 1980; Helle, 1981; Crête, Morneau & Nault, 1990; Thomas, Barry & Alaie, 1996; Arseneault et al., 1997; Bergerud, Luttich & Camps, 2008).

Differences in study design and sampling technique are inherent limitations when comparing data from multiple studies. Our data are based on values of lichens from mature lichen-dominant communities (43–264 y old), while some studies report the mean value of lichen biomass from all community types present. In addition, we separated the live portion of the lichen thallus from the base when measuring height values used to calculate biomass. We believe that this provides a more accurate depiction of the amount of lichen available to caribou and generates a more conservative measure of biomass. Furthermore, many researchers have

**Table IV. Lichen biomass measurements (kg ha⁻¹) for select winter ranges of caribou and reindeer (Rangifer tarandus).** Range types reported in the various studies included habitats used by caribou versus those not used by caribou, distinct age classes of habitat, lichen-dominated communities, heath forests, and all community types present. Thallus indicates whether or not the dead bases of lichen thalli were included in the biomass estimates.

<table>
<thead>
<tr>
<th>Location</th>
<th>Herd</th>
<th>Range type</th>
<th>Thallus</th>
<th>Biomass</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Northwest Territories</strong></td>
<td><strong>Bathurst</strong></td>
<td>Used unburned forest</td>
<td>No</td>
<td>2412</td>
<td>This study</td>
</tr>
<tr>
<td><strong>Northwest Territories</strong></td>
<td><strong>Bathurst</strong></td>
<td>Random unburned forest</td>
<td>No</td>
<td>2516</td>
<td>This study</td>
</tr>
<tr>
<td><strong>Northwest Territories</strong></td>
<td><strong>Beverly (west block)</strong></td>
<td>All present</td>
<td>No</td>
<td>2594</td>
<td>Thomas, Barry &amp; Alaie, 1996</td>
</tr>
<tr>
<td><strong>Northwest Territories</strong></td>
<td><strong>Beverly (east block)</strong></td>
<td>All present</td>
<td>No</td>
<td>6250</td>
<td>Thomas, Barry &amp; Alaie, 1996</td>
</tr>
<tr>
<td><strong>Northern Saskatchewan</strong></td>
<td><strong>Beverly / Kaminuriak</strong></td>
<td>Lichen-dominant</td>
<td>No</td>
<td>810</td>
<td>Scotter, 1970</td>
</tr>
<tr>
<td><strong>Northern Saskatchewan</strong></td>
<td><strong>Kaminuriak</strong></td>
<td>Lichen-dominant</td>
<td>Yes</td>
<td>5850</td>
<td>Miller, 1976</td>
</tr>
<tr>
<td><strong>Northern Manitoba</strong></td>
<td><strong>Leaf River</strong></td>
<td>Lichen-dominant</td>
<td>Unknown</td>
<td>1223</td>
<td>Crête, Morneau &amp; Nault, 1990</td>
</tr>
<tr>
<td><strong>Ungava</strong></td>
<td><strong>George River</strong></td>
<td>All present</td>
<td>Unknown</td>
<td>3170</td>
<td>Bergerud, Luttich &amp; Camps, 2008</td>
</tr>
<tr>
<td><strong>Northern Quebec</strong></td>
<td><strong>George / Leaf River</strong></td>
<td>Forests &lt; 30 y</td>
<td>No</td>
<td>530</td>
<td>Arseneault et al., 1997</td>
</tr>
<tr>
<td><strong>Northern Quebec</strong></td>
<td><strong>George / Leaf River</strong></td>
<td>All present</td>
<td>No</td>
<td>2800</td>
<td>Arseneault et al., 1997</td>
</tr>
<tr>
<td><strong>Northern Quebec</strong></td>
<td><strong>George / Leaf River</strong></td>
<td>Forests &gt; 90 y</td>
<td>No</td>
<td>8010</td>
<td>Arseneault et al., 1997</td>
</tr>
<tr>
<td><strong>Northeast Quebec</strong></td>
<td><strong>George / Leaf River</strong></td>
<td>Lichen-dominant</td>
<td>No</td>
<td>5440</td>
<td>Arseneault et al., 1997</td>
</tr>
<tr>
<td><strong>Central Yukon</strong></td>
<td><strong>Porcupine</strong></td>
<td>All present</td>
<td>Yes</td>
<td>508</td>
<td>Russell, Martell &amp; Nixon, 1993</td>
</tr>
<tr>
<td><strong>Central Alasca</strong></td>
<td><strong>Delta (traditional areas)</strong></td>
<td>All present</td>
<td>Unknown</td>
<td>100–850</td>
<td>Fleischman, 1990</td>
</tr>
<tr>
<td><strong>Central Alasca</strong></td>
<td><strong>Delta (peripheral areas)</strong></td>
<td>All present</td>
<td>Unknown</td>
<td>&gt; 2000</td>
<td>Fleischman, 1990</td>
</tr>
<tr>
<td><strong>Northwest Alaska</strong></td>
<td><strong>Western Arctic Herd</strong></td>
<td>Used unburned forest</td>
<td>Unknown</td>
<td>3007</td>
<td>Joly, Chapin &amp; Klein, 2010</td>
</tr>
<tr>
<td><strong>Northwest Alaska</strong></td>
<td><strong>Western Arctic Herd</strong></td>
<td>Random unburned forest</td>
<td>Unknown</td>
<td>1260</td>
<td>Joly, Chapin &amp; Klein, 2010</td>
</tr>
<tr>
<td><strong>Northwest Alaska</strong></td>
<td><strong>Western Arctic Herd</strong></td>
<td>Random burned forest</td>
<td>Unknown</td>
<td>818</td>
<td>Joly, Chapin &amp; Klein, 2010</td>
</tr>
<tr>
<td><strong>Northern Finland</strong></td>
<td><strong>Reindeer</strong></td>
<td>Heath forest</td>
<td>Unknown</td>
<td>520</td>
<td>Helle, 1981</td>
</tr>
<tr>
<td><strong>Norway</strong></td>
<td><strong>Reindeer</strong></td>
<td>Climax forest stands</td>
<td>Unknown</td>
<td>11000</td>
<td>Gaare &amp; Skogland, 1980</td>
</tr>
</tbody>
</table>

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included lichen biomass of *Stereocaulon* species in their assessments, while we did not.

Based on estimates provided by Bergerud, Luttich, and Camps (2008: pages 166, 495, 497, 500, 501), our data for lichen abundance suggest that conditions on the late-winter range of Bathurst caribou may support a herd density of approximately 1–2 animals per km² in unburned areas. Considering that the area of mature winter range (i.e., not classified as post-fire) below treeline totals approximately 240,186 km², current lichen stores could support between 240,186 and 480,372 caribou. Given the number of ecological factors that are known to affect barren-ground caribou populations (e.g., weather, insects, plant phenology; Post & Stenseth, 1999), this is a very simplistic index of population carrying capacity. A more conclusive analysis of winter range conditions would account for the size and distribution of mature lichen communities, since spatial variation influences foraging efficiency (Fleischman, 1990). Population dynamics aside, a change in the spatial availability of caribou can have large implications for access by harvesters. Our data suggest that wildfire can influence the distribution of caribou as they seek out individual stands or areas of the winter range with longer fire-return intervals and more abundant terrestrial lichen.

**Conclusion**

Specific habitat features such as lichen cover and stand age are important variables to consider when evaluating the availability of winter range for barren-ground caribou. In this study, caribou selected for mature habitats with a high percentage of ground cover of fruticose lichen and few or small conifer trees. Although the lichen resources present at winter range habitats are relatively abundant today (Table IV), more frequent and severe wildfires resulting from climate warming (Stocks et al., 1998; Rupp, Chapin & Starfield, 2000; McCoy & Burn, 2005) may reduce the quantity and quality (e.g., changes in the composition of lichen communities) of winter forage available to caribou (Joly et al., 2007; Sharma, Coutourier & Côté, 2009; Joly, Chapin & Klein, 2010). As demonstrated for other herds, such reductions could lead to declines in recruitment and body size of adult females (Skogland, 1986), as well as altered distribution patterns (Joly et al., 2003; 2007; Joly, Bente & Dau, 2007; Joly, Chapin & Klein, 2010).

Although forage was the most important variable to explain feeding-site selection during winter in this study, the observed pattern of caribou distribution may actually be a product of numerous environmental and cognitive factors that vary from early to late winter, and at broader spatial scales. Confounding factors related to foraging conditions but not quantified in this study include snow conditions, distribution of predators, and ease of mobility (e.g., steepness of terrain). A hierarchical analysis that examines foraging ecology at multiple spatial and temporal scales would more fully explain the effects of lichen abundance and associated stand attributes on caribou distribution during winter (Johnson, 1980; Johnson, Parker & Heard, 2001).

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