ÉCOSCIENCE 17 (3): 321-333 (2010)

Winter habitat selection by caribou in relation to lichen abundance, wildfires, grazing, and landscape characteristics in northwest Alaska[1]

Kyle JOLY[2], National Park Service, Gates of the Arctic National Park and Preserve, Arctic Network Inventory and Monitoring Program, 4175 Geist Road, Fairbanks, Alaska 99709, USA, and University of Alaska Fairbanks, Institute of Arctic Biology, Fairbanks, Alaska 99775, USA, e-mail: kyle_joly@nps.gov
F. Stuart CHAPIN III & David R. KLEIN, University of Alaska Fairbanks, Institute of Arctic Biology, Fairbanks, Alaska 99775, USA.

Abstract: Lichens are an important winter forage for large, migratory herds of caribou (*Rangifer tarandus granti*) that can influence population dynamics through effects on body condition and in turn calf recruitment and survival. We investigated the vegetative and physiographic characteristics of winter range of the Western Arctic Herd in northwest Alaska, one of the largest caribou herds in North America. We made 3 broad comparisons: habitats used by caribou *versus* random locations, burned *versus* unburned habitats, and habitats within the current winter range *versus* those in the historic winter range and potential winter ranges. We found that lichen abundance was more than 3 times greater at locations used by caribou than found at random. The current winter range does not appear to be overgrazed as a whole, but continued high grazing pressure and consequences of climate change on plant community structure might degrade its condition. Within the current winter range, lichen abundance was more than 4 times greater at unburned locations than at recently (< 58 y) burned locations. Other than lichen abundance, there were few vegetative differences between burned (mean = 37 ± 1.7 y) and unburned locations. The historic winter range has low lichen abundance, likely due to sustained grazing pressure exerted by the herd, which suggests that range deterioration can lead to range shifts. Recovery of this range may be slowed by continued grazing and trampling during migration of caribou to and from their current winter range, as well as by high wildfire frequency and other consequences of climate change. The area identified as potential winter range is unlikely to be utilized regularly by large numbers of caribou primarily due to low lichen abundance associated with extensive deciduous stands, large areas of riparian habitat, high moose (*Alces alces*) densities, and greater prevalence of wildfire. Our results suggest that lichens are important in the overwintering ecology of caribou that face the energetic costs of predator avoidance and migration.
Keywords: caribou, fire, grazing, lichens, range expansion, Western Arctic Herd.

Résumé : Les lichens sont un fourrage d'hiver important pour les grands troupeaux de caribous migrateurs (*Rangifer tarandus granti*) qui peut influencer la dynamique de population par des effets sur la condition physique et ainsi influencer le recrutement et la survie des veaux. Nous avons étudié les caractéristiques physiographiques et de la végétation de l'aire d'hivernage du troupeau de l'ouest de l'Arctique dans le nord-ouest de l'Alaska, un des plus grands troupeaux de caribous d'Amérique du Nord. Nous avons fait 3 grandes comparaisons : habitats utilisés par le caribou *versus* sites aléatoires, sites brûlés *versus* non brûlés et habitats à l'intérieur de l'aire actuelle d'hivernage *versus* ceux de l'aire historique et ceux d'une aire potentielle d'hivernage. Nous avons constaté que l'abondance de lichens était plus de 3 fois supérieure dans les sites utilisés par le caribou que dans des sites aléatoires. L'aire actuelle d'hivernage ne semble pas être surbroutée dans l'ensemble, mais la poursuite de la forte pression de broutement et les conséquences des changements climatiques sur la structure de la communauté végétale pourraient dégrader sa condition. Au sein de l'aire actuelle d'hivernage, l'abondance de lichens était plus de 4 fois supérieure dans les sites non brûlés que dans ceux brulés récemment (< 58 ans). À l'exception de l'abondance de lichens, il y avait peu de différences dans la végétation entre les sites brûlés (moyenne = 37 ± 1,7 ans) et non brûlés. L'aire historique d'hivernage a une faible abondance de lichens probablement en raison d'une pression continue de broutement par le troupeau ce qui suggère qu'une détérioration de l'habitat puisse mener à des changements dans l'aire de distribution. Le rétablissement de cette aire peut être ralenti par le broutement continu et le piétinement lors de la migration des caribous de leur présente aire d'hivernage et en direction de celle-ci, aussi bien que par la fréquence élevée de feu d'origine naturelle et d'autres conséquences des changements climatiques. Il est peu probable que la zone identifiée comme une aire potentielle d'hivernage soit utilisée régulièrement par un grand grand nombre de caribous principalement en raison de la faible abondance de lichens associée aux vastes peuplements feuillus, de grandes zones d'habitat riverain, d'une densité élevée d'orignal (*Alces alces*) et d'une plus grande prévalence de feu. Nos résultats suggèrent que les lichens sont importants dans l'écologie hivernale du caribou qui doit faire face aux dépenses énergétiques liées à l'évitement des prédateurs et à la migration.
Mots-clés : broutement, caribou, expansion de l'aire de répartition, feu, lichens, troupeau de l'ouest de l'Arctique.

Nomenclature: Brodo, Sharnoff & Sharnoff, 2001; Feldhamer, Thompson & Chapman, 2003; Viereck & Little, 2007.

[1]Rec. 2009-12-15; acc. 2010-07-05.
Associate Editor: Daniel Fortin.
[2]Author for correspondence.
DOI 10.2980/17-3-3337

Introduction

Caribou (*Rangifer tarandus*) distribution and population dynamics are driven by the complex interactions of numerous influences, including climate, predation, habitat, year-round forage quality, quantity, and availability, insects, parasites, diseases, density-dependence, disturbance, industrial development, and other factors (Bergerud, 1980; Messier *et al*., 1988; Klein, 1991; Post & Stenseth, 1999; Johnson *et al*., 2005; Brown *et al*., 2007; Joly *et al*., 2007; Pederson *et al*., 2007; Briand *et al*., 2009; Couturier *et al*., 2009; Hughes *et al*., 2009; Vors & Boyce, 2009). While it is important to understand that caribou population dynamics are a product of complex interactions among these factors, it is difficult to conduct research that simultaneously incorporates all of them. The quality of winter range has been a frequent focus of caribou research because range quality can affect body condition, fetal development, birth weights and growth rates of calves, and milk production (White, 1983; Parker, Barboza & Stephenson, 2005). Calf weights, in turn, are associated with herd productivity (Couturier *et al*., 2009). Thus, poor winter range conditions can have a pronounced impact on caribou population dynamics through its effects on recruitment.

Body condition, inclusive of available energy and protein stores, affects the ability of cervids to survive and reproduce (Parker, Barboza & Gillingham, 2009). High-protein forage is limited in its availability to cervids during late winter when gestational demands are high (Parker, Barboza & Stephenson, 2005; Brown *et al*., 2007). Caribou are unique among cervids in this respect because of the primary role lichens generally play in their winter diet. Lichens, though high in available energy, have a protein content that, by themselves, is below maintenance levels for most northern cervids (Person *et al*., 1980; Parker, Barboza & Stephenson, 2005). Although dietary protein requirements during winter are low in contrast to the summer period (White *et al*., 1981), an inadequate protein balance can cause catabolism of body tissues, reduce growth, or compromise *in utero* development in cervids (Parker, Barboza & Stephenson, 2005). Caribou acquire most protein during summer, when high-protein forage is available, and make greater use of lichens, which are high in digestible energy, in winter, when energy demands are high (Parker, Barboza & Gillingham, 2009). Caribou distribution in winter must balance the competing demands of acquiring enough quality forage to meet their energetic demands and avoiding predation (Brown *et al*., 2007; Parker, Barboza & Gillingham, 2009).

Large, migratory herds of barren-ground caribou generally rely heavily upon terricolous, fruticose lichens, especially those of the *Cladina* genus, during winter (Person *et al*., 1980; White *et al*., 1981; Klein, 1982; 1991; Heggberget, Gaare & Ball, 2002). The Western Arctic Herd (WAH), which ranges over 360 000 km^2 of northwest Alaska, represents a quintessential herd of this type (Davis, Valkenburg & Reynolds, 1980; Dau, 2007). Terricolous lichens constitute the majority of forage for WAH caribou during winter (Saperstein, 1996; Joly, Cole & Jandt, 2007). Some have suggested, however, that lichens are not essential for caribou during winter and that a graminoid-dominated diet may be adequate for sustaining caribou and reindeer (also *R. tarandus*) populations (Bergerud, 1974; Heggberget, Gaare & Ball, 2002; van der Wal, 2006). However, this assertion is based on low-density, insular, non-migratory, and/or predator- and parasitic insect–free populations. Recently (< 55 y old) burned habitats exhibit rapid and vigorous re-growth of graminoids (Jandt *et al*., 2008), but low lichen cover, and such habitats are avoided during winter by WAH caribou (Joly, Bente & Dau, 2007). An analysis of the winter diets of the WAH revealed that graminoids were selected against despite their increasing prevalence in the landscape (Joly, Cole & Jandt, 2007). These findings support the hypothesis that lichens are an important forage for this herd during winter.

The abundance of forage lichens is typically associated with particular plant community types, soil characteristics, topography, grazing pressure, and time since disturbance (Morneau & Payette, 1989; Swanson, 1996; Racine *et al*., 2004; Holt, McCune & Neitlich, 2006; 2008; Jandt *et al*., 2008). Abundance is greatest where competition from vascular species is low (such as on acidic or sandy soils) and where there is low frequency of disturbance by flooding or wildfire (Swanson, 1996; Holt, McCune & Neitlich, 2006; 2008). Following a wildfire, it can take several decades for forage lichens to return to their former levels (Racine *et al*., 2004; Dunford *et al*., 2006; Holt, McCune & Neitlich, 2008; Jandt *et al*., 2008). Grazing and trampling by large numbers of caribou or reindeer can also reduce lichen abundance at the landscape level (Klein, 1968; Moser, Nash & Thomson, 1979; Morneau & Payette, 1989; Arseneault *et al*., 1997; Joly *et al*., 2007).

Declining populations of *Rangifer* have been linked to climate change (Vors & Boyce, 2009). The influences of climate change are already apparent in the Arctic and are predicted to become more pronounced over time (Callaghan *et al*., 2004). Indeed, the largest changes in faunal populations of the western hemisphere are projected to occur in arctic tundra habitats (Lawler *et al*., 2009). Experimental, field, and theoretical studies suggest that climate change negatively impacts lichen abundance (see review by Joly, Jandt & Klein, 2009). Climate change–related factors that act to reduce lichen abundance include competition with vascular plant species (which will increase shading and leaf litter), wildfire, warming and associated drying, and sustained grazing by *Rangifer*. Future reduction of lichen abundance may negatively affect caribou population dynamics.

Our main goal was to identify characteristics of primary caribou winter range by comparing sites used by caribou to random locations. Secondarily, we quantified differences between burned and unburned habitat and among the herd's current, historic, and potential future winter ranges. Finally, we identified landscape-level and site-specific factors that were associated with the abundance of forage lichens. We hypothesized that caribou would seek out and locate areas of high lichen abundance, that unburned habitat would provide greater lichen abundance than recently (< 58 y) burned habitat, and that the herd's current winter range would provide greater lichen abundance than either the historic or potential

winter ranges. This research has implications for the relative importance of winter forage for caribou, will inform critical and costly decisions regarding fire management, and will assist in the management of caribou as a subsistence and economic resource for communities in the Arctic.

Methods

STUDY AREA

With a population size of 377 000 in 2007, the WAH is the largest caribou herd in Alaska (Dau, 2007). Herd size peaked in 2003 at 490 000 caribou (Dau, 2007). The annual range of the WAH covers all of northwest Alaska, some 360 000 km^2 (Figure 1; Davis, Valkenburg & Reynolds, 1980). WAH caribou can be found throughout most of this range during the winter when at high population levels (~300 000 caribou; Joly, Bente & Dau, 2007). Winter use has been concentrated in the "current winter range" since at least the 1990s (Figure 2; Dau, 2007). This range is dominated by the Nulato Hills, a region of rugged but low-lying hills. Recently (*circa* 1996), the herd expanded its winter range to include the Seward Peninsula (Dau, 2007). Vegetation ranges from coastal wet meadows to tussock tundra, alpine tundra, boreal forest, narrow riparian corridors, and brush (*Alnus* spp., *Salix* spp.) fields. In the past, winter use was concentrated further north, in the Selawik National Wildlife Refuge (NWR), the Kiana Hills, and the upper Kobuk River, referred to henceforth as the "historic winter range" (Figure 2). This region is more forested to the east and transitions to a vast wetland complex within the refuge. To the southeast of the current winter range lies the Koyukuk National Wildlife Refuge (NWR) and the Yukon Lowlands (Nowacki *et al*., 2001), where the Koyukuk River drains into the Yukon River.

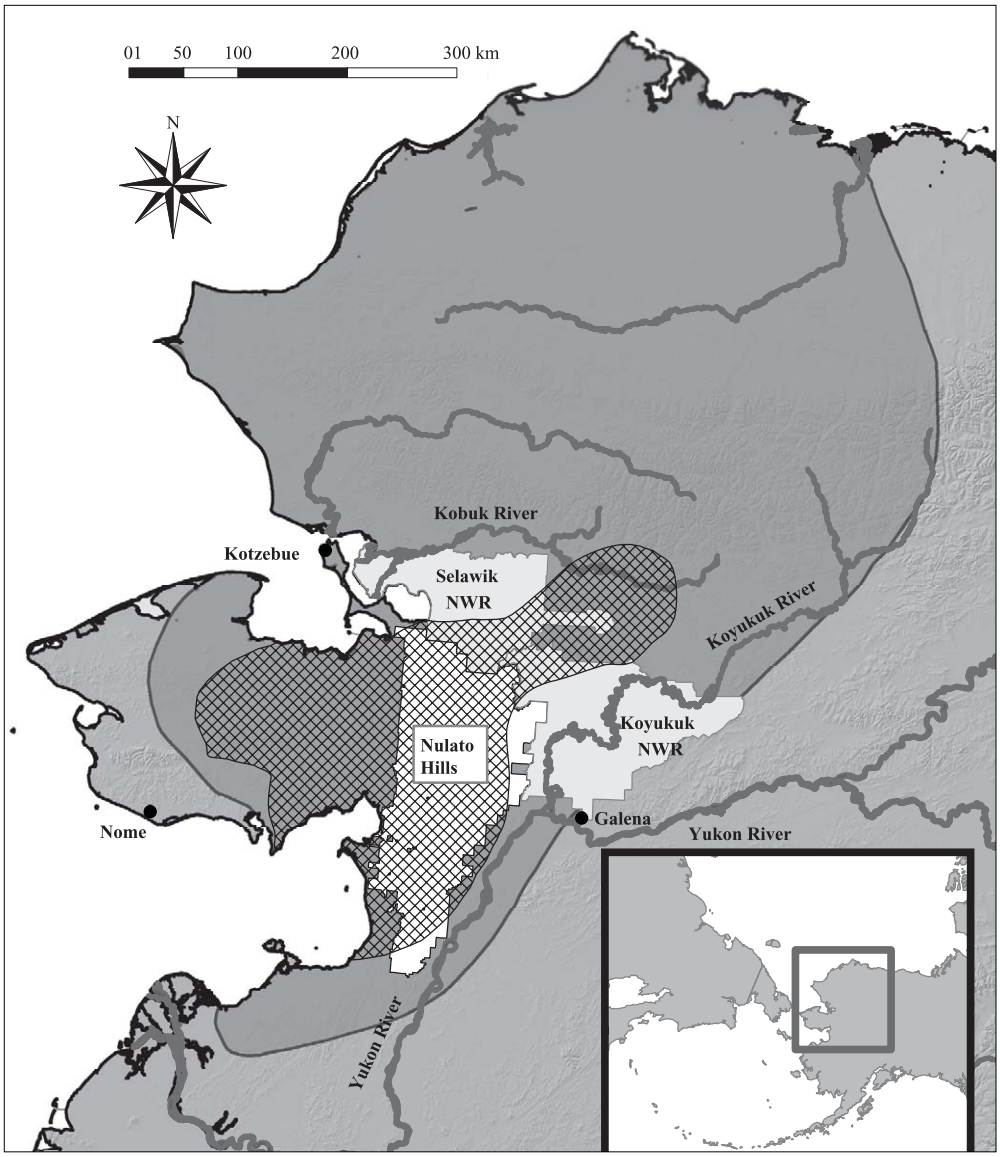

FIGURE 1. Range of the Western Arctic Caribou Herd, northwest Alaska, 2008. Annual range is shaded dark, while the current winter range is hatched. Courtesy of the Alaska Department of Fish and Game.

This region is dominated by boreal forest and contains vast riparian complexes. If the herd continues to expand its winter range, it might utilize this region, which we refer to as its "potential winter range" (Figure 2). For additional details, see Joly *et al*. (2009).

Vegetation plot location, data collection, and statistical analysis

We developed 8 treatment types for our study plots. Within the current winter range (Figure 2), we collected data at locations used by caribou that were unburned (T1) and burned (T2) and random locations that were unburned (T3) and burned (T4). In an area to the southeast of the current winter range, where the herd could potentially expand their winter range (hereafter potential winter range), we created plots using random locations that were unburned (T5) and burned (T6). Similarly, within the herd's historic winter range, in the Selawik National Wildlife Refuge, we created plots at random locations that were unburned (T7) and burned (T8). Plot locations used by caribou were randomly selected from a set of satellite telemetry locations from 1999 to 2005 (Joly, Bente & Dau, 2007). Caribou locations in the database were nearly unique (*i.e*., only 12 of 7049 [< 0.2%] had the same latitude and longitude as another caribou location), and thus the influence of frequency of usage was minimized. Unique, random locations were generated using ArcGIS 9.2 (ESRI, 2006). Burned status was determined using the Alaska Fire Service's Large Fire Database, which maps the perimeters of fires dating back to 1950 (data available at http://fire.ak.blm.gov/, accessed October 5, 2009). Thus, plots designated as burned did so within the past 58 y. However, the fire perimeters include unburned patches, also called inclusions, within the perimeter. We changed the designation of the plot treatment type if there was solid evidence that it was miscategorized using the Geographic Information System (GIS). For example, if a plot was designated T3 (random/unburned) but there were obvious

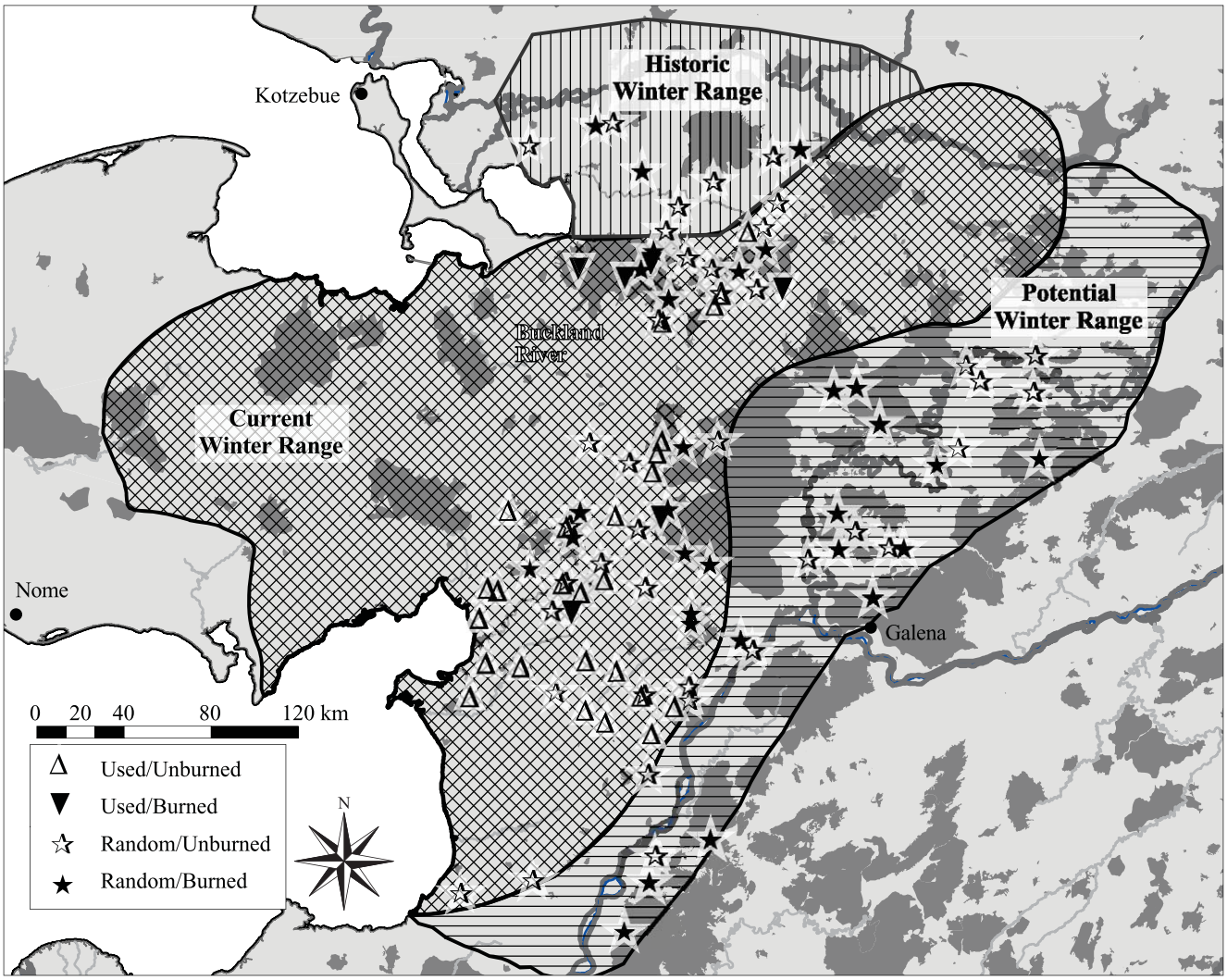

Figure 2. Study plot locations and winter ranges of the Western Arctic Caribou Herd, northwest Alaska, 2008. Plots designated as "Used" were determined by satellite telemetry locations of collared caribou. Plots designated as "Burned" did so recently (< 58 y). The darkly shaded polygons are the outlines of these recent burns (courtesy of the Alaska Fire Service). The current winter range is hatched, the historic winter range is identified by vertical lines, and a potential winter range (an area examined to see if caribou might expand their winter range there in the future) is identified by horizontal lines.

signs of burning (*i.e.*, standing burned poles or char), the plot would be re-designated T4 (random/burned). Similarly, presence of obvious caribou sign (*e.g.*, pellets, shed antlers, evidence of cratering) would cause the re-designation of a T3 plot to a T1 (used/unburned) plot type.

We used helicopters to access the plots, from 28 June to 22 July 2008, and hand-held Global Positioning System (GPS) units to navigate to the plot origin. A 10- × 10-m grid was formed from the origin. Vegetation was identified to species level, where possible, at 4 vertical layers every metre within the grid for a total of 100 intercepts per plot. The layers were ground (*e.g.*, lichens, mosses), herbaceous (*e.g.*, sedges, grasses, herbs), shrubs < 1 m (*e.g.*, *Ledum* spp., *Vaccinium* spp.), and canopy > 1 m (*e.g.*, *Picea* spp., *Populus* spp.). We used these data to determine percent cover. We considered *Cladina arbuscula/mitis* (referred to as *C. mitis* henceforth), *C. rangiferina/stygia* (referred to as *C. rangiferina* henceforth), *C. stellaris*, and *Cladonia uncialis* to be primary forage species and *Cetraria cucullata*, *C. ericetorum*, *C. islandica*, *C. nivalis*, *Cladonia amaurocraea,* and *C. gracilis* to be secondary forage species (Joly *et al*., 2007). For each primary and secondary caribou forage lichen that was encountered, we measured height to the nearest 0.5 cm using a blunt metal rod (3 mm ∅; Moen, Danell & Holt, 2007; also see Johnson, Parker & Heard, 2001). Total forage lichen is the combination of both primary and secondary lichens; all other lichen species were considered non-forage. Following Moen, Danell, and Holt (2007), we determined lichen volume by multiplying percent cover by height by plot area. Lichen volume is highly correlated with lichen biomass, so we used the formulas provided by Moen, Danell, and Holt (2007) to approximate lichen biomass from its volume. We did not develop correction factors for our study area, so the biomass estimates should be viewed cautiously. Additionally, we collected data on near-surface soil pH, depth of the organic layer, and amount of caribou utilization. Utilization was determined by identifying signs of use (*e.g.*, pellets, signs of cratering, trampling) within a 1-m arc at the end of each grid row (*sensu* Joly *et al*., 2007); recorded as the percentage of arcs with evidence.

We used pre-existing GIS data and recorded the following parameters for each plot: slope, aspect, elevation, habitat type (30-m National Land Cover Database of 2001, data available from the Multi-Resolution Land Characteristics Consortium, www.mrlc.gov, accessed October 5, 2009), and 2 measures of terrain ruggedness. These measures were determined using a vector ruggedness measure (VRM) at relatively fine (180 m) and coarse (1 km) scales (Sappington, Longshore & Thompson, 2007). For plots classified as burned, we used the Large Fire Database to determine stand age. We subjectively conferred a conservative age of 100 y to unburned plots for regression analyses and display purposes. Although fire rotation can be as short as 40–80 y in the boreal forest under the influence of the continental climate of eastern Alaska (Yarie, 1981; Johnstone *et al*., 2009), it is typically longer (100–200 y; Payette *et al*., 1989; Lynch *et al*., 2003; Kasischke, Rupp & Verbyla, 2006). Rotation period can be several hundreds of years in the tundra biome (Wein, 1976; Kasischke, Rupp & Verbyla, 2006). Mark *et al*. (1985) estimated the ages of unburned tussocks to be 150 y.

We used analysis of variance (ANOVA) to test for differences among treatment types, burned status, and winter ranges (*i.e.*, current, potential, and historic). We used linear regression to identify associations with plot lichen volume. Combinations of vegetation characteristics (herbaceous cover, moss cover, shrub cover, canopy cover), plot characteristics (latitude, longitude, pH, stand age), and GIS layers (elevation, slope, terrain ruggedness) were used, *a priori*, to develop potentially explanatory models. We used Akaike's Information Criterion (AIC_c) for small sample sizes and the change in AIC_c (ΔAIC_c; Burnham & Anderson, 2002) to determine the most parsimonious models. We calculated the variance inflation factor (VIF) to assess multicollinearity. We standardized the values of the covariates by subtracting their means and dividing by their standard deviations in order to show the relative influence of these factors (Neter *et al*., 1996; Schimdt *et al*., 2009). Significance for all tests was defined at $\alpha = 0.050$ level unless otherwise specified.

Results

Reassignment of plot treatment type

Ground observation of plots indicated that only 6 of 15 (40.0%) plots used by caribou within the mapped fire perimeters (T2) had actually burned. A total of 12 of 32 (37.5%) of the satellite-location–derived points were changed to a different plot type based on ground observations. Total forage lichen volume in plots reassigned to T1 (used/unburned) (1037.2 ± 256.4 $dm^3 \cdot 100\ m^{-2}$) was significantly greater than those that remained as T2 (used/burned) plots (125.0 ± 296.1 $dm^3 \cdot 100\ m^{-2}$; $F_{1, 13} = 5.42$, $P = 0.038$). Total forage lichen volumes in the remaining T2 (used/burned) plots were not significantly different than T4 plots (random/burned; $P > 0.100$).

A full 60% of plots determined by satellite telemetry to be within a burn but used by caribou did not fit this categorization. Part of this error rate is undoubtedly due to lack of precision in the large fire database, but it strongly highlights the need for much more accurate caribou locations. All 6 remaining T2 (used/burned) plots were based on caribou locations from outside the mid-winter (*i.e.*, December through mid-April) period.

Used *versus* random unburned plots within the current winter range

Total forage lichen volume was significantly greater in locations used by caribou that were unburned (1427.3 ± 194.0 $dm^3 \cdot 100\ m^{-2}$) than at randomly located unburned sites (447.8 ± 206.2 $dm^3 \cdot 100\ m^{-2}$; $F_{1, 48} = 11.97$, $P = 0.001$). In addition to having greater cover of forage lichens, areas in the current winter range used by caribou had lower cover of mosses, forbs, and shrubs compared to random points (Table I).

Unburned *versus* burned plots

In the current winter range, for both used and random plots, total forage lichen volume was

significantly ($F_{1, 70}$ = 9.79, P = 0.003) greater in unburned plots (967.52 ± 133.43 $dm^3 \cdot 100\ m^{-2}$) than on burned plots (217.49 ± 1991.3 $dm^3 \cdot 100\ m^{-2}$). Forage lichen cover was also significantly ($F_{1, 70}$ = 11.97, P = 0.001) greater in unburned plots (23.3 ± 2.9%) than in burned plots (5.1 ± 4.4%). We did not detect any other significant vegetation differences between burned and unburned plots. The average age of burned plots was 37 ± 1.7 y. Though total forage lichen volume was nearly twice as much in random unburned plots (447.79 ± 136.84 $dm^3 \cdot 100\ m^{-2}$) than in random burned plots (252.18 ± 164.06 $dm^3 \cdot 100\ m^{-2}$) within the current winter range, the difference was not statistically significant ($F_{1, 38}$ = 0.84, P = 0.366).

TABLE I. Differences in vegetation between unburned locations used by caribou and randomly selected unburned locations within the current winter range of the Western Arctic Caribou Herd, northwest Alaska, 2008.

	Caribou locations		Random locations		$F_{1, 48}$
Vegetation (layer)	% Cover	SE	% Cover	SE	
Forage lichen (ground)	34.6	4.1	10.6	4.4	16.00**
Moss (ground)	25.3	4.4	38.0	4.7	3.81*
Forb (herb)	8.8	3.4	22.0	3.6	7.03**
Graminoid (herb)	22.5	3.5	16.5	3.7	1.37
Alder (shrub)	0.2	0.5	2.0	0.5	6.35**
Tall shrub (shrub)	27.7	3.9	43.5	4.2	7.67**
Willow (shrub)	1.9	2.6	12.2	2.8	7.28**
Alder (canopy)	0.1	1.4	4.3	1.4	4.60**
Willow (canopy)	0.3	2.3	11.2	2.5	10.33**
Total shrub (canopy)	0.7	2.7	17.3	2.9	18.06**
Total tree (canopy)	1.0	0.8	2.6	0.8	1.86
Total (canopy)	1.7	2.9	19.9	3.1	18.70**

* P < 0.100; ** P < 0.050.

Forage lichen cover and volume in the potential winter range were not significantly different between random unburned and burned locations. Dwarf birch (*Betula* spp.) cover in the shrub layer was significantly greater ($F_{1, 22}$ = 8.45, P = 0.008) in burned (8.1 ± 1.5%) than in unburned plots (1.5 ± 1.7%). Tree ($F_{1, 22}$ = 5.41, P = 0.030) and total ($F_{1, 22}$ = 8.01, P = 0.010) canopy cover were significantly greater in unburned plots (24.5 ± 6.7%, 31.9 ± 7.1%, respectively) than burned plots (3.9 ± 5.8%, 5.2 ± 6.2%, respectively) in the potential winter range. The average age of burned plots was 25 ± 3.4 y.

Forage lichen cover and volume were not significantly different between random unburned and burned locations in the historic winter range. Dwarf birch cover in the shrub layer was significantly greater ($F_{1, 10}$ = 7.55, P = 0.023) in burned (11.5 ± 2.4%) than in unburned plots (3.1 ± 1.8%) in the historic winter range, similar to the pattern found in the potential winter range. The average age of burned plots was 37 ± 0.1 y.

DIFFERENCES IN VEGETATION AMONG UNBURNED CURRENT, POTENTIAL, AND HISTORIC WINTER RANGES

Although total forage lichen volume in the potential (274.97 ± 221.59 $dm^3 \cdot 100\ m^{-2}$) and historic (108.77 ± 264.86 $dm^3 \cdot 100\ m^{-2}$) winter ranges were only 62% and 24%, respectively, of that of the current (447.79 ± 146.11 $dm^3 \cdot 100\ m^{-2}$) winter range, the differences were not statistically significant ($F_{2, 39}$ = 0.70, P = 0.505) due to high variability. The same held true for forage lichen cover (Table II). Small sample sizes (Table II) likely hindered our statistical analyses. Although there were relatively few statistically significant differences in vegetation between the current winter range and either the historic or the potential winter range, there were some

TABLE II. Percent lichen cover by treatment type among winter ranges of the Western Arctic Caribou Herd, northwest Alaska, 2008. Total cover includes all types of lichens, whereas forage lichen includes only primary and secondary forage species. "Used" notation under "Treatment" represents a plot where a caribou was located as determined by satellite telemetry data. "Burned" means that the location recently (< 58 y) burned.

Winter range	Treatment	n	Total (%)	SE	Forage (%)	SE
Current	T1 – Used/Unburned	26	41.1	26.7	34.6	3.1
Current	T2 – Used/Burned	6	7.5	10.1	3.5	6.6
Current	T3 – Random/Unburned	23	14.8	19.9	10.6	3.3
Current	T4 – Random/Burned	16	16.3	19.0	5.8	4.0
Potential	T5– Random/Unburned	10	7.6	13.7	4.9	5.1
Potential	T6 – Random/Burned	13	18.8	18.6	7.5	4.5
Historic	T7– Random/Unburned	7	6.4	5.9	3.7	6.1
Historic	T8 – Random/Burned	4	13.5	7.3	4.5	8.0

TABLE III. Relative differences in vegetation among random unburned locations within the current (C), potential (P), and historic (H) winter ranges of the Western Arctic Caribou Herd, northwest Alaska, 2008. Significance level of * P < 0.100 and ** P < 0.050.

	Current		Potential		Historic		$F_{2, 39}$	Relative
Vegetation (layer)	% Cover	SE	% Cover	SE	% Cover	SE		differences
Dwarf birch (shrub)	9.5	1.4	1.5	2.1	3.1	2.5	6.27	C > P, H**
Crowberry (shrub)	3.0	0.7	0.2	1.1	0.6	1.3	3.23	C > P, H*
All shrubs (shrub)	57.5	4.6	52.1	6.9	31.1	8.3	3.87	C > H**
Broadleaf trees (canopy)	0.7	3.3	15.2	5.0	0.0	0.0	3.2	P > C, H*
Conifer trees (canopy)	1.9	1.9	9.3	2.9	5.4	3.5	2.27	
Tall shrubs (canopy)	17.3	3.3	7.4	5.1	1.0	6.1	3.27	C > H**
All trees (canopy)	2.6	3.4	24.5	5.2	5.4	6.3	6.21	P > C**

ecologically important trends (Table III). In the shrub layer, both dwarf birch and crowberry (*Empetrum nigrum*) had significantly ($P < 0.100$ for the latter) greater cover in the current winter range than in the potential or historic winter ranges, and total shrub cover was greater in the current winter range than in the historic winter range. In the canopy layer, there were no significant differences among the current, potential, and historic winter ranges except for a lower tree canopy in the current than the potential winter range and greater tall shrub canopy cover in the current than the historic winter range (just as observed in the shrub layer). In general, these results indicate that the current winter range tended to have considerably more lichens than the historic or potential winter ranges and had significantly less tree cover than the potential winter range and more shrub cover than the historic winter range.

Lichen use by caribou

Total forage lichen volume was positively associated with signs of caribou use ($R^2 = 17.2$, $F = 21.44$, df = 104, $P < 0.001$). Only 4 of 53 plots (7.5%) with forage lichen cover < 5% showed any signs of utilization by caribou. Total forage lichen volume was negatively associated with latitude ($R^2 = 15.8$, $F = 19.30$, df = 104, $P < 0.001$). Primary and secondary lichen covers were negatively associated with latitude ($R^2 = 18.4$, $F = 23.20$, df = 104, $P < 0.001$ and $R^2 = 5.0$, $F = 5.44$, df = 104, $P = 0.022$, respectively), but non-forage lichen cover was not ($R^2 = 0.01$, $F = 0.59$, df = 104, $P = 0.444$).

Associations with lichen abundance

Stand age, moss cover, latitude, soil pH, and herbaceous cover parameters were in all of the most parsimonious models ($\Delta AIC_c < 4.0$) predicting lichen volume for classes containing primary forage lichens (*i.e.*, total forage, primary forage, *Cladina rangiferina*, and *Cladina mitis*; Table IV). The most parsimonious model predicting *Cetraria cucullata* volume (the most common secondary forage lichen) included stand age, moss cover, longitude, soil pH, canopy cover of shrubs, terrain ruggedness (1 km scale), and elevation parameters (Table IV). A complete listing of the candidate models

Table IV. The most parsimonious models ($\Delta AIC_c < 4.0$) predicting volume of different lichen classes within the winter range of the Western Arctic Caribou Herd, northwest Alaska, 2008. Abbreviations for the model parameters are "Age" for stand age, "Moss" for moss cover, "Lat" for latitude, "Long" for longitude, "pH" for soil pH, "Herb" for total herbaceous cover, "Shrub" for shrub cover in the canopy layer, "A" for alder in the shrub layer, "VRM180" for terrain ruggedness at the 180-m scale, "VRM1K" for terrain ruggedness at the 1-km scale, and "Elev" for elevation. "Sample" is the sample size used in the analysis, "*K*" is the number of degrees of freedom in the model, and "w_i" is the Akaike weight of the model.

Lichen class	Model parameters	Sample	*K*	Adj. R^2	ΔAIC_c	w_i
Total forage	Age, Moss, Lat, Long, pH, Herb, Shrub	104	8	53.4	0.0	0.33
	Age, Moss, Lat, pH, Herb, A	104	7	52.7	0.1	0.31
	Age, Moss, Lat, pH, Herb, A, VRM180	104	8	52.7	1.6	0.15
	Age, Moss, Lat, pH, Herb, Shrub, VRM180, Elev	104	9	53.1	1.9	0.13
	Age, Moss, Lat, Long, pH, Herb, VRM180	104	8	52.1	2.9	0.08
Primary forage	Age, Moss, Lat, pH, Herb, A	104	7	51.8	0.0	0.39
	Age, Moss, Lat, pH, Herb, A, VRM180	104	8	52.9	1.7	0.17
	Age, Moss, Lat, Long, pH, Herb, VRM180	104	8	51.6	1.8	0.16
	Age, Moss, Lat, pH, Herb, Shrub, VRM180, Elev	104	9	52.2	1.9	0.15
	Age, Moss, Lat, Long, pH, Herb, Shrub	104	8	51.5	2.0	0.14
Secondary forage	Age, Moss, Long, pH, Shrub, VRM1K, Elev	104	8	37.5	0.0	0.34
	Age, Moss, Lat, pH, Herb, Shrub, VRM180, Elev	104	9	37.9	0.7	0.24
	Age, Moss, Lat, Long, pH, Herb, Shrub	104	8	37.1	0.7	0.24
	Age, Moss, Lat, Long, pH, Herb, VRM180	104	8	35.7	3.0	0.08
	Age, Moss, Lat, pH, Herb, A	104	7	34.5	3.6	0.06
Cladina rangiferina	Age, Moss, Lat, Long, pH, Herb, VRM180	104	8	38.7	0.0	0.34
	Age, Moss, Lat, pH, Herb, Shrub, VRM180, Elev	104	9	39.1	0.7	0.24
	Age, Moss, Lat, Long, pH, Herb, Shrub	104	8	37.9	1.2	0.19
	Age, Moss, Lat, Long, pH, Herb	104	7	36.6	1.9	0.013
	Age, Moss, Lat, pH, Herb, A, VRM180	104	8	38.6	3.4	0.06
Cladina mitis	Age, Moss, Lat, Long, pH, Herb, VRM180	104	8	44.4	0.0	0.49
	Age, Moss, Lat, pH, Herb, Shrub, VRM180, Elev	104	9	44.3	1.4	0.24
	Age, Moss, Lat, pH, Herb, A	104	7	42.5	2.1	0.17
Cetraria cucullata	Age, Moss, Long, pH, Shrub, VRM1K, Elev	104	8	30.7	0.0	0.79
Total forage[1]	Age, Lat, Long	105	4	25.7	0.0	0.26
	Age, Lat, Long, Slope	105	5	26.3	0.4	0.21
	Age, Lat, Slope	105	4	24.7	1.46	0.12
	Age, Lat, Long, Elev	105	5	25.4	1.59	0.12
	Age, Lat, Long, VRM180, Slope	105	6	25.8	2.32	0.08
	Age, Lat, Long, Elev, Slope	105	6	25.6	2.53	0.07
	Age, Lat, Long, VRM1K, Slope	105	6	25.6	2.62	0.07
	Age, Lat	105	3	22.7	3.01	0.06

[1]Using only covariates that are available in existing GIS databases.

is provided in Table V. All VIF values were low (< 4.0), suggesting multicollinearity was not problematic. Using only pre-existing covariates available as GIS layers, the best model explaining variability of forage lichen volume included latitude, longitude, and stand age (Table IV). Elevation, terrain ruggedness (1-km scale), and slope were all significantly and positively associated (independently) with forage lichen volume. The relative influence of the covariates and directionality (positive or negative) of their associations are depicted in Figure 3. Latitude had a relatively strong negative association with lichen abundance, while stand age showed the opposite relationship.

In relation to shrubs specifically, forage lichen volume was associated positively with crowberry and dwarf birch cover, even using just the data from unburned plots. Forage lichen volume was negatively associated with alder (*Alnus* spp.) and willow (*Salix* spp.) cover in the shrub layer and with the depth of the organic layer ($R^2 = 23.0$, $F = 5.24$, df = 93, $P < 0.001$). Forage lichen volume also varied among habitat classes (Table VI). Approximations of lichen biomass from the volumes we calculated, as well as others we found in the literature, are listed in Table VII. Lichen biomass at caribou locations was much greater than found at random locations within Alaska but still much lower than climax lichen communities in Quebec and Scandinavia.

TABLE V. List of candidate models and number (*K*) of parameters used. Abbreviations for the model parameters are "Age" for stand age, "Moss" for moss cover, "Lat" for latitude, "Long" for longitude, "pH" for soil pH, "Herb" for total herbaceous cover, "Shrub" for shrub cover in the canopy layer, "A", "Db", "W" for alder, dwarf birch, and willow (respectively) in the shrub layer, "VRM180" for terrain ruggedness at the 180-m scale, "VRM1K" for terrain ruggedness at the 1-km scale, and "Elev" for elevation.

Model	*K*
Age, Moss, Lat, pH, Herb, Shrub, VRM180, Elev	8
pH, Herb, Shrub, A, Db, W, VRM1K	7
Lat, Long, pH, Herb, Shrub, VRM180, Elev	7
Age, Moss, Lat, Long, pH, Herb, Shrub	7
Age, Moss, Lat, pH, Herb, A, VRM180	7
Age, Moss, Long, A, Db, W, Elev	7
Age, Moss, Lat, Long, pH, Herb, VRM180	7
Age, Moss, Long, pH, Shrub, VRM1K, Elev	7
Age, Moss, Lat, pH, Herb, A	6
Age, pH, Herb, Shrub, VRM180, Elev	6
Age, Moss, Lat, Long, pH	5
Age, Moss, Lat, Long	4
Age, pH, Shrub	3
Moss, Herb, Shrub	3
Age	1

TABLE VI. Lichen volume ($dm^3 \cdot 100\ m^{-2}$) per plot by habitat type (from the National Land Cover Map of 2001).

Habitat	*n*	Volume	SE
Sedge/Herb	5	1461.1	375
Dwarf scrub	41	892.5	131
Shrub/Scrub	30	365.5	153
Woody wetlands	12	278.6	242
Herb wetlands	3	130.0	484
Evergreen forest	10	113.5	265
Grassland	1	60.0	0
Deciduous forest	1	0.0	0
Mixed forest	2	0.0	0

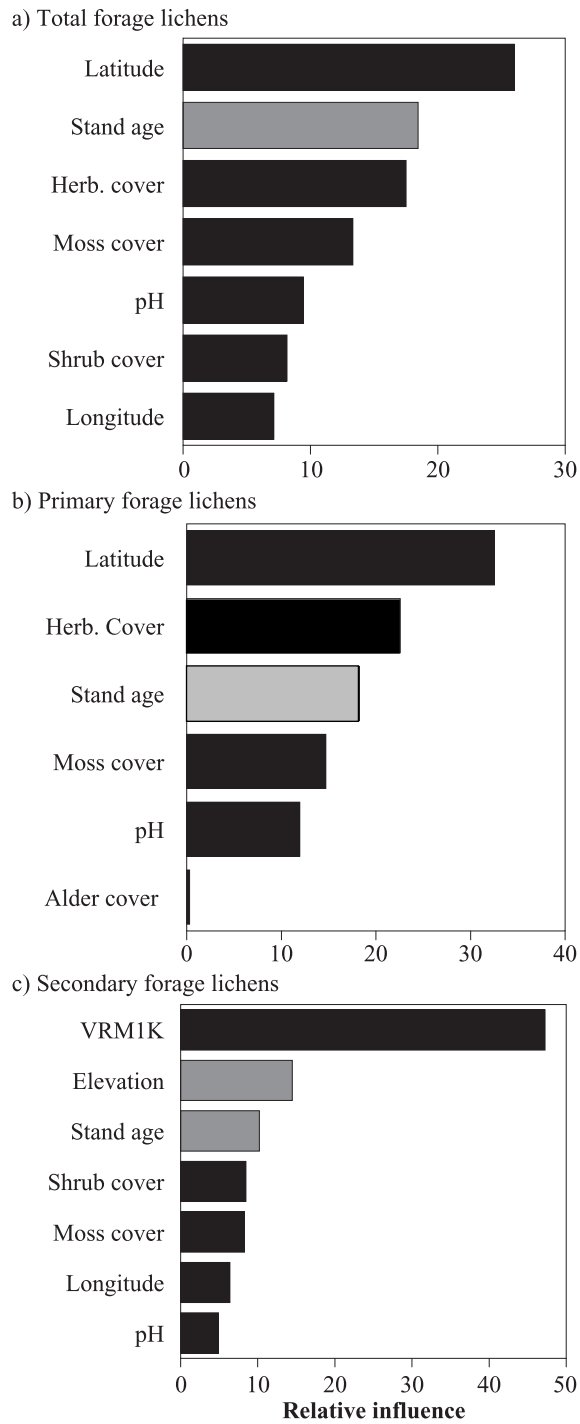

FIGURE 3. Relative influence (regression coefficients standardized by subtracting their means and dividing by their standard deviations) of covariates on modelling lichen abundance in the winter range of the Western Arctic Caribou Herd, northwest Alaska, 2008. Black bars indicate a negative association, while grey bars indicate a positive association.

TABLE VII. Comparison of lichen biomass (kg·ha^{-1}) among different ranges.

Study area	Range	Plot type	Biomass	Reference
Northwest Alaska	Current	Used by caribou (Unburned)	3007	this study
	Current	Random (Unburned)	1260	this study
	Current	Random (Burned)	818	this study
	Historic	Random (Unburned)	435	this study
	Potential	Random (Unburned)	873	this study
Northwest Alaska	Historic	Used by caribou (Unburned)	1400	Saperstein, 1993
East Alaska	Current	Used by caribou	1045	Collins *et al*., in press
	Current	Random	414	Collins *et al*, in press
	Historic	Random	224	Collins *et al*, in press
Quebec			1223	Crête, Morneau & Nault, 1990
Quebec		< 30 y old	530	Arseneault *et al*, 1997
Quebec		> 90 y old	8010	Arseneault *et al*, 1997
Finland		Ungrazed pasture	8000	Väre, Ohtonen & Mikkola, 1996
Norway		Climax stands	11 000	Gaare & Skogland, 1980

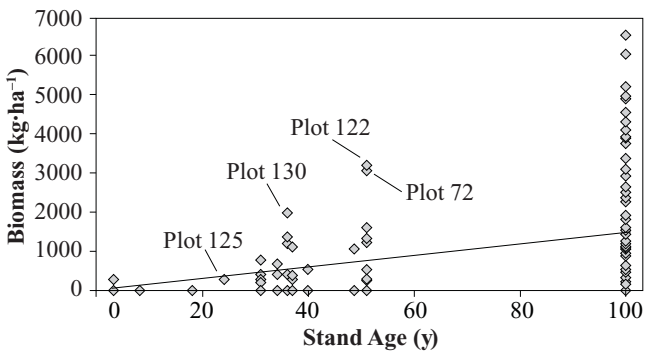

FIGURE 4. Forage lichen abundance *versus* stand age in the winter range of the Western Arctic Caribou Herd, northwest Alaska, 2008. Plots determined to be "unburned" were subjectively assigned a stand age of 100 y (see Methods).

While increasing lichen abundance was associated with stand age (Figure 4), there were a few somewhat anomalous study plots of interest. Plots #72 and #122, which burned in 1957 (stand age = 51 y) had 74% and 45% lichen cover, 31% and 36% of which were forage lichens, respectively. On the sandy soils of plot #130, which burned in 1972 (stand age = 36 y), lichen cover reached 50%, with 31% forage (predominately *Cladina mitis*) lichen cover. Aspen (*Populus tremuloides*) was quickly colonizing this area, so the high lichen cover may be a short-lived phase. Finally, plot #125, which burned in 1984 (stand age = 24 y) had a lichen cover of 42% (primarily *Cladonia* spp.), but with only 4% forage lichen cover.

Discussion

Lichens are a critical component of the winter diet of caribou in large, migratory herds with high energy expenditure for predation avoidance and migration, such as the WAH. The abundance of lichens can affect caribou body condition, which in turn can have multiplier effects that affect herd population dynamics (White, 1983; Parker, Barboza & Gillingham, 2009). WAH caribou selected sites that had more than 3 times greater lichen abundance (both percent cover and volume) of terricolous forage lichens than was found at random, unburned locations within the herd's current winter range. Additionally, locations used by caribou had lower moss, forb, shrub, and canopy cover than these random locations. Caribou utilized habitats that had less cover of tall shrubs; it is unclear if this is because of the lower lichen abundance in these habitat types, deeper snow, increased risk of predation, or a combination of these factors.

Lichen abundance was greatest in the current winter range and lowest in the historic winter range. Moreover, we found much lower lichen abundance on the historic range than was found there less than 20 y ago (Table VII), though the 2 studies are not directly comparable because methodologies and study sites varied. Northern areas of the current winter range have endured sustained heavy grazing (Joly *et al*., 2007), which was followed by the expansion of the herd's winter range onto the Seward Peninsula around 1996. From these findings, we infer that range deterioration can lead to range shifts, which is congruent with other research (*e.g.*, Ferguson, Gauthier & Messier, 2001). Our results reveal, however, that there are still large portions of current winter range with relatively high abundance of forage lichens.

We hypothesized that an indicator of severe overgrazing of winter range would be the lack of, or loose, association between forage lichen volume or biomass and lichen cover. Instead, we found that forage lichen volume was highly associated with forage lichen cover, from which we infer that the winter range of the WAH has not been overgrazed. In addition, signs of caribou use were associated with forage lichen abundance, while areas containing less than 5% cover of forage lichens had very low use, in agreement with other studies (Arseneault *et al*., 1997; Joly *et al*., 2007). We found forage lichen cover to be 10.6% and biomass to be 1260 kg·ha^{-1}; this also suggests to us that the range is not overgrazed, but it does have substantially less lichen biomass than some other *Rangifer* ranges (Table VII). Grazing and trampling by *Rangifer* are important factors in landscape-level reductions in lichen cover (Klein; 1968; Pegau, 1969; Moser, Nash & Thomson, 1979; Messier *et al*., 1988; Arseneault *et al*., 1997; Joly *et al*., 2007; Klein & Shulski, 2009). Forage lichen cover was reduced by a third in just 10 y in the northern portion of the WAH's current winter range (Joly *et al*., 2007); reductions of this order of magnitude could drive forage lichen abundance below desired thresholds in the current winter range (see Kumpula, Colpaert & Nieminen, 2000). In view of the

current low abundance of forage lichens in the historic winter range, the continuing damage to the lichens from trampling, associated loss of lichen biomass through foraging during the traditional semi-annual migration through the historic winter range, and reduced lichen growth due to climate warming, we expect that lichen cover and biomass will be slow to recover and that this area will be used less as winter range than during the historic period (Kumpula, Colpaert & Nieminen, 2000).

We hypothesized that associations between lichen abundance and latitude would be affected by caribou usage and/or climatic influences. Caribou can utilize northern portions of their winter range on both their fall and spring migration; thus, these areas may be subject to greater usage. Since caribou cross these areas during migrations and the areas are less energetically demanding to reach (Fancy & White, 1987), we should expect to see a negative relationship between forage lichen abundance and latitude if caribou usage was affecting lichen abundance. If lichens declined universally from south to north, this would be suggestive of climatic factors. Forage lichen abundance was negatively associated with latitude (Figure 3), but non-forage cover was not significantly associated. While total lichen cover (12.5%) was similar between an area of concentrated use in the northern portion of the current winter range (Joly *et al*., 2007) and random unburned plots in our study (14.8%), forage lichen cover was less than half in this northern area (4.6%) *versus* the present study (10.6%). These results suggest caribou usage is negatively impacting lichen abundance – although climatic factors may be doing so as well. This therefore provides evidence that large, migratory herds of barren-ground caribou both affect and respond to lichen availability (also see Moser, Nash & Thomson, 1979; Arsenault *et al*. 1997).

The abundance of forage lichens was also negatively associated with soil pH and the cover of moss, herbaceous layer, and shrubs in the canopy. The negative association between lichen abundance and vascular plant species has been reported in other studies (Klein, 1987; Swanson, 1996; Cornelissen *et al*., 2001; Graglia *et al*., 2001; Joly *et al*., 2007; Holt, McCune & Neitlich, 2008; 2009). Taller physiognomy shrubs with greater leaf biomass (*e.g*., alders and willows) appear to inhibit lichens through shading and smothering (from the shrub leaf litter). Another indirect, negative impact is that these taller shrubs can alter patterns of snow accumulation and delay snow melt, which could further enhance the competitive advantage of vascular species (Sturm *et al*., 2005; Forbes, Fauria & Zetterberg, 2010) at the expense of lichens. In contrast, covers of crowberry and dwarf birch were positively associated with lichen abundance. This relationship was the same using just unburned plots and thus is likely not an artifact of both being positively associated with time since last burn. The negative association with pH was also anticipated as acidic soils restrict vascular plants that compete with lichens (Swanson, 1996; Holt, McCune & Neitlich, 2007; 2009). However, our finding of a negative association with moss cover contrasts with that of Holt, McCune, and Neitlich (2008) on the Seward Peninsula. Our sampling universe covered a much greater range of habitat types, which may explain this discrepancy. Plots with well-drained soils, which are uncommon on the Seward Peninsula, can have high lichen but low moss abundance, resulting in the association that we found. The disparity may also be due to differences in methodology. Because we could only determine the ages of recently burned plots, we are not able to address the potential regenerative role of fire in lichen stands in the long-term (*e.g*., 200 y) and whether mosses may outcompete lichen on this time horizon, as occurs elsewhere (Sulyma & Coxson, 2001).

Forage lichen abundance was positively associated with stand age, elevation, coarse scale terrain ruggedness, and slope. Lichen abundance was very low for at least 30–35 y following fire, which is in agreement with other studies from this region (Swanson, 1996; Racine *et al*., 2004; Holt, McCune & Neitlich, 2006; 2008; Jandt *et al*., 2008). Areas of low elevation, topographic complexity, and slope tend to be associated with large riparian habitats. Terricolous lichens do not compete well in these habitats due to competition with vascular plants, smothering by leaf litter, and burial by sediments (Swanson, 1996; Holt, McCune & Neitlich, 2008). The positive association with elevation, terrain complexity, and slope will have limits; as these factors get too great, exposure, unstable soils, and avalanches can reduce lichen abundance (Swanson, 1996; Holt, McCune & Neitlich, 2008). Most of our plots were found at intermediate elevations, topographic complexity, and slopes and thus did not approach the upper limits that would restrict forage lichen abundance.

The abundance of forage lichens was more than 4 times greater in unburned plots as compared to burned plots within the current winter range. Limited differences, aside from lichen abundance, between burned and unburned plots support the hypothesis that caribou avoid burned habitat in this region because of limited availability of forage lichens during winter (Joly, Bente & Dau, 2007). Additionally, many caribou locations initially thought to be within burned areas were outside actual burn perimeters or were within unburned inclusions within the larger fire perimeter. Islands of unburned habitat may also be attractive feeding sites for caribou (Miller, 2000). The large proportion of T2 (used/burned) plots that had to be reassigned to T1 (used/unburned) plots suggests that the avoidance of burned habitat in winter by caribou in this region is likely much greater than previously reported. All T2 (used/burned) plots that were not reassigned were based on caribou locations during more migratory (*e.g*., October or late April) periods.

Traditional satellite and GPS-based telemetry systems use different methodologies and satellite platforms to determine locations, with accuracies of approximately 500 m (Fancy *et al.,* 1989) for traditional satellites and 30 m (Joly, 2005) for GPS telemetry in caribou studies. We recommend transitioning from traditional satellite to GPS telemetry technology for determining caribou locations in habitat use studies due to the high percentage of misclassification of plot treatment type (*i.e.*, the satellite location indicated it was not in a burn but ground-truthing revealed it clearly was in a burn).

Differences between forage lichen abundance at burned and unburned plots were not detected within the historic and potential winter ranges, likely due to caribou reducing lichens on unburned plots in the historic range to the point

that differences between grazing and burning impacts could not be statistically differentiated and that other factors (*e.g.*, more tall shrubs) might have made unburned habitats less suitable for lichens in the potential winter range. Indeed, we detected few significant differences between burned and unburned plots in these areas, which is likely related to the ability of vascular vegetation to recover quickly after fire (average stand age of burned areas was 37 and 25 y in the historic and potential winter ranges, respectively), though small samples sizes may have hampered our ability to detect differences. We were able to determine that cover of dwarf birch was greater at burned locations than at unburned locations in both the historic and potential winter ranges. Increased abundance of dwarf birch following a wildfire should be expected given its adaptations to fire (de Groot & Wein, 1999). Dwarf birch is predicted to increase in abundance and distribution under climate warming scenarios (de Groot & Wein, 1999; Bret-Harte *et al*., 2001; Euskirchen *et al.*, 2009) and could enhance a positive feedback mechanism that would further increase wildfire in tundra ecosystems (Higuera *et al*., 2008; 2009).

We believe that the likelihood of the WAH expanding its range into the potential range is low for many reasons. First, biomass of forage lichens is low. Although there are peat plateau habitats in this region that support high lichen abundance, their extent is limited and they are present only on the southeast side of the Koyukuk River (Figure 2). This large, meandering river creates vast riparian habitats with low biomass of forage lichens, and these habitats support high densities of moose (*Alces alces*), which could facilitate the maintenance of year-round high densities of wolves (*Canis lupus*), the primary predator of caribou during winter. The low-elevation hills to the west of the Koyukuk River are blanketed with habitat types that caribou avoid in winter (*e.g*., deciduous forests, alder and willow thickets; this study). Tree cover in the potential winter range (25%) was much greater than in the current (3%) or historic (5%) winter ranges. The extent and frequency of fires is also much greater in the potential winter range than the current winter range (Joly *et al*., 2009). So the herd would have to cross wide expanses of poor-quality winter range with potentially high predator densities to reach the spatially limited but higher quality peat plateau habitats. Thus, we infer it is unlikely that the herd will utilize the Koyukuk country as winter range regularly or in large numbers.

Large, migratory herds of caribou seek out winter range with abundant lichen biomass. These herds can substantially affect this resource. Once their range areas are depleted, caribou may expand or shift their distribution to find new areas with high lichen abundance. The additional energetic expense of migrating further, combined with additional predation risk, may be detrimental to caribou populations. Moreover, recovery of depleted winter ranges may take decades (Henry & Gunn, 1990). This recovery period may be extended due to changes in climate (Joly, Jandt & Klein, 2009; Klein & Shulski, 2009). Increased wildfire activity and shrub abundance combined with expansion of deciduous forests, all of which are predicted under climate change scenarios, will further retard lichen growth. This may in turn negatively impact caribou and the subsistence users that rely upon this critical resource.

Acknowledgements

Funding for this project was generously provided by the Bureau of Land Management – Central Yukon Field Office, the US Fish and Wildlife Service – Selawik National Wildlife Refuge, and the National Park Service – Gates of the Arctic National Park and Preserve. S. Jacobson, L. A. Ayres, and T. Liebscher were instrumental in getting the project supported. T. Jorgenson (ABR, Inc.), K. Sonnen (NRCS), P. Neitlich (NPS), and T. Miller (ABR, Inc.) provided expert advice for the design of the study. T. Miller led the field crews collecting data within the Selawik National Wildlife Refuge. D. Gustine, P. Neitlich, J. Schmidt, D. Swanson, L. Saperstein, C. Roland, D. Fortin, and anonymous reviewers provided insights and comments that improved this manuscript.

Literature cited

Arsenault, D., N. Villeneuve, C. Boismenu, Y. Leblanc & J. Deshaye, 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of northern Québec: An application of fire history and Landsat data. Journal of Applied Ecology, 34: 65–78.

Bergerud, A. T., 1974. Decline of caribou in North America following settlement. Journal of Wildlife Management, 38: 757–770.

Bergerud, A. T., 1980. A review of the population dynamics of caribou and wild reindeer in North America. Proceedings of the International Reindeer/Caribou Symposium, 2: 556–581.

Bret-Harte, M. S., G. R. Shaver, J. P. Zoerner, J. F. Johnstone, J. L. Wagner, A. S. Chavez, R. F. Gunkelman, S. C. Lippert & J. A. Laundre, 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. Ecology, 82: 18–32.

Briand, Y., J. P. Ouellet, C. Dussault & M. H. St.-Laurent, 2009. Fine-scale habitat selection by female forest-dwelling caribou in managed boreal forest: Empirical evidence of a seasonal shift between foraging opportunities and antipredator strategies. Écoscience, 16: 330–340.

Brodo, I. M., S. D. Sharnoff & S. Sharnoff (eds), 2001. Lichens of North America. Yale University Press, New Haven, Connecticut.

Brown, G. S., L. Landriault, D. J. H. Sleep & F. F. Mallory, 2007. Comment arising from a paper by Wittmer *et al.*: Hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics. Oecologia, 154: 485–492.

Burnham, K. P. & D. R. Anderson, 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd Edition. Springer-Verlag, New York, New York.

Callaghan, T. V., L. O. Björn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, S. Schaphoff, S. Sitch & C. Zöckler, 2004. Key findings and extended summaries. Ambio, 33: 386–392.

Collins, W. B., B. W. Dale, L. G. Adams, D. E. McElwain & K. Joly, in press. Fire, grazing history, lichen abundance, and winter distribution of barren-ground caribou in Alaska's taiga. Journal of Wildlife Management.

Cornelissen, J. H. C., T. V. Callaghan, J. M. Alatalo, A. Michelsen, E. Graglia, A. E. Hartley, D. S. Hik, S. E. Hobbie, M. C. Press, C. H. Robinson, G. H. R. Henry, G. R. Shaver, G. K. Phoenix, D. Gwynn Jones, S. Jonasson, F. S. Chapin III, U. Molau, C. Neill, J. A. Lee, J. M. Melillo, B. Sveinbjornsson & R. Aerts, 2001. Global change and arctic ecosystems: Is lichen decline a function of increases in vascular plant biomass? Journal of Ecology, 89: 984–994.

Couturier, S., S. D. Côté, R. D. Otto, R. B. Weladji & J. Huot, 2009. Variation in calf body mass in migratory caribou: The role of habitat, climate, and movements. Journal of Mammalogy, 90: 442–452.

Crête, M., C. Morneau & R. Nault, 1990. Biomasse et espèces de lichens terrestres pour le caribou dans le nord du Québec. Canadian Journal of Botany, 68: 2047–2053.

Dau, J., 2007. Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24 and 26A caribou management report. Pages 174–231 *in* P. Harper (ed.). Caribou Management Report of Survey and Inventory Activities 1 July 2004–30 June 2006. Alaska Department of Fish and Game. Project 3.0. Juneau, Alaska.

Davis, J. L., P. Valkenburg & H. V. Reynolds, 1980. Population dynamics of Alaska's Western Arctic Caribou Herd. Proceedings of the International Reindeer/Caribou Symposium, 2: 595–604.

de Groot, W. J. & R. W. Wein, 1999. *Betula glandulosa* Michx. response to burning and postfire growth temperature and implications of climate change. International Journal of Wildland Fire, 9: 51–64.

Dunford, J. S., P. D. McLoughlin, F. Dalerum & S. Boutin. 2006. Lichen abundance in the peatlands of northern Alberta: Implications for boreal caribou. Écoscience, 13: 469–474.

ESRI, 2006. ArcGIS version 9.2. Redlands, California.

Euskirchen, E. S., A. D. McGuire, F. S. Chapin III, S. Yi & C. C. Thompson, 2009. Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: Implications for climate feedbacks. Ecological Applications, 19: 1022–1043.

Fancy, S. G. & R. G. White, 1987. Energy expenditures for locomotion by barren-ground caribou. Canadian Journal of Zoology, 65:122–128.

Fancy, S. G., L. F. Pank, K. R. Whitten & W. L. Regelin, 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. Canadian Journal of Zoology, 67: 644–650.

Ferguson, M. A. D., L. Gauthier & F. Messier, 2001. Range shift and winter foraging ecology of a population of Arctic tundra caribou. Canadian Journal of Zoology, 79: 746–758.

Feldhamer, G. A., B. C. Thompson & J. A. Chapman (eds), 2003. Wild Mammals of North America: Biology, Management, and Conservation. 2nd Edition. Johns Hopkins University Press, Baltimore, Maryland.

Forbes, B. C., M. M. Fauria & P. Zetterberg, 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. Global Change Biology, 16: 1542–1554.

Gaare, E. & T. Skogland, 1980. Lichen–reindeer interaction studied in a simple case model. Proceedings of the International Reindeer/Caribou Symposium, 2: 47–56.

Graglia, E., S. Jonasson, A. Michelsen, I. K. Schmidt, M. Havström & L. Gustavsson, 2001. Effects of environmental perturbations on abundance of subarctic plants after three, seven and ten years of treatment. Ecography, 24: 5–12.

Heggberget, T. M., E. Gaare & J. P. Ball, 2002. Reindeer (*Rangifer tarandus*) and climate change: Importance of winter forage. Rangifer, 22: 13–32.

Henry, G. H. R. & A. Gunn, 1990. Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. Arctic, 44: 38–42.

Higuera, P. E., L. B. Brubaker, P. M. Anderson, T. A. Brown, A. T. Kennedy & F. S. Hu, 2008. Frequent fires in ancient shrub tundra: Implications of paleorecords for Arctic environmental change. PLoS ONE, 3(3):e0001744. doi:10.1371/journal.pone.0001744.

Higuera, P. E., L. B. Brubaker, P. M. Anderson, F. S. Hu & T. A. Brown, 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecological Monographs, 79: 201–219.

Holt, E. A., B. McCune & P. Neitlich, 2006. Defining a successional metric for lichen communities in the Arctic tundra. Arctic, Antarctic, and Alpine Research, 38: 373–377.

Holt, E. A., B. McCune & P. Neitlich, 2007. Succession and community gradients of arctic macrolichens and their relation to substrate, topography, and rockiness. Pacific Northwest Fungi, 2: 1–21.

Holt, E. A., B. McCune & P. Neitlich, 2008. Grazing and fire impacts on macrolichen communities of the Seward Peninsula, Alaska, USA. Bryologist, 111: 68–83.

Holt, E. A., B. McCune & P. Neitlich, 2009. Macrolichen communities in relation to soils and vegetation in the Noatak National Preserve. Botany, 87: 241–252.

Hughes, J., S. D. Albon, R. J. Irvine & S. Woodin, 2009. Is there a cost of parasites to caribou? Parasitology, 136: 253–265.

Jandt, R. R., K. Joly, C. R. Meyers & C. Racine, 2008. Slow recovery of lichen on burned caribou winter range in Alaska tundra: Potential influences of climate warming and other disturbances. Arctic, Antarctic and Alpine Research, 40: 89–95.

Johnson, C. J., K. L. Parker & D. C. Heard, 2001. Foraging across a variable landscape: Behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia, 127: 590–602.

Johnson, C. J., M. Boyce, R. L. Case, H. D. Cluff, R. J. Gau, A. Gunn & R. Mulders, 2005. Cumulative effects of human developments on arctic wildlife. Wildlife Monographs, 160: 1–36.

Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin III & M. C. Mack, 2009. Changes in boreal fire regime break the legacy lock on successional trajectories in the Alaskan boreal forest. Global Change Biology, 15: 1281–1295.

Joly, K., 2005. The effects of sampling regime on the analysis of movements of over-wintering female caribou in east-central Alaska. Rangifer, 25: 67–74.

Joly, K., P. Bente & J. Dau, 2007. Response of overwintering caribou to burned habitat in northwest Alaska. Arctic, 60: 401–410.

Joly, K., M. J. Cole & R. R. Jandt, 2007. Diets of overwintering caribou, *Rangifer tarandus*, track decadal changes in arctic tundra vegetation. Canadian Field-Naturalist, 121: 379–383.

Joly, K., R. R. Jandt & D. R. Klein, 2009. Decrease of lichens in arctic ecosystems: Role of wildfire, caribou and reindeer, competition, and climate change. Polar Research, 28: 433–442.

Joly, K., R. R. Jandt, C. R. Meyers & M. J. Cole, 2007. Changes in vegetative cover on Western Arctic Herd winter range from 1981–2005: Potential effects of grazing and climate change. Rangifer Special Issue, 17: 199–207.

Joly, K., T. S. Rupp, R. R. Jandt & F. S. Chapin III, 2009. Fire in the range of the Western Arctic Caribou Herd. Alaska Park Science, 8: 68–73.

Kasischke, E. S., T. S. Rupp & D. L. Verbyla, 2006. Fire trends in the Alaskan boreal forest. Pages 285–301 *in* F. S. Chapin III, M. W. Oswood, K. Van Cleve, L. A. Viereck & D. L. Verbyla (eds). Alaska's Changing Boreal Forest. Oxford University Press, Oxford.

Klein, D. R., 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management, 32: 350–367.

Klein, D. R., 1982. Wildfire, lichens and caribou. Journal of Range Management, 35: 390–395.

Klein, D. R., 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. Journal of Range Management, 40: 336–338.

Klein, D. R., 1991. Limiting factors in caribou population ecology. Rangifer Special Issue, 7: 30–35.

Klein, D. R. & M. Shulski, 2009. Lichen recovery following heavy grazing by reindeer delayed by climate warming. Ambio, 38: 11–16.

Kumpula, J., A. Colpaert & M. Nieminen, 2000. Condition, potential recovery rate, and productivity of lichen (*Cladonia* spp.) ranges in the Finnish reindeer management area. Arctic, 53: 152–160.

Lawler, J. J., S. L. Shafer, D. White, P. Kareiva, E. Maurer, A. R. Blaustein & P. J. Bartlein, 2009. Projected climate-induced faunal change in the western hemisphere. Ecology, 90: 588–597.

Lynch, J. A., J. S. Clark, N. H. Bigelow, M. E. Edwards & B. P. Finney, 2003. Geographic and temporal variations in fire history in boreal ecosystems of Alaska. Journal of Geophysical Research, 108: 1–17.

Mark, A. F., N. Fetcher, G. R. Shaver & F. S. Chapin III, 1985. Estimated ages of mature tussocks of cotton sedge, *Eriophorum vaginatum* along a latitudinal gradient in central Alaska. Arctic and Alpine Research, 17: 1–5.

Messier, F., J. Huot, D. Le Henaff & S. Luttich, 1988. Demography of the George River Caribou Herd: Evidence of population regulation by forage exploitation and range expansion. Arctic, 41: 279–287.

Miller, D., 2000. Lichens, wildfire, and caribou on the taiga ecosystem of northcentral Canada. Rangifer Special Issue, 12: 197–207.

Moen, J., O. Danell & R. Holt, 2007. Non-destructive estimation of lichen biomass. Rangifer, 27: 41–46.

Morneau, C. & S. Payette, 1989. Postfire lichen–spruce woodland recovery at the limit of boreal forest in northern Québec. Canadian Journal of Botany, 67: 2770–2782.

Moser, T. J., T. H. Nash III & J. W. Thomson, 1979. Lichens of Anaktuvuk Pass, Alaska, with emphasis on the impact of caribou grazing. Bryologist, 82: 393–408.

Neter, J., M. H. Kutner, C. J. Nachtsheim & W. Wasserman, 1996. Applied Linear Statistical Models. 4th Edition. McGraw-Hill, Boston, Massachusetts.

Nowacki, G., P. Spencer, M. Fleming, T. Brock & T. Jorgenson, 2001. Ecoregions of Alaska: 2001. Open File Report 02-297. US Geological Survey, Washington, DC.

Parker, K. L., P. S. Barboza & M. P. Gillingham, 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology, 23: 57–69.

Parker, K. L., P. S. Barboza & T. R. Stephenson, 2005. Protein conservation in female caribou (*Rangifer tarandus*): Effects of decreasing diet quality during winter. Journal of Mammalogy, 86: 610–622.

Payette, S., C. Morneau, L. Sirois & M. Desponts, 1989. Recent fire history of the northern Québec biomes. Ecology, 70: 656–673.

Pederson, A. B., K. E. Jones, C. L. Nunn & S. Altizer, 2007. Infectious diseases and extinction risk in wild mammals. Conservation Biology, 21: 1269–1279.

Pegau, R. E., 1969. Effect of reindeer trampling and grazing on lichens. Journal of Range Management, 23: 95–97.

Person, S. J., R. E. Pegau, R. G. White & J. R. Luick, 1980. In vitro and nylon-bag digestibilities of reindeer and caribou forages. Journal of Wildlife Management, 4: 613–622.

Post, E. & N. C. Stenseth, 1999. Climatic variability, plant phenology, and northern ungulates. Ecology, 80: 1322–1339.

Racine, C. H., R. Jandt, C. Meyers & J. Dennis, 2004. Tundra fire and vegetation change along a hillslope on the Seward Peninsula, Alaska, USA. Arctic, Antarctic, and Alpine Research, 36: 1–10.

Saperstein, L. B., 1993. Winter forage selection by barren-ground caribou: Effects of fire and snow. M.Sc. thesis, University of Alaska, Fairbanks, Alaska.

Saperstein, L. B., 1996. Winter forage selection by barren-ground caribou: Effects of fire and snow. Rangifer Special Issue, 9: 237–238.

Sappington, J. M., K. M. Longshore & D. B. Thompson, 2007. Quantifying landscape ruggedness for animal habitat analysis: A case study using Bighorn sheep in the Mojave Desert. Journal of Wildlife Management, 71: 1419–1426.

Schimdt, J. H., M. S. Lindberg, D. S. Johnson, B. Conant & J. King, 2009. Evidence of Alaskan trumpeter swan population growth using Bayesian hierarchical models. Journal of Wildlife Management, 73: 720–727.

Sturm, M., J. Schimel, G. Michaelson, J. M. Welker, S. F. Oberbauer, G. E. Liston, J. Fahnestock & V. E. Romanovsky, 2005. Winter biological processes could help convert arctic tundra to shrubland. BioScience, 55: 17–26.

Sulyma, R. & D. S. Coxson, 2001. Microsite displacement of terrestrial lichens by feather moss mats in late seral pine–lichen woodlands of north-central British Columbia. Bryologist, 104: 505–516.

Swanson, D. K., 1996. Fruticose lichen distribution in the Kobuk Preserve Unit, Gates of the Arctic National Park, Alaska. Technical Report NPS/AFA RNR/NRTR-96/28. US Department of Agriculture, Natural Resources Conservation Service, Washington, DC.

van der Wal, R., 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. Oikos, 114: 177–186.

Väre, H., R. Ohtonen & K. Mikkola, 1996. The effect and extent of heavy grazing by reindeer in oligotropic pine heaths in northeastern Fennoscandia. Ecography, 19: 245–253.

Viereck, L. A. & E. L. Little, 2007. Alaska Trees and Shrubs. University of Alaska Press, Fairbanks, Alaska.

Vors, L. S. & M. S. Boyce, 2009. Global declines of caribou and reindeer. Global Change Biology, 15: 2626–2633.

Wein, R. W., 1976. Frequency and characteristics of arctic tundra fires. Arctic, 29: 213–222.

White, R. G., 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos, 40: 377–384.

White, R. G., F. L. Bunnell, E. Gaare, T. Skogland & B. Hubert, 1981. Ungulates on arctic ranges. Pages 397–483 *in* L. C. Bliss, O. W. Heal & J. J. Moore (eds). Tundra Ecosystems: A Comparative Analysis. Cambridge University Press, Cambridge.

Yarie, J., 1981. Forest fire cycles and life tables: A case study from interior Alaska. Canadian Journal Forest Research, 11: 554–562.