



Research Article

Fire, Grazing History, Lichen Abundance, and Winter Distribution of Caribou in Alaska's Taiga

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ABSTRACT In the early 1990s the Nelchina Caribou (*Rangifer tarandus*) Herd (NCH) began a dramatic shift to its current winter range, migrating at least an additional 100 km beyond its historic range. We evaluated the impacts of fire and grazing history on lichen abundance and subsequent use and distribution by the NCH. Historic (prior to 1990) and current (2002) winter ranges of the NCH had similar vascular vegetation, lichen cover ($P = 0.491$), and fire histories ($P = 0.535$), but the former range had significantly less forage lichen biomass as a result of grazing by caribou. Biomass of forage lichens was twice as great overall ($P = 0.031$) and 4 times greater in caribou selected sites on the current range than in the historic range, greatly increasing availability to caribou. Caribou on the current range selected for stands with >20% lichen cover ($P < 0.001$), greater than 1,250 kg/ha ($P < 0.001$) forage lichen biomass and stands older than 80 yr postfire ($P < 0.001$). After fires, forage lichen cover and biomass seldom recovered sufficiently to attract caribou grazing until after ≥ 60 yr, and, as a group, primary forage lichen species did not reach maximum abundance until 180 yr postfire. Recovery following overgrazing can occur much more quickly because lichen cover, albeit mostly fragments, and organic substrates remain present. Our results provide benchmarks for wildlife managers assessing condition of caribou winter range and predicting effects of fires on lichen abundance and caribou distribution. Of our measurements of cover and biomass by species, densities and heights of trees, elevation, slope and aspect, only percentage cover by *Cladonia amaurocraea*, *Cladina rangiferina*, *Flavocetraria cuculata*, and lowbush cranberry (*Vaccinium vitis-idaea*) were necessary for predicting caribou use of winter range. © 2011 The Wildlife Society

KEY WORDS Alaska, caribou, fire, grazing history, lichen, range management, *Rangifer tarandus*.

The Nelchina Caribou (*Rangifer tarandus*) Herd (NCH) declined from a peak population of 70,000 in the mid-1960s to approximately 10,000 in the early 1970s (Siniff and Skoog 1964, Bos 1975, Lieb et al. 1988). From 1977 to 1995, the herd rebounded, reaching about 45,000 caribou and surpassing the Alaska Department of Fish and Game management objective of 30,000. During this time, forage lichens only partially recovered from previous overgrazing, raising concerns about negative impacts by caribou on lichen standing crops within the herd's winter range (Lieb 1994). Since the mid-1990s, increased harvests have been used to reduce herd size to the management objective, and numbers have fluctuated between about 30,000 and 35,000 caribou.

In the early 1990s as the NCH reached high numbers and lichens were overgrazed, the herd began a dramatic shift from its historic wintering range in the Copper River Basin and southern Alaska Range to its current winter range in the

Tanana Hills and western Yukon Territory (Valkenburg et al. 2002). This was the first shift in approximately 100 yr for which records are available, and it required additional migration of ≥ 100 km. Prior to arrival of the NCH, the current winter range had not been grazed since collapse of the Fortymile Caribou Herd approximately 40 yr earlier.

Fire is a dominant ecological force in taiga as found in the Copper River Basin and Tanana Hills. Fire stimulates early succession vegetation important to many wildlife species, but it simultaneously decreases the value of habitat for wintering barren-ground caribou by eliminating lichens, a principal food of caribou (Miller 1980, Joly et al. 2003). Lichens are particularly vulnerable to fire and slow to reestablish following fire (Bliss and Wien 1972, Joly et al. 2003, Dunford et al. 2006). Some researchers have hypothesized that fire benefits caribou in the long term by removing trees, moss, and herbaceous flora that compete with lichens in older stands (Vioreck and Schandelmeier 1980, Klein 1982). Some resource managers have considered fire much less important to lichen availability in the historic winter range of NCH than in caribou ranges north of the Alaska Range.

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An understanding of the role of fire is particularly important to management in areas where fires are suppressed to protect property or resource values or where prescribed burning is used to manage fuels or enhance habitat for other species. Our objective was to determine effects of fire and grazing on the availability of forage lichens and the subsequent winter distribution of the NCH. We hypothesized that 1) fire has had less effect on lichen availability in the historic winter range of NCH than in range north of the Alaska Range and that 2) fire benefits caribou in taiga by reducing vascular plants that compete with lichen production.

STUDY AREA

We evaluated the historic (prior to 1990) and current (2002) winter ranges of the NCH, an area including the Copper River Basin, portions of the Alaska Range, and the Tanana Uplands (61–64°N, 141–150°W; Fig. 1). Due to the international boundary, we did not include minor portions of current NCH range in the western Yukon Territory, Canada. Elevations ranged from 300 m to >5,000 m, though caribou usually stayed below 1,500 m in winter.

Black spruce (*Picea mariana*) forest was the dominant cover type. Aspen (*Populus tremuloides*), birch (*Betula papyrifera*), and white spruce (*Picea glauca*) were also present as small stands interspersed within the black spruce forest. At elevations >1,100 m, forest gave way to shrubs (Alder [*Alnus* spp.], birch [*Betula* spp.]) and alpine communities. Muskegs and tussock tundra were common in poorly drained, low-lying areas. Climate was continental, with range to the northeast being the coldest and driest. Mean annual snowfall was 96 cm (National Oceanic and Atmospheric Administration 2002).

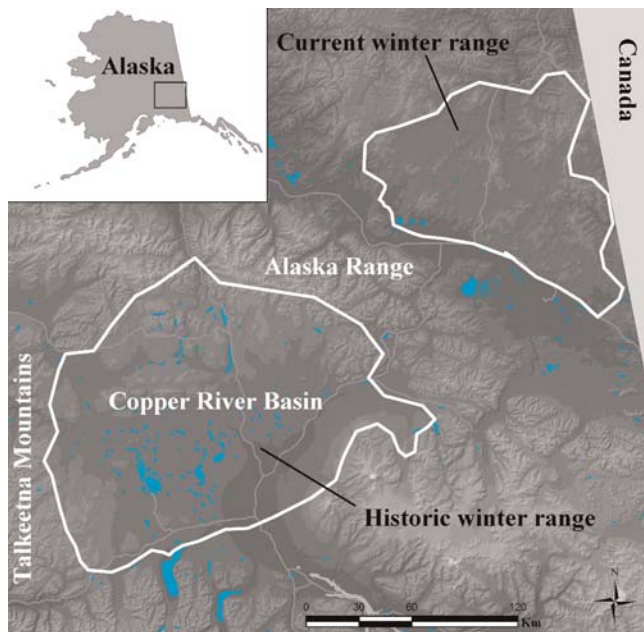


Figure 1. Winter ranges of Nelchina Caribou Herd, Alaska, USA. The herd primarily wintered in the Copper River Basin before 1990, but currently (2002) winters primarily north of the Alaska Range.

METHODS

Vegetation Sampling

We sampled vegetation characteristics and lichen abundance at random points and at locations of individual caribou across most of the current and historic winter ranges of the NCH in 2001 and 2002. We generated random coordinates using a Geographic Information System (GIS) and obtained coordinates of caribou locations from a randomly selected subset of points where radiocollared caribou were visually located during radiotracking by airplane during winters 1984–1985 and 1985–1986 in the historic NCH range south of the Alaska Range (Pitcher 1987) and during winters 1999–2000 and 2000–2001 in the current NCH range north of the Alaska Range (Joly et al. 2003). Locations south of the Alaska Range were recorded on topographic maps (Pitcher 1987), whereas those north of the range were entered into a Global Positioning System (GPS) as the plane passed over the animal (Joly et al. 2003). We accessed sampling locations by helicopter and on foot, using a hand-held GPS unit to locate random points and the previously observed locations of caribou. Given the large patch sizes and homogeneity of stands in the study area, we were confident that our vegetation measurements coincided with stands where caribou had been located, with few exceptions. We excluded those exceptions (i.e., locations within 60 m of a stand edge) from results.

At each random point or caribou location, we established a randomly oriented 60-m transect with its midpoint at the point coordinates. We measured slope and aspect at the midpoint of each transect. We recorded overstory and under-story cover by species at each 0.5-m interval along each transect. We grouped lichen species according to preference; primary species were those preferred by caribou, secondary species were less preferred, and non-selected species included all other lichens (Scotter 1964, Boertje 1981, Johnson et al. 1998). We grouped *Cladonia mitis* and *C. arbuscula* as one forage species because of difficulty in readily distinguishing them in the field, and we grouped non-selected *Cladonia* spp. We determined lichen biomass by collecting 20 randomly located 7.3-cm-diameter plugs of ground cover from along each transect. We separated lichens from plugs by species, then dried (overnight at 60°C) and weighed them. We recorded tree density by height category (<0.1 m, 0.1–1 m, 1–2 m, 2–4 m, 4–6 m, and >6 m) within a 1 × 60-m belt plot parallel and adjacent to the transect. We determined stand age by cutting or coring trees representative of the overstory at each point and counting annual rings.

We determined percent change in forage lichen abundance within the historic range for the period 1989–2001 by reevaluating 16 range stations established 1955–1960 (Pegau and Hemming 1972) and last measured in 1989. We estimated standing crop at the stations by multiplying lichen cover by its height, the same method used in 1989 (Lieb 1994). By treating the change in standing crop as an index to change in biomass, we adjusted our 2001 estimates of total forage lichen biomass accordingly to estimate forage lichen biomass near the times of Pitcher's (1987) radiolocations of caribou

and when caribou began migrating to their current winter range.

Statistical Analyses

We used the Kolmogorov–Smirnov goodness-of-fit (GOF) test (KS; Zar 1984) to compare stand age distributions on current and historic winter ranges, stand ages selected at random and by radiocollared caribou for each winter range, and lichen cover and biomass selected at random and by radiocollared caribou for each winter range. We also compared lichen cover and biomass between current and historic winter ranges with *t*-tests. We evaluated relationships among forage lichen cover, forage lichen biomass, and stand age by fitting quadratic equations via least squares linear regression. If the predicted maximum for the regression fell within the range of stand ages that occurred on our study area, we used that maximum as an estimate of the stand age and value for peak lichen cover or biomass. We also employed linear regression to assess relationships between lichen cover and biomass for each winter range.

We developed a resource selection function for measurements taken on the current winter range to examine which variables could best predict use. We ran univariate regressions on each of 61 variables we recorded for used and random sites, and we retained those variables with significance $P > 0.1$ as candidates for final model selection. Several variables were highly correlated ($r > 0.7$), either as sums of other variables or as biomass measures of the analogous percentage covers. We likewise eliminated these as candidates. We selected the final model by backward selection from the remaining variables. We assessed GOF by the Hosmer–Lemeshow GOF test as well as by examining the area under the Receiver Operating Characteristic (ROC) curve (Hosmer and Lemeshow 2000). For all statistical tests, we considered $P \leq 0.05$ indicative of significance.

RESULTS

Stand ages amongst randomly sampled sites in historic ($n = 48$) and current ($n = 88$) winter ranges were similarly distributed (KS = 0.15, $P = 0.535$) indicating peak disturbance by fire at approximately 90 yr and 160 yr before present (BP), with an intervening lull around 130 yr BP (Fig. 2).

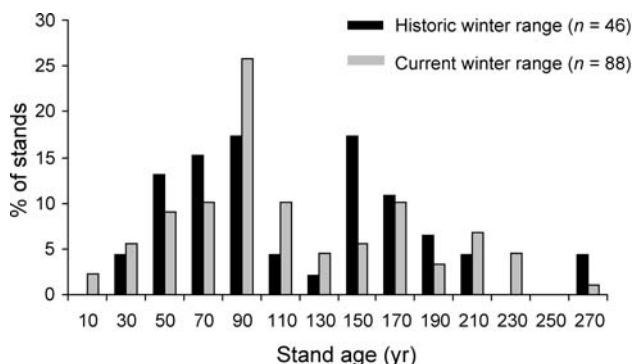


Figure 2. Stand age distributions for historic (1986) and current (2002) winter ranges of the Nelchina Caribou Herd, Alaska, USA.

Fires were essentially absent from the historic range during the last 37 yr, infrequent on the current range during the same period, and also infrequent on both ranges 121–140 yr BP. Stand age averaged 126 (SD = 60) yr in the historic range and 101 (SD = 64) yr in the current range. We found black spruce as old as 435 yr in a few small, relict sites apparently isolated from fuels that could carry fire. However, stands older than 220 yr were rare on both winter ranges due to the fire frequencies we observed, and cover by black spruce stabilized at approximately 17% after 200 yr.

On the current winter range, caribou preferentially selected stands older than 80 yr postfire (Fig. 3; KS = 0.30, $n = 86$, $P = 0.001$). Selected stands also had >20% total forage lichen cover more often than the relative availability of those stands (Fig. 4; KS = 0.47, $n = 88$, $P < 0.001$). Stands with forage lichen biomass <1,000 kg/ha were used little relative to their availability, whereas stands >1,250 kg/ha were selected disproportionately more than their availability (KS = 0.39, $n = 86$, $P < 0.001$).

Forage lichen cover in caribou-selected stands of the current winter range averaged 29.7%, versus 8.2% in random stands (Table 1), and forage lichen biomass was 1,045 kg/ha versus 414 kg/ha in the same stands, respectively. Of our measurements of cover and biomass by species, densities and heights of trees, elevation, slope and aspect, only percentage cover by *Cladonia amaurocraea*, *Cladonia rangiferina*, *Flavocetraria cucullata*, and lowbush cranberry were necessary for predicting caribou use.

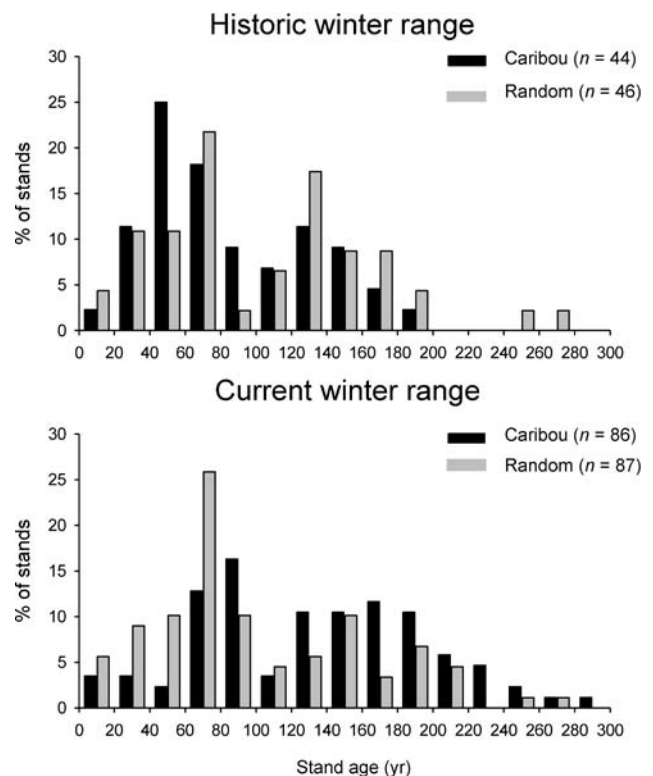


Figure 3. Stand ages of caribou-selected sites and random sites on historic (1986) and current (2002) winter ranges of the Nelchina Caribou Herd, Alaska, USA.

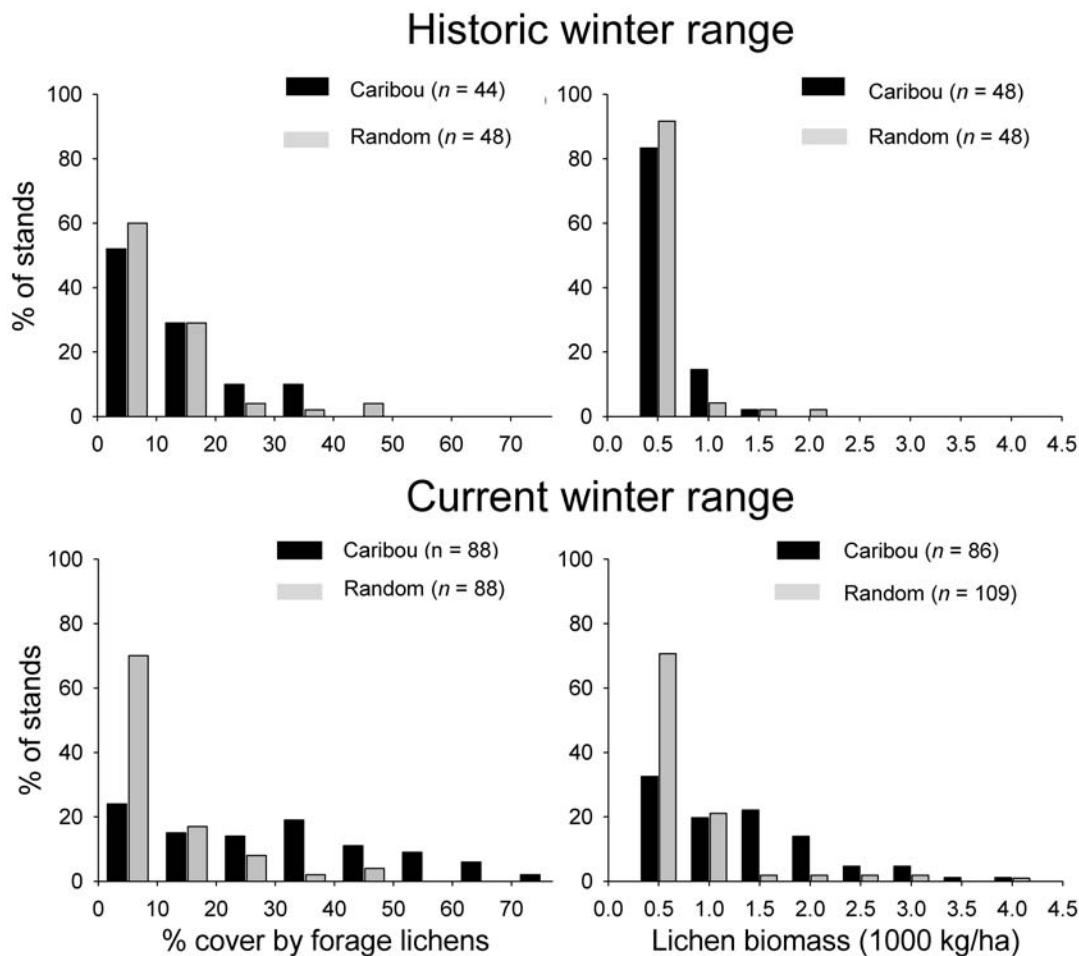


Figure 4. Forage lichen cover and biomass on caribou-selected sites and random sites on historic (1986) and current (2002) winter ranges of the Nelchina caribou herd, Alaska, USA, 2002.

In 2001, most forage lichens in the historic range showed little evidence of recovery from overgrazing that occurred prior to the mid-1990s. Those forage lichens remaining intact after being cropped or dislodged by grazing exhibited 3–5 yr of new growth. Standing crop of lichens at range stations in the historic range declined 39% during the period 1989–2001, presumably by the mid-1990s after most caribou stopped wintering in that range. Therefore, to estimate forage lichen abundance for the historic range shortly after radiocollared caribou were last located there, we raised our 2001 estimates of total forage lichen biomass in randomly

selected and caribou-selected sites to reflect the decrease during the same period, producing estimates of 367 kg/ha and 418 kg/ha, respectively.

Age distributions of random and caribou-selected stands in the historic winter range were not different ($KS = 0.16$, $n = 44$, $P = 0.614$), unlike in the current range where caribou preferred older stands (Fig. 3). Following overutilization by the high caribou population prior to the mid-1990s and, after that, a period of limited recovery, forage lichen cover in the historic winter range averaged 12.7% in caribou-selected stands versus 9.5% in random

Table 1. Mean forage lichen biomass (kg/ha) and cover (%) at random and caribou-selected locations in the historic and current winter ranges of the Nelchina Caribou Herd, Alaska, USA, 2002.

Variable	Historic winter range				Current winter range			
	Random		Caribou location		Random		Caribou location	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Primary forage lichen biomass (kg/ha)	155	18.4	189	20.9	147	30.3	486	51.3
Secondary forage lichen biomass (kg/ha)	69	20.9	66	11.7	267	45.2	559	48.9
Total forage lichen biomass (kg/ha)	224	32.4	255	25.7	414	65.5	1045	85.1
Primary forage lichen cover (%)	7.8	0.8	9.0	0.9	4.6	0.7	15.5	1.3
Secondary forage lichen cover (%)	1.7	0.3	3.7	1.3	3.6	0.6	14.2	1.1
Total forage lichen cover (%)	9.5	1.1	12.7	1.0	8.2	1.2	29.7	2.0

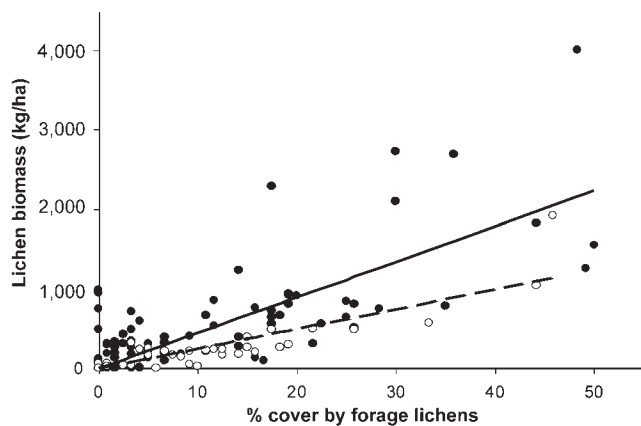


Figure 5. Forage lichen cover and biomass on the historic (dashed line, open circles) and current (solid line, filled circles) winter ranges of the Nelchina Caribou Herd, Alaska, USA, 2002.

stands (Table 1), and forage lichen biomass was essentially the same in caribou-selected stands as in random stands. Thus, caribou showed no preference for stands relative to forage lichen cover ($KS = 0.08$, $n = 44$, $P = 1.000$) or biomass ($KS = 0.08$, $n = 48$, $P = 1.000$).

Lichen cover and biomass were strongly correlated within both winter ranges, but forage lichen biomasses were

significantly higher on the current winter range for any given cover value (Fig. 5). Mean forage lichen cover was similar on the 2 ranges (Table 1; $t = 0.69_{df=139}$, $P = 0.491$), but biomass of forage lichens on the current winter range was about twice that on the historic winter range (Table 1; $t = 2.18_{df=138}$, $P = 0.031$). Only 7.5% of stands on the historic winter range had lichen exceeding 500 kg/ha, versus 30.1% of stands on the current winter range (Fig. 4).

On both ranges, lichen cover seldom exceeded 1–2% until 60–70 yr postfire when an abrupt increase occurred (Fig. 6). Forage lichen cover and biomass peaked on the current winter range at 149 yr and 141 yr, respectively, whereas we did not detect peaks on the historic winter range (Table 2). On the current winter range, biomass of secondary forage lichens peaked at 115 yr postfire, whereas biomass of primary forage lichens did not peak until 180 yr postfire. Biomass of *Cladina rangiferina*, a preferred forage species, was low for the first 160 yr postfire but then steadily increased to the limit of stand ages occurring in our study area, based on quadratic regression analyses.

With regard to specific lichen cover, the best correlation in the current range was between *Cladina rangiferina* and stand age ($r = 0.452$, $n = 88$). The best correlation with cover by *Cladina arbuscula*–*C. mitis* was with cover by *Cladonia amaurocraea* ($r = 0.533$, $n = 88$). *Cladina stellaris*, another

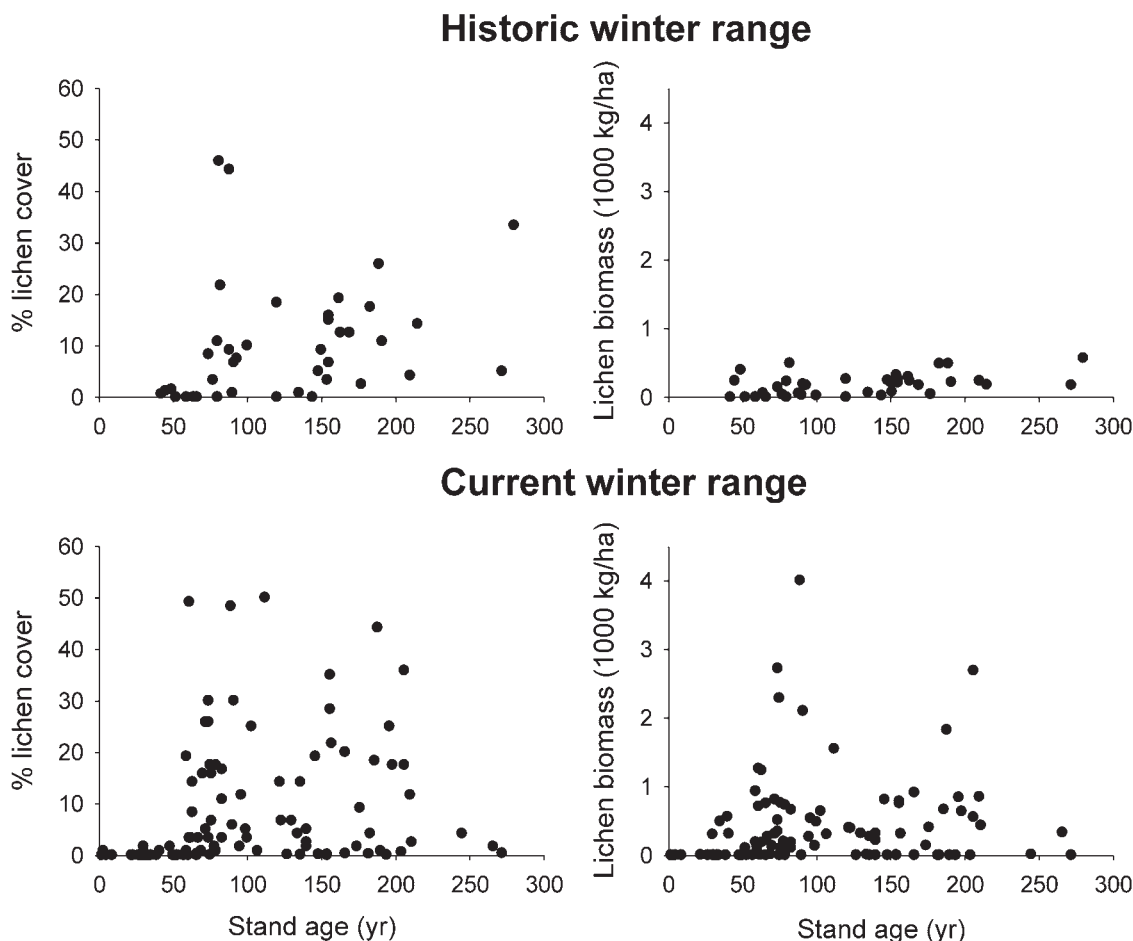


Figure 6. Cover and biomass of forage lichens relative to stand age in historic (1986) and current (2002) winter ranges of the Nelchina Caribou Herd, Alaska, USA, 2002.

Table 2. Regression analyses for forage lichen biomass (kg/ha) and cover (%) with stand age of randomly selected stands in the winter ranges of the Nelchina Caribou Herd, Alaska, USA, 2002.

Variable	Max. ^a	Age (yr) ^b	R ²	P	P (x ²) ^c	Eq
Current winter range						
Primary biomass	249	180	0.068	0.031	0.176	$y = -0.0094x^2 + 3.3573x - 52.282$
Secondary biomass	335	115	0.019	0.391	0.177	$y = -0.0142x^2 + 3.2765x + 146.9909$
Total biomass	561	141	0.032	0.202	0.121	$y = -0.0236x^2 + 6.6338x + 94.7089$
Primary cover	7.6	164	0.104	0.004	0.037	$y = -0.0003x^2 + 0.1143x - 1.7874$
Secondary cover	5.6	132	0.079	0.017	0.007	$y = -0.0004x^2 + 0.0977x - 0.8443$
Total cover	13.0	149	0.115	0.003	0.006	$y = -0.0007x^2 + 0.2198x - 3.3073$
Historic winter range						
Primary biomass	142	72	0.069	0.260	0.465	$y = 0.0052x^2 - 0.7463x + 168.996$
Secondary biomass	ND ^d	ND	0.016	0.742	0.852	$y = -0.0015x^2 + 0.0024x + 97.345$
Total biomass	ND	ND	0.005	0.903	0.775	$y = 0.0037x^2 - 0.7439x + 266.3415$
Primary cover	ND	ND	0.043	0.443	0.630	$y = 0.0000x^2 - 0.0002x + 0.0721$
Secondary cover	ND	ND	0.011	0.809	0.610	$y = 0.0000x^2 - 0.0002x + 0.0354$
Total cover	ND	ND	0.036	0.498	0.521	$y = 0.0000x^2 - 0.0005x + 0.1144$

^a We estimated max. biomass and cover from best fit regression lines.

^b Stand age is the computed age at which maximums occur.

^c Probability from *t*-test that the quadratic (x²) regression coeff was different from zero.

^d Not detected. Regression relationship was either concave or did not reach a maximum within the range of stand ages used in analysis of the historic winter range (0–220 yr).

Table 3. Variables we evaluated relative to distribution of the Nelchina Caribou Herd in its current winter range, Alaska, USA, 2002. We recorded percent cover for 104 additional species or species groups, but due to scarcity of observations we did not included those records in analysis and did not list them here.

Physical	Density	% cover	% cover (continued)
Age ^a	<i>Picea</i> spp. seedlings	<i>Cladina arbuscula-mitis</i> ^{a,b}	<i>Sphagnum</i> spp.
Slope ^a	<i>Picea</i> spp. <0.1 m ht	<i>Cladina rangiferina</i> ^{a,b}	<i>Polytrichum</i> spp. ^a
Aspect	<i>Picea</i> spp. 0.1–1 m ht	<i>Cladina stellaris</i> ^b	<i>Brachythecium</i> spp.
Degrees from north	<i>Picea</i> spp. 1–2 m ht ^a	Total primary forage lichens	Total moss
	<i>Picea</i> spp. 2–4 m ht ^a	<i>Cladonia amaurocraea</i> ^{a,c}	<i>Eriophorum vaginatum</i>
Biomass			
<i>Cladina arbuscula-mitis</i> ^b	<i>Picea</i> spp. 4–6 m ht	<i>Flavocetraria cuculata</i> ^{a,c}	<i>Carex</i> spp.
<i>Cladina rangiferina</i> ^b	<i>Picea</i> spp. > 6 m ht	<i>Cetraria islandica</i> ^{a,c}	<i>Gramineae</i>
<i>Cladina stellaris</i> ^b	Deciduous tree spp. seedlings	<i>Cladonia uncialis</i> ^{a,c}	<i>Betula papyrifera</i> ^a
Total primary forage lichens	Deciduous tree spp. <0.1 m ht	<i>Stereocaulon</i> spp. ^c	<i>Alnus</i> spp. ^a
<i>Cladonia amaurocraea</i> ^c	Deciduous tree spp. 0.1–1 m ht	Total secondary forage lichens	<i>Salix</i> spp. ^a
<i>Flavocetraria cuculata</i> ^c	Deciduous tree spp. 1–2 m ht	<i>Peltigera apthosa</i> ^d	<i>Betula nana</i>
<i>Cetraria islandica</i> ^c	Deciduous tree spp. 2–4 m ht	<i>Peltigera</i> spp. ^d	<i>Vaccinium vitis-idaea</i> ^a
<i>Cladonia uncialis</i> ^c	Deciduous tree spp. 4–6 m ht	Total <i>Peltigera</i> spp.	<i>Picea mariana</i> ^a
<i>Stereocaulon</i> spp. ^c	Deciduous tree spp. >6 m ht	<i>Hylocomium splendens</i>	<i>Picea glauca</i> ^a
Total secondary forage lichens		<i>Pleurozium shreberi</i>	<i>Populus tremuloides</i>

^a Candidate variables for Resource Selection Function estimation.

^b Primary forage lichens.

^c Secondary forage lichens.

^d Non-selected lichens.

Table 4. Resource Selection Function parameters for the current winter range of the Nelchina Caribou Herd, Alaska, USA, 2002. The odds ratio reflects the odds for a 1% increase in cover for each respective lichen species, keeping all else constant.

Variable	Parameter estimate	SE	P-value	Odds ratio	95% CI
Intercept	−2.40	0.415	<0.001		
% cover <i>Cladonia amaurocraea</i>	0.138	0.055	0.013	1.15	1.03, 1.28
% cover <i>Cladina rangiferina</i>	0.195	0.046	<0.001	1.22	1.11, 1.33
% cover <i>Flavocetraria cuculata</i>	0.066	0.032	0.037	1.07	1.003, 1.14
% cover <i>Vaccinium vitis-idaea</i>	0.026	0.010	0.008	1.03	1.006, 1.047

forage species typically important on caribou ranges, was rare on both ranges.

The resource selection model only used 4 of the 17 variables retained after the univariate and correlative inclusion criteria (Tables 3 and 4). Percent cover by *Cladonia amaurocraea*, *Cladina rangiferina*, *Flavocetraria cuculata*, and lowbush cranberry were sufficient for predicting caribou use

(Table 4; GOF $\chi^2 = 14.2_{df=8}$, $P = 0.078$). Area under the ROC curve was 0.82 ($n = 195$, $P < 0.001$), which indicates excellent discrimination for used sites compared to random sites. Although a 1% increase in *Cladina rangiferina* cover increased odds of use by 22% (95% CI = 11–33%), *Cladina rangiferina* was about half as abundant as *Cladonia amaurocraea*, which only increased odds of

use by 15% for every 1% increase in cover; *Cladonia amaurocraea* was thus a more discriminating factor in the model (Table 4).

DISCUSSION

Our measurements of stand age documented high fire frequency in both the historic and current winter ranges of the NCH and indicated that fire had an equivalent role in vegetation succession and lichen availability in the 2 ranges. We, therefore, rejected our hypothesis that fire had less effect on lichen availability in the historic versus the current range of the NCH.

Regardless of the equivalent role of fire in the 2 ranges, forage lichen biomass was much greater in the current range. This difference in lichen biomass was not the result of fire and probably not due to other environmental differences between the 2 ranges, given the similar cover and growth rates by forage lichens in the 2 ranges. However, overgrazing in the historic range was an important difference affecting forage lichens in that range. Although cover by forage lichens was slightly greater in the historic range, overgrazing had reduced those lichens to primarily fragments or young plants that provided little biomass. Forage lichens in the historic range showed limited signs of recovery by the time of our observations, and thus our estimates of forage lichen availability were representative of range conditions the NCH had abandoned by the mid-1990s and continued to bypass in 2001.

In response to the declining lichen abundance in 1989, Lieb (1994:27) reported that a continuation in that trend could lead to "increased use of peripheral areas outside of the traditional Nelchina range, and possibly emigration." Indeed, by the mid-1990s, the NCH was migrating ≥ 100 km beyond its historic winter range, far beyond peripheral areas. By doing so, caribou were able to utilize stands with 4 times the forage lichen biomass of stands they had previously selected in the historic winter range. The neighboring Delta Caribou Herd responded similarly to increasing herd size by wintering in peripheral areas where lichen biomass was 5 times greater and where they were able to increase intake by 60–90% (Fleischman 1991).

Without caribou, overgrazed lichen stands within the NCH's historic range should recover much more quickly than stands destroyed by fire, because overgrazed but formerly productive lichen patches retain lichen fragments as propagules and favorable microclimatic conditions of intact organic substrates. Therefore, substantial recovery following overgrazing may only require 20 yr or so rather than the ≥ 60 yr required after fire (Henry and Gunn 1991, this study).

The significance of fire to lichen abundance was clearly manifest by the relationships of stand age to forage lichen cover and biomass in the current range. However, in the historic range, these relationships were obscured as a result of the confounding influence of grazing. The caribou's shift toward use of younger stands in the historic range indicated the influence of grazing, in that depletion of forage in older

stands resulted in younger stands having comparable forage availability and attractiveness to caribou.

Destruction of forage lichen stands, rather than reduced competition from associated flora, was the primary influence fire had upon lichen abundance. After fires, forage lichens seldom recovered sufficiently to attract grazing until after ≥ 60 yr, and as a group, primary forage lichen species did not reach maximum productivity until after 180 yr. Although forage lichens are shade intolerant and expected to decrease with increasing overstory, we observed that forage lichen biomass continued to increase beyond the time black spruce cover had stabilized. Biomass of *Cladonia rangiferina*, one of the most preferred forage species, continued to increase across the range of stand ages occurring in our study area.

Competition from associated plant species did not prevent forage lichen biomass from increasing through the full range of stand ages we measured. We therefore rejected our hypothesis that fire benefits caribou in taiga by reducing vascular plants that compete with lichens. Although it is theoretically possible that vascular plants could compete with lichens in stands older than we observed, the frequency of fires within the range of the NCH does not allow this to occur.

Relationships of lichen to stand age vary widely among locations throughout the circumpolar range of *Rangifer*, but few studies addressed these relationships in Alaska's taiga (Andreev 1954, Hale 1973). A review of literature by Kelsall et al. (1977) resulted in estimates of between 50 yr and 150 yr for recovery of lichen stands in boreal forests in the Canadian north. In northern Saskatchewan, Scotter (1964) found that forage lichen biomass continued to increase to 120 yr (the oldest stands present in his study area). Similar to our results, Scotter (1964) also observed that forage lichens of moderate value (roughly analogous to our secondary species) stabilized between 50 yr and 120 yr, whereas species of high forage value (our primary species) continued to increase to at least 120 yr. The slow recovery, low biomass, and low cover we observed compared to that in other ranges (Klein and White 1978, Crête et al. 1990, Saperstein 1993) may be the result of lower annual precipitation, lower winter temperatures, and poorer drainage.

Cladonia amaurocraea was a secondary forage lichen species in terms of caribou preference, but as the most ubiquitous of forage lichens it had the most influence on caribou distribution. In addition to cover by important forage lichens (i.e., *Cladonia amaurocraea*, *Cladonia rangiferina*, and *Flavocetraria cuculata*), cover by lowbush cranberry was also a discriminating factor in prediction of caribou use because it was a principal component of caribou diets (W. B. Collins, Alaska Department of Fish and Game, unpublished data) and was typically abundant where forage lichens occurred. In the current winter range where overgrazing did not obscure relationships between cover, biomass, and caribou distribution, we found that caribou selected older sites with greater lichen cover and biomass than in randomly selected sites, thus indicating that, within the limitations of snow conditions (Fancy and White 1985, Collins and Smith 1991), winter range selection was associated primarily with presence

of forage lichens and secondarily with other environmental factors.

Caribou locate forages by scent and are able to smell lichens buried beneath snow (Pruitt 1959, Bergerud 1974, Johnson et al. 1998). Locally, caribou are initially attracted to crater (excavate snow) where cover by forage lichens is highest, as that is where forage can be most readily detected (Johnson et al. 1998). As foraging reduces lichen availability in the most productive sites, caribou shift their effort to sites where forage lichen biomass and corresponding efficiency for consuming lichens is at least comparable. Thus, as biomass was depleted in older, more productive stands in the historic range, caribou broadened their selection to include younger stands having less lichen cover but forage lichen biomass comparable to higher-cover stands where biomass was already depleted. On a larger scale, as the entire historic range became overgrazed, caribou extended their search for winter forage to include the current range, which at that time had greater forage lichen biomass, albeit similar forage lichen cover to the historic range.

MANAGEMENT IMPLICATIONS

In Alaska's taiga, caribou abandoned winter range after forage lichen availability in caribou-selected stands declined to approximately 400 kg/ha or to levels characteristic of stands <60 yr old. Although abandonment favors recovery of overgrazed range, winter utilization of lichens by the NCH in the current range will eventually compete with recovery and re-colonization by the Fortymile Caribou Herd. Low availability of forage lichens in the historic range was not only indicative of overstocking leading up to the mid-1990s, but distribution of the NCH during that period highlighted the importance of retaining mid and late successional habitat as the principal source of winter forages for caribou. In cases such as the historic NCH range, where herd population objectives were developed during a period of limited impact by fire, return to average or greater fire frequency will further limit carrying capacity for caribou. Whether increased fire occurs naturally, as in response to a climatic warming trend, or through management, there will be major tradeoffs for habitat enhancement for early seral species versus retention of mid-to-late successional vegetation for caribou. Management to ensure sustained availability of productive caribou range requires lead time of ≥ 60 yr.

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