

Winter habitat use by female caribou in relation to wildland fires in interior Alaska

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Abstract: The role of wildland fire in the winter habitat use of caribou (*Rangifer tarandus*) has long been debated. Fire has been viewed as detrimental to caribou because it destroys the slow-growing climax forage lichens that caribou utilize in winter. Other researchers argued that caribou were not reliant on lichens and that fire may be beneficial, even in the short term. We evaluated the distribution of caribou relative to recent fires (<50 years old) within the current winter range of the Nelchina caribou herd in east-central Alaska. To address issues concerning independence and spatial and temporal scales, we used both conventional very high frequency and global positioning system telemetry to estimate caribou use relative to recent, known-aged burns. In addition, we used two methods to estimate availability of different habitat classes. Caribou used recently burned areas much less than expected, regardless of methodologies used. Moreover, within burns, caribou were more likely to use habitat within 500 m of the burn perimeter than core areas. Methods for determining use and availability did not have large influences on our measures of habitat selectivity.

Résumé : Le rôle des feux de toundra sur l'utilisation de l'habitat par le caribou (*Rangifer tarandus*) en hiver fait l'objet de longs débats. Le feu est considéré comme nuisible au caribou, car il détruit les lichens à croissance lente du climax que le caribou utilise en hiver. D'autres chercheurs pensent que le caribou n'est pas dépendant des lichens et que le feu peut être bénéfique, même à court terme. Nous avons évalué la répartition des caribous en fonction des feux récents (<50 ans) dans les aires d'hivernage actuelles du troupeau de caribous Nelchina dans le centre-est de l'Alaska. Pour résoudre les questions relatives à l'indépendance et aux échelles spatiales et temporelles, nous avons utilisé à la fois la télémétrie conventionnelle à très haute fréquence et la télémétrie basée sur le système de positionnement global pour estimer l'utilisation par les caribous de surfaces récemment brûlées d'âge connu. De plus, nous avons utilisé deux méthodes pour estimer la disponibilité des différentes classes d'habitat. Les caribous utilisent les surfaces récemment incendiées beaucoup moins que prévu, quelle que soit la méthodologie employée. De plus, sur les surfaces incendiées, les caribous sont plus susceptibles d'utiliser les habitats situés à moins de 500 m du périmètre de la surface brûlée que la région centrale. Les méthodes employées pour déterminer l'utilisation et la disponibilité n'ont pas d'influence importante sur nos mesures de sélectivité de l'habitat.

[Traduit par la Rédaction]

Introduction

Recurrent and often expansive wildland fires are a natural component of boreal forest ecosystems (Lutz 1956). Indeed, wildland fire is the dominant ecological process determining the vegetative landscape of interior Alaska. Fire recurrence is related to age of vegetation, physiography, and local environmental conditions (Rowe et al. 1974). Patterns of postfire succession (Van Cleve and Viereck 1981, 1983) and fire cycle effects on the forest mosaic are well described for boreal forests (Bergeron and Dansereau 1993). Although wildland fires increase overall vegetative diversity and productivity, they destroy fruticose lichens. These lichens, if available, are major constituents of winter diets of caribou (*Rangifer*

tarandus; Boertje 1984; Thomas 1998). Forage lichens are associated with late successional seres of boreal forest (Klein 1982) and require long periods of recovery following fire or other disturbance (Viereck and Schandelmeier 1980; Thomas and Kiliaan 1998).

Since at least the 1920s, it has been suggested that wildland fires are harmful to caribou populations (Klein 1982). Early research suggested that fires had negative effects on caribou populations because of losses of mature forest stands with substantial lichen biomass (Kelsall 1960; Scotter 1965, 1970; Thomas 1969). However, other studies indicated little or no impact of fire on the population dynamics of caribou (Skoog 1968; Bergerud 1972; Johnson and Rowe 1975). These divergent findings precipitated research in Canada to evaluate the influences of fire history on winter habitat use of caribou (Miller 1976, 1980; Schaefer and Pruitt 1991; Thomas 1991; Thomas et al. 1998). The research revealed that caribou avoided recent fires (up to 60 years) and that caribou herds may expand their ranges to compensate for burned portions of wintering areas. Klein (1982) and Schaefer and Pruitt (1991) concluded that although wildland fire may be detrimental to caribou populations in the near term by destroying forage lichens, fire might be requisite in the long term to maintain high lichen productivity by destroying competing mosses and rejuvenat-

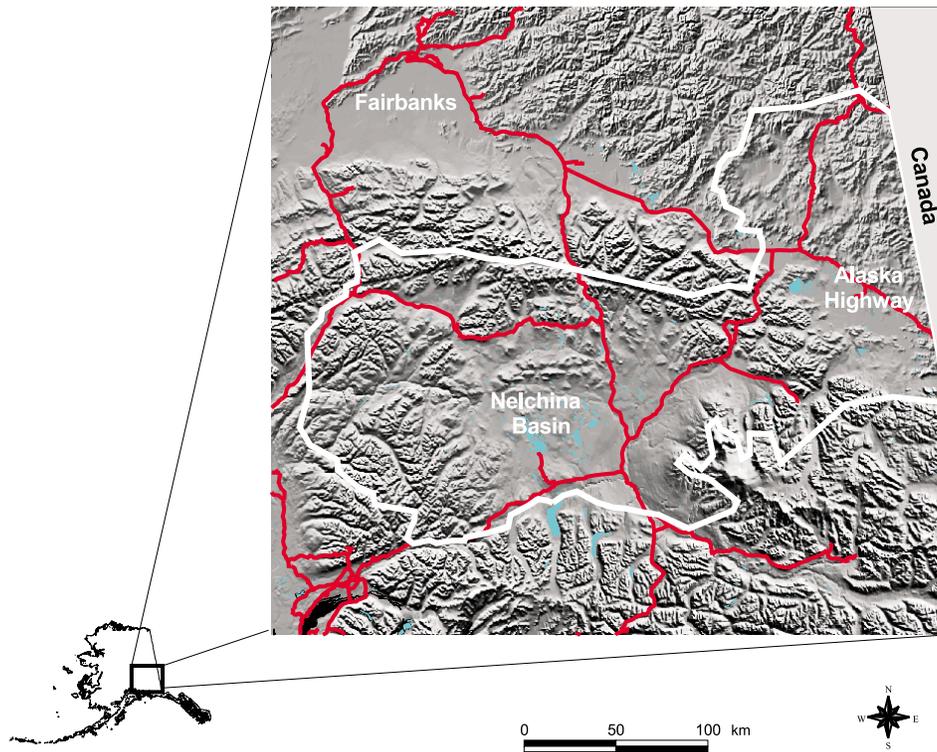
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Fig. 1. Annual range of the Nelchina caribou (*Rangifer tarandus*) herd in eastern Alaska, 1999–2001. The herd historically wintered in the Nelchina Basin (before 1990), but currently winters primarily north of the Alaska Highway (after 1990).



ing senescent lichen mats in very old stands (Miller 1980; Schaefer and Pruitt 1991). Additionally, avoidance of recent burns by caribou may alleviate the detrimental effects of grazing and trampling, allowing recolonizing lichen mats to recover in these stands (Lutz 1956; Ahti and Hepburn 1967; Rowe et al. 1975; Kershaw 1977).

For the past decade, most of the 31 000 caribou of the Nelchina caribou herd (NCH) have migrated northeast out of the Nelchina Basin, their traditional wintering grounds, to overwinter north of the Alaska Highway (Fig. 1). Less than 1% of the Nelchina Basin has burned recently (≤ 50 years), whereas the herd's current winter range is much more susceptible to wildland fire (Fig. 2). The current winter range is composed largely of rolling hills of black spruce (*Picea mariana*) woodlands where fire is the primary force in determining vegetative cover. This shift to fire-prone winter range appears to run counter to current theory. Therefore, the NCH provides an excellent opportunity to investigate the effects of wildland fire on habitat use of interior caribou herds.

Our objective was to evaluate habitat use by caribou relative to fire history. Specifically, we compared the use by caribou with the gross availability of burned areas ≤ 50 years old, assessed differences in selection among successional stages of these burned areas, and evaluated the use of burn edges versus their core areas. We hypothesized that although caribou would avoid stands ≤ 50 years old in general, they may make more use of the 10- to 20-year-old stands that would have the greatest availability of shrubs. Burn edges provide the juxtaposition of unburned habitats with adequate forage and relatively open, burned areas that could provide additional security from predators.

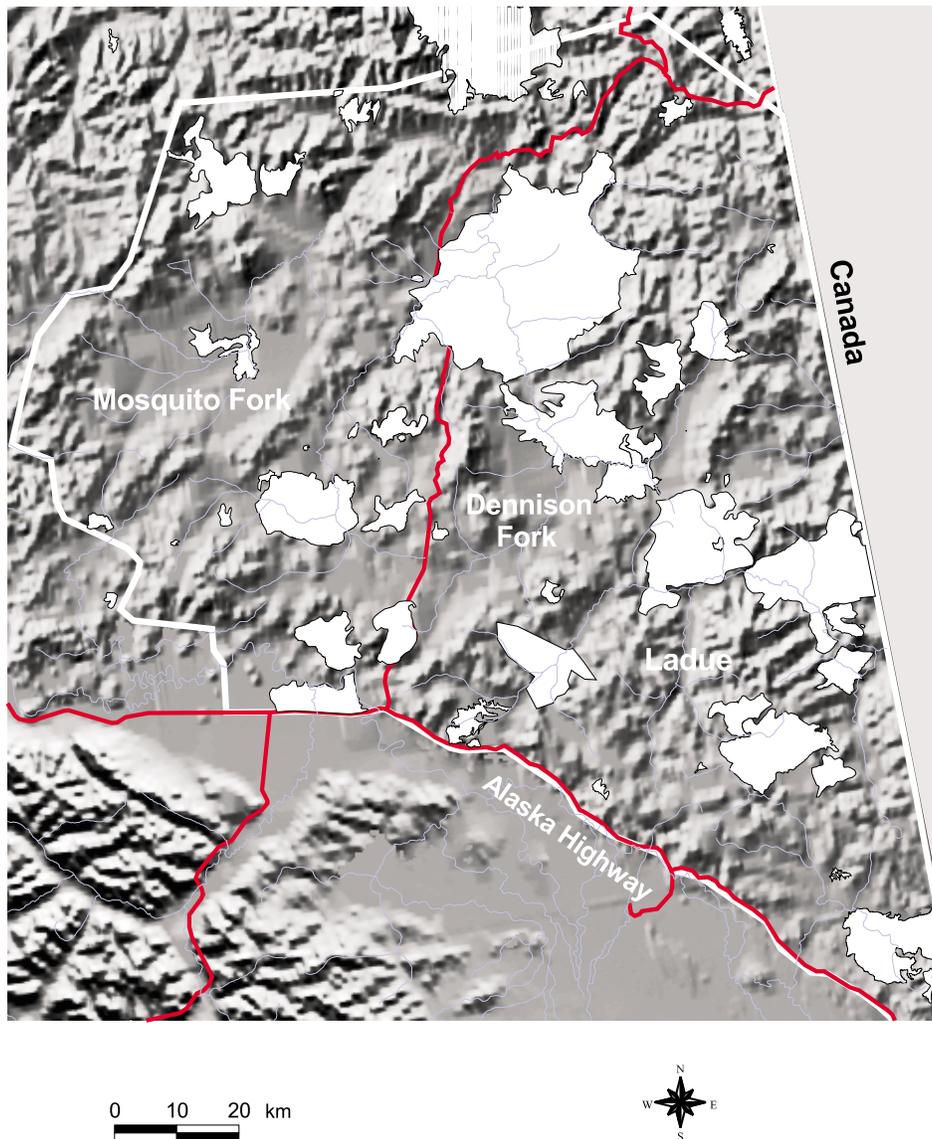
Habitat use–availability analyses can be compromised by study design limitations, lack of independence among animals and locations, and how available habitat is determined (Johnson 1980; Alldredge and Ratti 1986, 1992; Thomas and Taylor 1990). Additionally, spatial and temporal scales of an investigation can affect apparent selection (Johnson 1980; Porter and Church 1987; Levin 1992; Rettie and Messier 2000). To address these issues, we used a combination of conventional very high frequency (VHF) and global positioning system (GPS) technology. Furthermore, we used two methods to estimate habitat availability on scales appropriate for each location dataset.

Materials and methods

Study area

The study area, located in the eastern interior of Alaska (141° – $143^{\circ}30'W$, 63° – $64^{\circ}N$), is bounded on the south by the Alaska Highway and on the east by the U.S. – Canada border and includes the Mosquito and Dennison forks of the Fortymile River and the Ladue River drainages (Fig. 2). The region is characterized by archetypal boreal forest, with black spruce dominating the landscape with white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*) occurring on more xeric sites. The absence of jack pine (*Pinus banksiana*) is the most conspicuous difference between the forests of central Canada and interior Alaska. Shrub and wetland communities occur throughout the region but are not nearly as extensive as forested areas. Alpine communities are found above 1100 m, but these elevations are relatively rare in the region. The

Fig. 2. Distribution of recent burns (≤ 50 years old) within the winter range study area for the Nelchina caribou herd between October and April of 1999–2001.



continental climate of the region is typified by long, cold winters with warm, dry summers. Snow accumulation usually increases throughout the winter, reaching maximum depth in late March or early April. Fires are typically ignited by lightning strikes; however, human-caused fires (including prescribed burns) also affect this region. Ignitions occur between May and September; however, most fires originate in early summer (Viereck 1973). Other works provide more detailed accounts of the physiography and vegetation of this region (Skoog 1956; Curatolo 1975).

Mapping fire history

We obtained geographical information system (GIS) coverage of burn perimeters dating back to 1950 (Fig. 2) from the Alaska Fire Service (AFS). Before 1993, fires that disturbed less than 405 ha (1000 acres) were not mapped, whereas since 1993, the mapping threshold was reduced to 40.5 ha (100 acres). Furthermore, we searched archived AFS records and incorporated additional unmapped fires to the

extent possible. We assigned fires to four different age classes: ≤ 10 , 11–20, 21–50, and >50 years. The categories were based on patterns of succession in the region (Viereck 1973; Collins and Schwartz 1998). The last category (>50 years) included some areas that burned during the last 50 years but were not mapped because of mapping thresholds or fires that were not detected. However, we believe that these mischaracterizations represent a minor fraction of the area burned within our study area during the last 50 years and should not unduly influence our results.

Caribou movements

Female caribou, including calves, yearlings, and cows, were captured using standard helicopter darting techniques (Adams et al. 1987, 1995) and were fitted with VHF transmitters during October 1999, April 2000, October 2000, and April 2001. The relatively inexpensive cost of VHF collars allowed us to deploy samples of 93 and 89 caribou during the 1999–2000 and 2000–2001 winters, respectively, which

Table 1. Habitat composition relative to stand age for winter range of the Nelchina caribou (*Rangifer tarandus*) herd, east-central Alaska, 1999–2001.

Method*	Type	Area (km ²)	Available habitat (%)	Number of caribou locations (%)
VHF–MCP	Available habitat	11 495	100	849 (100)
	All burns	2 517	21.9	46 (5.4)
	0–10 years	1 342	11.7	33 (3.9)
	11–20 years	70	0.6	5 (0.6)
	21–50 years	1 105	9.6	8 (0.9)
GPS–MCP	Available habitat	10 211	100	12 117 (100)
	All burns	2 303	22.6	698 (5.8)
	0–10 years	1 128	11.1	398 (3.3)
	11–20 years	70	0.7	47 (0.4)
	21–50 years	1 105	10.8	253 (2.1)
GPS–circle [†]	Available habitat	1 204 134	100	12 117 (100)
	All burns	135 256	11.2	698 (5.8)
	0–10 years	79 886	6.6	398 (3.3)
	11–20 years	6 334	0.5	47 (0.4)
	21–50 years	49 036	4.1	253 (2.1)

*VHF–MCP, a minimum convex polygon (MCP) was created using the VHF dataset to derive the extent of available habitat; GPS–MCP, a MCP was created using the GPS dataset to derive the extent of available habitat; GPS–circle, circles (radius = 5658 m) around each GPS data point delineated available habitat.

[†]Areas determined using the circle method are larger than the MCP because of overlap of the 12 117 circles.

were monitored on a monthly schedule using fixed-wing aircraft. Locations of each caribou were determined with GPS units onboard the aircraft. Of these caribou, 16 and 13 cows each winter, respectively, wore collars that also incorporated a GPS unit programmed to calculate and store locations every 7 h. The cows were recaptured at the end of winter to download the digital GPS archive.

Habitat analysis

We used individual relocations as our observational units for habitat use analyses, though we did investigate variation among individual GPS-collared cows. Habitat use analyses can be significantly influenced by how available habitat is determined (Johnson 1980). Therefore, we used two methods to quantify the proportions of available habitat within each stand age category. The first method was to create separate minimum convex polygons (MCPs) for the VHF and GPS datasets (*sensu* Bradshaw et al. 1995; Poole et al. 2000; Rettie and Messier 2000) and to determine the proportion of each stand age class within the MCPs from the fire history GIS coverage. These MCPs were used to determine the northern and western boundaries of the winter range of the NCH. The Alaska Highway defined the southern boundary, and the Canadian border, the eastern boundary. None of the collared caribou that migrated through the Alaska Range, in either year, wintered south of the Alaska Highway, so we considered relocations south of the highway as migratory. Lack of fire perimeter data in Canada prompted our decision for using the border as the eastern study area boundary and because only two caribou relocations (both VHF) fell east of the border.

The second method used to determine habitat availability was based on only the GPS data. Each location served as the center of a circle with a radius equal to the maximum dis-

tance that a caribou was likely to travel in the 7 h between relocations (99th percentile movement = 5658 m; *sensu* Arthur et al. 1996). The area within each circle represented available habitat. This approach (subsequently termed the “circle method”) addresses the concern that instrumented caribou simply could not reach all areas contained within the MCP in the 7 h between GPS relocations (Johnson 1980; Alldredge and Ratti 1986, 1992; Thomas and Taylor 1990; Aebischer et al. 1993). ArcView GIS (ESRI 1996) was used to create these circles and to determine the areal extent of each stand age class and the areal extent of fires within three different derivations of available habitat (VHF–MCP, GPS–MCP, and GPS–circle).

To investigate influences of edges of burned areas on habitat selection of caribou, we used ArcView to create 500 m wide buffers inside and outside burn perimeters and compared use by caribou in these areas with habitat >500 m outside burned areas and in the core of burned areas (Neu et al. 1974).

We calculated standardized selectivity indices and their 95% confidence intervals according to Manly et al. (1993) to evaluate use of burned areas. We used χ^2 analysis to detect significant differences in the use of burned areas by collar type, caribou age class, year, and month (Zar 1984).

Results

The areal extent of available habitat and proportion burned was dependent on the location data set (VHF versus GPS) used and methodology used to determine available habitat (MCP versus circle; Table 1). Approximately 50% less burned area was defined as available when we used the circle methodology. Burns ≤ 10 years old made up most of total area burned and number of fires, whereas burns >20 years old were much less common but accounted for a large

Fig. 3. Chronology of acres burned during 1950–2001 in the winter range study area for the Nelchina caribou herd in eastern Alaska. The numbers above the bars represent the number of burns within that category.

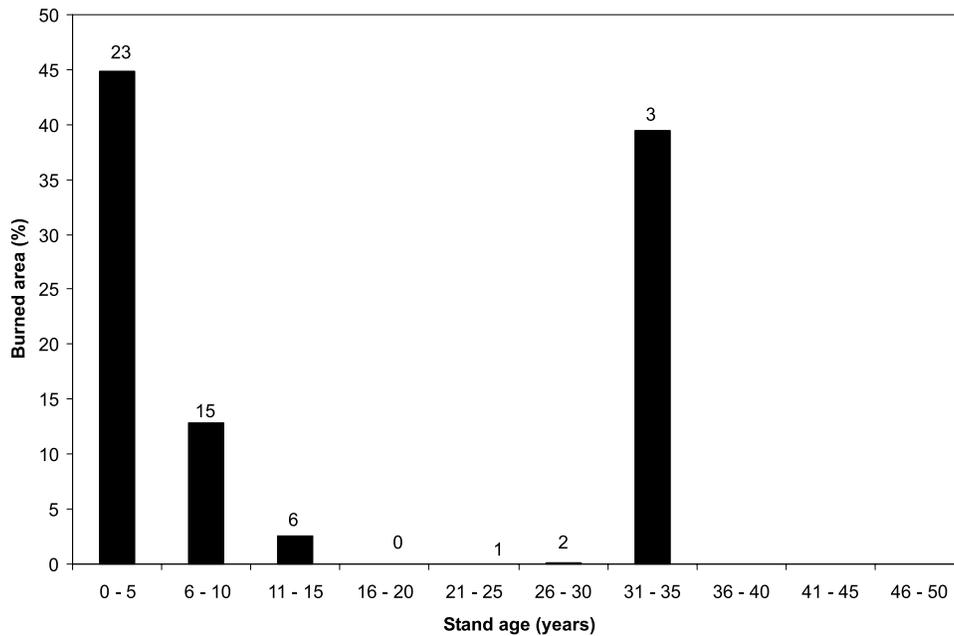
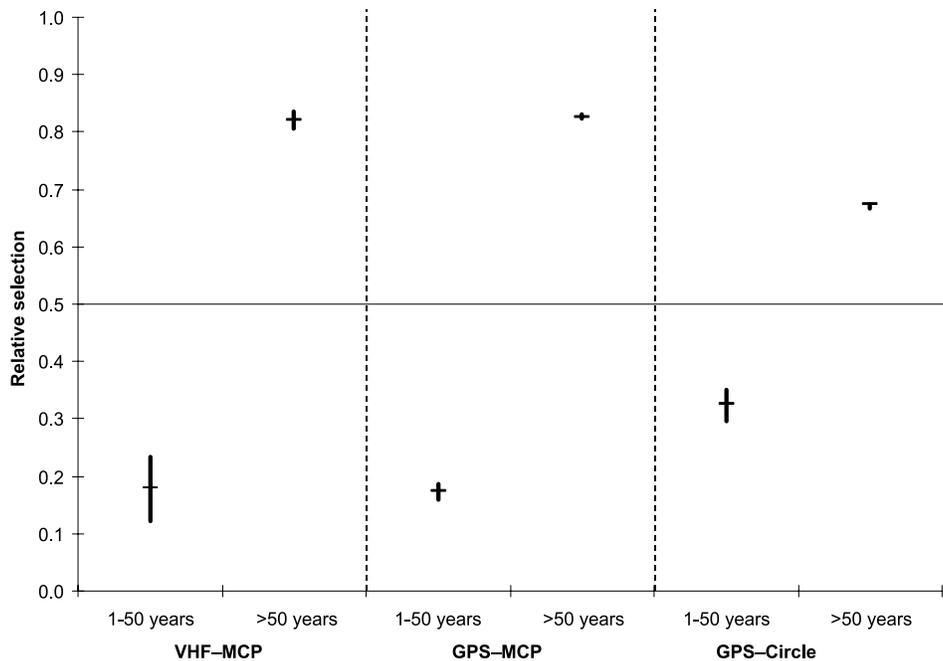


Fig. 4. Habitat selection indices (and 95% CI) for the Nelchina caribou herd cows on their wintering grounds in east-central Alaska, 1999–2001. Available habitat was categorized as either recently burned (1–50 years) or >50 years. A selectivity index of 0.5 implies use in proportion to availability. Two different datasets were used (VHF and GPS), as well as two methods for determining the amount of available habitat (MCP and circle).

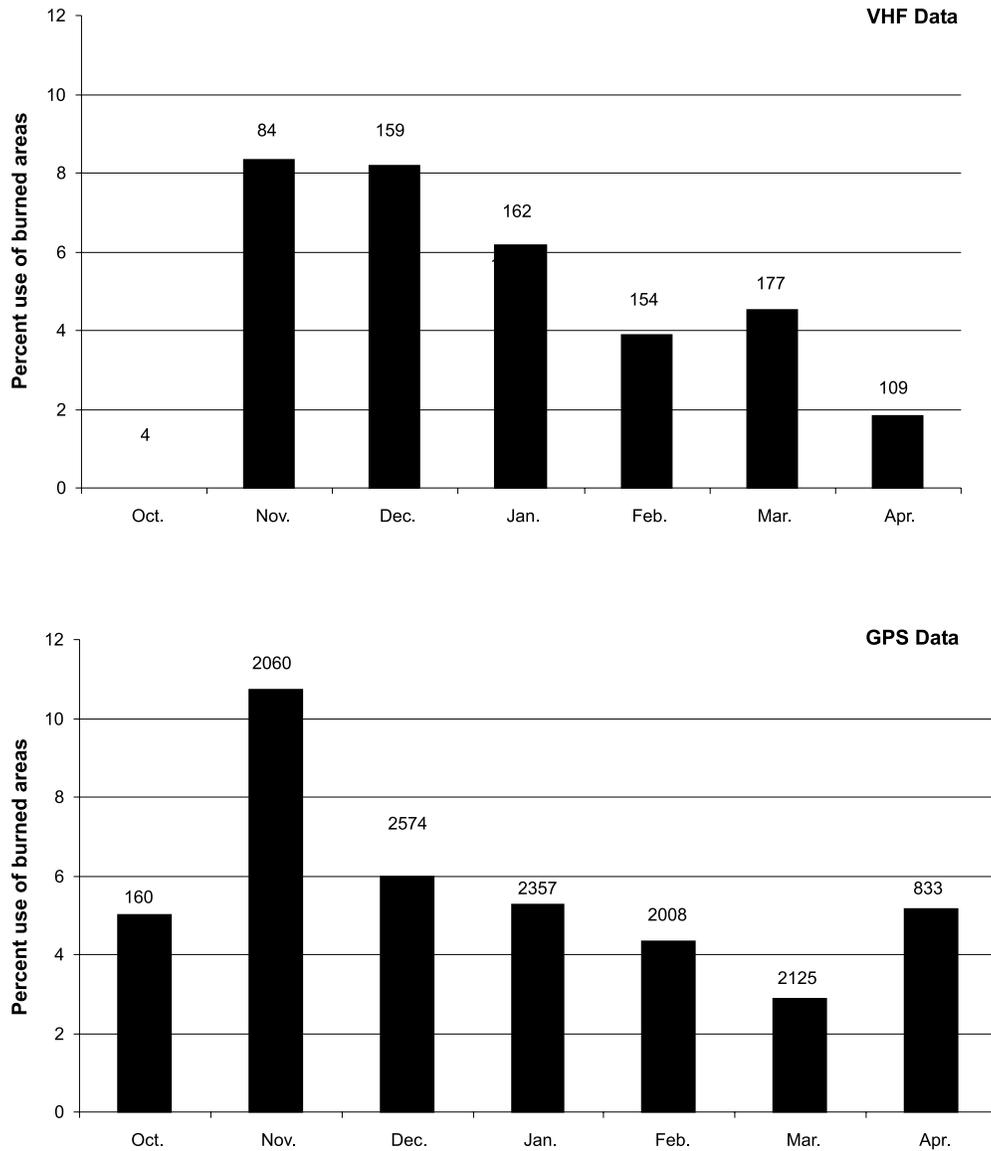


proportion of the total area burned (Table 1; Fig. 3). There were relatively few burns in the 11- to 20-year-old category, accounting for $\leq 1\%$ of the total area, and none in the 35- to 50-year-old category (Fig. 3).

We acquired 849 VHF relocations within the study area, of which 46 (5.4%) were within mapped fire perimeters. GPS collars furnished 12 117 relocations, including 698 (5.8%) within fire perimeters. The GPS collars, on average, successfully acquired relocations 82.5% of the time (range 42.2–98.9%).

Individual use of burned areas by GPS-collared cows averaged 6.4% (range 0.6–17.0%), with an average sample size of 527 (range 19–987). Use of burned areas did not differ among caribou age classes ($\chi^2 = 2.42$, $df = 2$, $P = 0.298$), and therefore these data were pooled. Use of burned areas did not vary between years ($\chi^2 = 0.28$, $df = 1$, $P = 0.594$) for caribou with VHF transmitters but did for animals wearing GPS units ($\chi^2 = 9.34$, $df = 1$, $P = 0.002$). GPS-collared caribou were located within fire perimeters slightly more during

Fig. 5. Use of burned areas by month during the winters of 1999–2000 and 2000–2001 for the Nelchina caribou herd, Alaska. Sample size (number of caribou relocations) is denoted above percentage bar.



the second winter (387 of 6038 relocations; 6.4%) compared with the first year (311 of 6160 relocations; 5.1%). However, we pooled the data between years for subsequent analyses because the difference in proportion of use between years was relatively small and statistical significance was enhanced by extremely large numbers of relocations.

Caribou use of burned areas ≤ 35 years old was considerably less than availability, regardless of dataset or method used to determine available habitat (Fig. 4). The proportion of locations within burns did not differ between the GPS and VHF datasets ($\chi^2 = 0.17$, $df = 1$, $P = 0.678$). Use of burned areas ≤ 35 years old differed among months with the GPS dataset ($\chi^2 = 135.9$, $df = 6$, $P < 0.001$) but not with the VHF information ($\chi^2 = 7.87$, $df = 6$, $P = 0.248$). In general, use of burned areas declined throughout the winter (Fig. 5). Caribou use of young (< 10 years old) and relatively older stands (21–50 years old) was consistently less than expected for all three approaches (Fig. 6). Stands 11–20 years old may have been used relatively more than other burned areas, but preci-

sion of selectivity indices was poor because of the limited extent of this stand age class (Figs. 3, 6).

Use of interior 500-m buffers was nearly in proportion to their availabilities, whereas use of core areas of burns was much less than expected (Fig. 7). Although the 500-m interior buffer consisted of $\sim 25\%$ of the burned area, more than 60% of VHF and GPS locations within burned areas occurred in the buffer. The GPS data revealed that use of the exterior 500-m buffers was slightly greater than their availability (Fig. 7). The exterior 500-m buffer had a lower selectivity index than areas > 500 m away from burns, when an MCP was used to determine habitat availability, but not using the circle method.

Discussion

Caribou selected for relatively mature stands (> 50 years old) and avoided stands ≤ 35 years old. We could not determine if caribou avoided burns in the 35- to 50-year age class

Fig. 6. Habitat selection indices (and 95% CI) for Nelchina caribou herd cows on their wintering grounds in east-central Alaska, 1999–2001. Available habitat was categorized as into 4 age classes (1–10, 11–20, 21–50, and >50 years) based on the last time that the stand burned. A selectivity index of 0.25 implies use in proportion to availability. Two different datasets were used (VHF and GPS), as well as two methods for determining the amount of available habitat (MCP and circle).

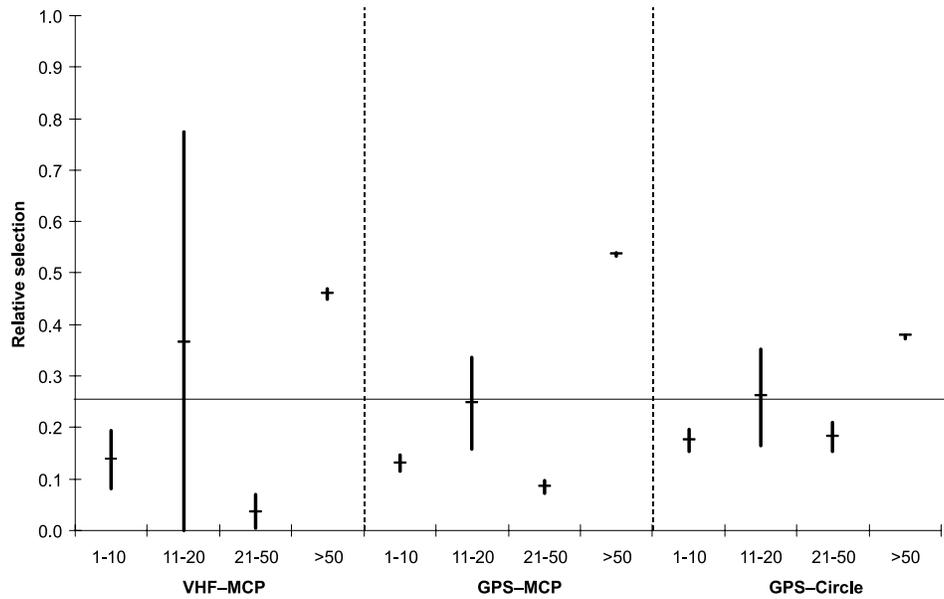
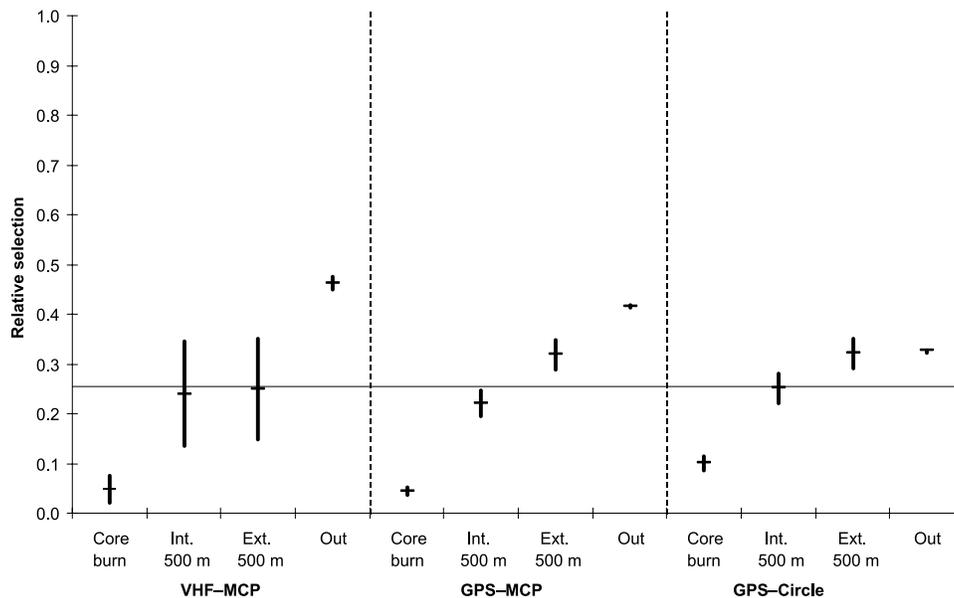


Fig. 7. Habitat selection indices (and 95% CI) for Nelchina caribou herd cows on their wintering grounds in east-central Alaska, 1999–2001. Available habitat was classified into four categories: within a recent (<50 years) burn and >500 m from the perimeter (Core burn); within a recent burn and <500 m from the perimeter (Int. 500 m); outside a recent burn but within 500 m of a burn perimeter (Ext. 500 m); or >500 m from a recent burn perimeter (Out). A selectivity index of 0.25 implies use in proportion to availability. Two different datasets were used (VHF and GPS), as well as two methods for determining the amount of available habitat (MCP and circle).



because that age class was not represented within the study area. However, because stands in this age range are dominated by maturing deciduous forest, we speculate that caribou may avoid stands in that age range as well. The limited use of recently burned areas by caribou corroborated findings from central Canada for both resident woodland caribou

(Schaefer and Pruitt 1991) and migratory populations (Thomas et al. 1996, 1998).

Researchers have posited that wildland fire might be beneficial to caribou, even in the short term (Johnson and Rowe 1975), by increasing vascular forage. Our research reveals that caribou strongly selected against burned areas through-

out the winter. Early successional vascular forages present in burns may be more attractive to caribou in early winter and spring, giving rise to greater use of burned areas during these periods. However, in the range of the NCH, these alternate forage species may only be attractive for very short periods at the beginning of winter before snow accumulates and in early spring as the caribou are migrating to the calving grounds. Although foraging within burns during these brief periods may provide important nutrients, it appears to occur on a limited temporal basis. Therefore, coupled with our finding of lack of selection for burned areas in winter, our data provide little support for the theory that wildland fire benefits caribou in the short term (<50 years) in interior Alaska.

Habitat in the 0- to 10-year and 21- to 35-year age classes received less use than expected based on availability. Caribou may have used 11- to 20-year-old stands more than other age classes of burns, but our results are equivocal because this age class was rare in our study area. Burns <10 years old are devoid of lichen suitable for caribou forage, and access to vascular forage is limited. Caribou migrate out of the winter range just as or before vascular species, such as *Eriophorum* spp., become available in spring. Greater use of 11- to 20-year-old stands could occur because of increased abundance of vascular forages (Collins and Schwartz 1998). The 21- to 50-year-old stands may provide little forage for caribou, as vascular forage species become less palatable and lichens remain sparse (Viereck and Schandelmeier 1980; Thomas and Kiliaan 1998).

Our analyses suggest that burn perimeters are not sought out for foraging, predator avoidance, or other ecological benefit because caribou underutilized all burned habitat. However, when locations were inside burned areas, they tended to be within 500 m of the perimeter. Use of the interior buffer was essentially in proportion to their availabilities, but core burned areas were the least selected for habitat type. Use of habitat more than 500 m away from burned areas was greater than expected based on availability. The GPS data revealed that use of the exterior buffer was greater than expected based on availability.

The degree to which caribou avoid recently burned areas was so great that analyses using either the VHF or GPS dataset were able to reveal this relationship. We infer from this that either type of sampling technique was acceptable for detecting gross differences in winter range habitat use (e.g., selection between burned and unburned habitat) at the scales used here. One disparity that was revealed was that differences between years and months could be detected with the GPS data but not with the VHF data. Analysis of the VHF data set resulted in larger confidence intervals compared with the GPS data, primarily as a result of differences in sample size. This was especially apparent when analyzing habitat types with limited areal extent (i.e., the 11- to 20-year-old age class and buffers). The scale and objectives of the research must be considered when deciding between use of traditional VHF versus GPS technology, but as our research suggests, there are spatial and temporal scales at which either technology can be appropriate.

Determining available habitat using the circle methodology eliminated problems associated with using a boundary based

on an aggregated dataset, such as an MCP. The proportion of available burned habitat defined by the circle method was ~50% of the amount defined by the MCPs because caribou strongly avoided core area of burns and therefore these areas were discounted using the circle methodology. The amount of available habitat will vary with different radii of the circle. At one extreme, a circle with a radius of 0 m is equivalent to the point locations, and use equals availability. On the other extreme, in circles with very large radii, availability will be the same as determined by using MCPs. We believe that the circle method results in more conservative estimates of habitat use than MCPs because the broad-scale selection against the core of burn areas is already factored into the analysis. The degree of avoidance contributed to the concurrence between the two methods that caribou selected against recently burned areas. Disparities may arise when selection behaviors are subtler or when research is more focused, such as analyzing buffers or different stand age classes.

Wildland fires destroy caribou forage lichens, and we hypothesize that this is the primary factor influencing caribou habitat selection. Unfavorable snow conditions and deadfalls have also been implicated as factors that may contribute to the avoidance of burned areas by caribou (Schaefer and Pruitt 1991; Thomas et al. 1996). These factors may increase foraging costs or reduce the ability of caribou to evade predators. Although we cannot infer consequences for individual fitness or population dynamics, wildland fire influences overwinter nutritional performance of caribou in the boreal forest by essentially eliminating large expanses of habitat for decades or by increasing their migratory movements to find additional lichen-rich winter range.

Climatic changes and pressure to initiate prescribed burns are factors that could potentially increase the areal extent of burns in boreal forests in the future. Although the rejuvenating effects of wildland fire have been noted as being beneficial to some wildlife species, such as moose (*Alces alces*), this relationship does not hold for all species. The implication for caribou is that increasing wildland fires will result in a reduction of winter habitat for several decades.

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References

- Adams, L.G., Valkenburg, P., and Davis, J.L. 1987. Efficacy of carfentanil citrate and naloxone for field immobilization of Alaskan caribou. *In* Proceedings of the 3rd North American Caribou Workshop, Chena Hot Springs, Alaska, 4–6 November 1987. Alaska Department of Fish and Game, Juneau. pp. 167–168.

- Adams, L.G., Dale, B.W., and Mech, L.D. 1995. Wolf predation on caribou calves in Denali National Park, Alaska. *In Ecology and conservation of wolves in a changing world. Edited by L.N. Carbyn, S.H. Fritts, and D.R. Seip.* Can. Circumpolar Inst. Occas. Publ., Edmonton, Alta., No. 35. pp. 245–260.
- Aebischer, N.J., Robertson, P.A., and Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, **74**: 1313–1325.
- Ahti, T., and Hepburn, R.L. 1967. Preliminary studies on woodland caribou range, especially on lichen stands, in Ontario. Ontario Department of Lands and Forests Res. Rep. No. 74.
- Allredge, J.R., and Ratti, J.T. 1986. Comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manag.* **50**: 157–165.
- Allredge, J.R., and Ratti, J.T. 1992. Further comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manag.* **56**: 1–9.
- Arthur, S.M., Manly, B.F.J., McDonald, L.L., and Garner, G.W. 1996. Assessing habitat selection when availability changes. *Ecology*, **77**: 215–227.
- Bergeron, Y., and Dansereau, P.R. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. *J. Veg. Sci.* **4**: 827–832.
- Bergerud, A.T. 1972. Food habits of Newfoundland caribou. *J. Wildl. Manag.* **36**: 913–923.
- Boertje, R.D. 1984. Seasonal diets of the Denali Caribou Herd, Alaska. *Arctic*, **37**: 161–165.
- Bradshaw, C.J.A., Hebert, D.M., Rippin, A.B., and Boutin, S. 1995. Winter peatland habitat selection by woodland caribou in north-eastern Alberta. *Can. J. Zool.* **73**: 1567–1574.
- Collins, W.B., and Schwartz, C.C. 1998. Logging in Alaska's boreal forest: creation of grasslands or enhancement of moose habitat. *Alces*, **34**: 355–374.
- Curatolo, J.A. 1975. Factors influencing local movements and behavior of barren-ground caribou (*Rangifer tarandus granti*). M.Sc. thesis, University of Alaska, Fairbanks.
- Environmental Systems Research Institute. 1996. ArcView version 3.2. Environmental Systems Research Institute, Redlands, Calif.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**: 65–71.
- Johnson, E.A., and Rowe, J.S. 1975. Fire in the subarctic wintering ground of the Beverley Caribou Herd. *Am. Midl. Nat.* **94**: 1–14.
- Kelsall, J.P. 1960. Cooperative studies of barren-ground caribou 1957–58. *Can. Wildl. Manag. Bull. Ser. 1*, No. 15.
- Kershaw, K.A. 1977. Studies on lichen-dominated systems. XX. An examination of some aspects of the northern boreal lichen woodlands in Canada. *Can. J. Bot.* **55**: 393–410.
- Klein, D.R. 1982. Fire, lichens, and caribou. *J. Range Manag.* **35**: 390–395.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology*, **61**: 65–71.
- Lutz, H.J. 1956. Ecological effects of forest fires in the interior of Alaska. U.S. Department of Agriculture Tech. Bull. No. 1133.
- Manly, B.F.J., McDonald, L.L., and Thomas, D.L. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London.
- Miller, D.R. 1976. Wildfire and caribou on the taiga ecosystem of northcentral Canada. Ph.D. thesis, University of Idaho, Moscow, Idaho.
- Miller, D.R. 1980. Wildfire effects on barren-ground caribou wintering on the taiga of north-central Canada. *In Proceedings of the 2nd International Reindeer/Caribou Symposium. Edited by E. Reimers, E. Gaare, and S. Skjemneberg.* Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway. pp. 84–89.
- Neu, C.W., Byers, C.R., and Peek, J.M. 1974. A technique for analysis of utilization–availability data. *J. Wildl. Manag.* **38**: 541–545.
- Poole, K.G., Heard, D.C., and Mowat, G. 2000. Habitat use by woodland caribou near Takla Lake in central British Columbia. *Can. J. Zool.* **78**: 1552–1561.
- Porter, W.F., and Church, K.E. 1987. Effects of environmental pattern on habitat preference analysis. *J. Wildl. Manag.* **51**: 681–685.
- Rettie, J.W., and Messier, F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, **23**: 466–478.
- Rowe, J.S., Bergsteinsson, J.L., Padbury, G.A., and Hermesh, R. 1974. Fire studies in the Mackenzie Valley. Indian and Northern Affairs Publ. No. QS-1567-000-EE-A1.
- Rowe, J.S., Spittlehouse, D., Johnson, E., and Jasieniuk, M. 1975. Fire studies in the Upper Mackenzie Valley and adjacent Precambrian uplands. Indian and Northern Affairs Publ. No. QS-8045-000-EE-A1.
- Schaefer, J.A., and Pruitt, W.O. 1991. Fire and woodland caribou in southeastern Manitoba. *Wildl. Monogr.* No. 116.
- Scotter, G.W. 1965. Study of the winter range of barren-ground caribou with special reference to the effects of forest fires. *Can. Wildl. Serv. Prog. Rep.* No. 3.
- Scotter, G.W. 1970. Wildfires in relation to the habitat of barren-ground caribou in the taiga of northern Canada. *Ann. Proc. Tall Timbers Fire Ecol. Conf.* **10**: 85–106.
- Skoog, R.O. 1956. Range, movements, population, and food habits of the Steese–Fortymile Caribou Herd. M.Sc. thesis, University of Alaska, Fairbanks.
- Skoog, R.O. 1968. Ecology of caribou in Alaska. Ph.D. thesis, University of California–Berkeley.
- Thomas, D.C. 1969. Population estimates of barren-ground caribou March to May, 1967. *Can. Wildl. Serv. Rep. Ser.* 9.
- Thomas, D.C. 1991. Adaptations of barren-ground caribou to snow and burns. *In Proceedings of the 4th North American Caribou Workshop, St. John's, Nfld., 31 October – 3 November 1989.* Newfoundland and Labrador Wildlife Division, St. John's. pp. 482–500.
- Thomas, D.C. 1998. Fire–caribou relationships. (V) Winter diet of the Beverly Herd in northern Canada, 1980–87. *Tech. Rep. Ser. No. 312, Canadian Wildlife Service, Prairie and Northern Region, Edmonton, Alta.*
- Thomas, D.C., and Kiliaan, H.P.L. 1998. Fire–caribou relationships. (IV) Recovery of habitat after fire on winter range of the Beverly Herd. *Tech. Rep. Ser. No. 312, Canadian Wildlife Service, Prairie and Northern Region, Edmonton, Alta.*
- Thomas, D.L., and Taylor, E.J. 1990. Study designs and tests for comparing resource use and availability. *J. Wildl. Manag.* **54**: 322–330.
- Thomas, D.C., Barry, S.J., and Alaie, G. 1996. Fire–caribou–winter range relationships in northern Canada. *Rangifer*, **16**: 57–67.
- Thomas, D.C., Kiliaan, H.P.L., and Trotter, T.W.P. 1998. Fire–caribou relationships. (III) Movement patterns of the Beverly Herd in relation to burns and snow. *Tech. Rep. Ser. No. 311, Canadian Wildlife Service, Prairie and Northern Region, Edmonton, Alta.*
- Van Cleve, K., and Viereck, L.A. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. *In Forest succession: concepts and application. Edited by D.C. West, H.H. Shugart, and D.B. Botkin.* Springer-Verlag, New York. pp. 185–211.

- Van Cleve, K., and Viereck, L.A. 1983. A comparison of successional sequences following fire on permafrost-dominated and permafrost-free sites in interior Alaska. *Proc. Int. Conf. Permafrost*, **4**: 1286–1291.
- Viereck, L.A. 1973. Wildfire in the Taiga of Alaska. *J. Quat. Res.* **3**: 465–495.
- Viereck, L.A., and Schandelmeier, L.A. 1980. Effects of fire in Alaska and adjacent Canada — a literature review. Bureau of Land Management – Alaska Tech. Rep. 6.
- Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall Inc., Englewood Cliffs, N.J.