Long-term fluctuations of a caribou population revealed by tree-ring data

Claude Morneau and Serge Payette

Abstract: We used a dendroecological approach that involved examination of debarking lesions (trampling scars) produced by caribou (*Rangifer tarandus*) hooves on surficial roots and low branches of conifers to assess caribou activity in the summer range of the Rivière George caribou herd in northeastern Quebec–Labrador over the last 100 years. We deduced changes in caribou activity from the age-frequency distributions of trampling scars in three widely spaced (>100 km) old-growth conifer stands in the Rivière George area. We used the fluctuating patterns in age distributions, described by residuals of the log-linear regression, as an index of the number of trampling scars with time. This index indicated that caribou activity at the three sites followed a general decreasing trend from the turn of the last century to around 1950. There were two stages of rapid decline, around 1905–1915 and 1940, separated by a minor increase in the 1920–1930s. A sustained increase occurred from the 1950s to the 1980s. A comparison with survey and historical data for caribou suggested that these fluctuations in this common signal of activity at the three sites resulted mainly from fluctuations in caribou abundance that occurred throughout the 20th century in northeastern Quebec–Labrador. The increase in caribou activity during the 1920–1930s suggested by the frequency of trampling scars is not reported in the historical record. Caribou trampling scars on conifers may offer a new opportunity to assess large-scale spatial and temporal population trends of caribou in subarctic and boreal zones.

Résumé : Nous avons utilisé une approche dendroécologique basée sur les cicatrices de piétinement produites sur les racines superficielles et les branches basses des conifères par les sabots du Caribou (*Rangifer tarandus*), dans le but d'évaluer l'activité des caribous dans l'aire d'été du troupeau de la Rivière George, dans le nord-est du Québec–Labrador, au cours des derniers 100 ans. Nous avons identifié les changements d'activité à partir de la distribution de fréquence de l'âge des cicatrices de piétinement dans trois vieilles formations conifériennes, distantes de plus de 100 km les unes des autres, de la région de la Rivière George. Nous avons utilisé les patrons de fluctuations des fréquences d'âge, décrits par les résidus de la régression log-linéaire, comme un indice du nombre de cicatrices de piétinement au cours du temps. L'indice montre que l'activité du caribou aux trois sites a suivi une tendance générale décroissante à partir du début du siècle jusqu'à 1950 environ. Il s'est produit deux phases de déclin rapide, vers 1905–1915 et 1940, séparées par une phase de recrudescence durant les années 1920–1930. Une augmentation soutenue est survenue des années 1950 aux années 1980. La comparaison avec les données d'inventaires et les données historiques disponibles pour le caribou suggère que ces changements synchrones d'activité dans les trois sites résultent surtout des fluctuations d'abondance qui ont prévalu pendant tout le 20e siècle dans le nord-est du Québec–Labrador. L'augmentation d'activité durant les années 1920–1930 révélée par les données de cicatrices de piétinement n'a pas été identifiée par les documents historiques. Les cicatrices de piétinement produites sur les conifères par le caribou semblent donc offrir de nouvelles opportunités d'évaluer, dans l'espace et dans le temps, les fluctuations de population de caribous dans les zones subarctique et boréale.

Introduction

Caribou (*Rangifer tarandus*) in mainland North America form large migratory herds that characteristically winter on the northern fringes of the boreal forest and summer on the arctic tundra. These herds have fluctuated widely in the past and the causes of these fluctuations are much debated. Causal factors such as predation and hunting (Banfield 1954; Kelsall 1968; Bergerud 1974, 1980), climate (Klein 1991; Caughley and Gunn 1993), and food limitation due to overgrazing (Messier et al. 1988; Crête and Huot 1993; Messier 1995) have been proposed. The dynamics of migratory caribou herds remain largely unknown, however, because reliable records of long-term population changes are lacking.

Recently we presented a new method for evaluating past caribou activity during the snow-free period using tree-ring records from conifer stands (Morneau and Payette 1998). The method is based on debarking lesions (trampling scars) produced by caribou hooves on surficial roots and low branches of conifers. Scars left on conifers by trampling may persist for several decades in wood and can be dated dendrochronologically because radial growth stops at the lesion. Morneau and Payette (1998) analyzed factors influencing production and loss of caribou trampling scars in open lichen–woodland sites and concluded that changes in scar frequency adequately reflected changes in caribou activity. It appeared to be possible to use age-frequency distributions of trampling scars to

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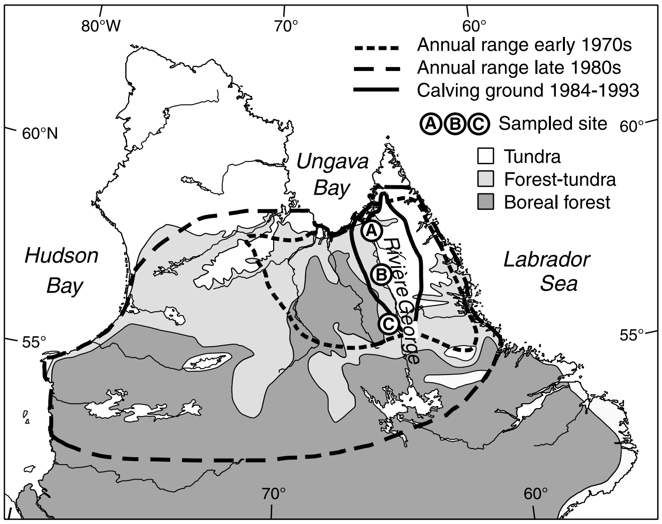

Fig. 1. Locations of the three sampled sites in the Rivière George area. The annual range of the Rivière George caribou herd (RGCH) in the early 1970s and late 1980s is according to Messier et al. (1988) and Couturier et al. (1990). The composite calving ground for 1984–1993 is according to Crête et al. (1991) and Couturier et al. (1996). Vegetation zones are after Payette (1983).

assess large-scale spatial and temporal trends in caribou populations in subarctic and boreal zones.

The Rivière George caribou herd (RGCH), inhabiting northeastern Quebec–Labrador and numbering 800 000 individuals in 1993 (Couturier et al. 1996), has undergone large fluctuations in size and distribution over the last century. Historical documents suggest that the population reached a peak in the second part of the 19th century (Low 1896), declined rapidly between 1905 and 1916 (Elton 1942), and remained scarce until the 1960s (Banfield and Tener 1958; Bergerud 1967). Recent dynamics of the RGCH were characterized by steady growth from the mid-1950s to the mid-1980s (Messier et al. 1988) and relative stabilization since then (Couturier et al. 1990; Hearn et al. 1990; Crête et al. 1991; Couturier et al. 1996; Crête et al. 1996). Description of population changes before the 1970s, however, is based on fragmentary information and superficial scientific surveys.

The tundra plateaux between Rivière George and the Labrador Sea are traditionally used by caribou during spring and summer (Low 1896; Elton 1942; Banfield and Tener 1958; Messier et al. 1988; Couturier et al. 1996). This region appears to correspond to the “center of habitation” (Skoog 1968) of the RGCH, meaning that animals use it regardless of herd size. Accordingly, changes in herd size should lead to concomitant changes in the intensity of use of the region. The recent phase of growth of the RGCH was accompanied by an increase in the number of caribou utilizing these high plateaux (Messier et al. 1988; Couturier et al. 1990).

We reconstructed trends in caribou activity over the last 100 years in the Rivière George area, a part of the traditional spring and summer range of the RGCH, by using caribou trampling scars. We deduced trends in caribou activity from the age structures of trampling scars in three widely spaced old-growth conifer stands. To verify the extent to which the tree-ring records of caribou activity were related to the population dynamics of caribou, we examined the fluctuating patterns present in each of the three age structures of trampling scars and compared them with survey and historical data available for the RGCH.

Methods

Study area

The study sites were located in the forest–tundra between 56° and 59°N in the vicinity of Rivière George, just west of the shrub tundra that stretches on high plateaux to the Labrador Sea (Fig. 1). Mesic and dry tundra–heath and shrub communities are the predominant vegetation types in the Rivière George area. Conifer stands (forest and krummholz) are distributed in the most protected sites (Payette 1983; Manseau et al. 1996). Black spruce (*Picea mariana*) is the dominant tree species and tamarack (*Larix laricina*) and white spruce (*Picea glauca*) are common.

Caribou used to migrate across the Rivière George area during spring, summer, and fall (Low 1896; Elton 1942; Messier and Huot 1985). Surveys of the RGCH since the 1970s indicate that the area has been continuously used during calving and in summer (Messier and Huot 1985; Crête et al. 1991; Couturier et al. 1996). Dense trail systems are present throughout the area and ground vegetation was severely damaged by caribou grazing and trampling following the recent expansion of the herd (Manseau et al. 1996; Morneau 1999). The recent increase in population size was accompanied by range expansion toward new winter foraging sites west and south of the Rivière George area (Fig. 1). Summer distribution of the herd also expanded west and south in the 1980s, encroaching on the winter range (Messier and Huot 1985; Vandal et al. 1989; Russell et al. 1996).

Selection of sampling sites

We selected sampling sites to provide long chronologies of trampling scars. However, intensive caribou use of the Rivière George area during recent decades made the reconstruction of past caribou activity over long periods difficult. The dense trail systems in the area, where the large majority of trampling scars were produced, were developed during the current phase of caribou abundance (after the 1960s) (Morneau and Payette 1998). Collecting trampling scars within caribou trails selected randomly or systematically greatly reduces the possibility of obtaining age structures of trampling scars that cover a period extending back to before the last herd expansion. Therefore, after making a general survey of old-growth conifer stands in the subarctic area that extends on both sides of the Rivière George north of 56°N (ca. 15 000 km^2), we directed sampling to trails where old scars were evident. We avoided sites corresponding to major migration routes, owing to high mortality of parts of conifers resulting from trampling. The three selected sites were those that showed a potential for long-term reconstruction of caribou activity based on a relatively large number of trampling scars formed before 1960. The presence of old scars in trails was checked by taking sections of several roots or stems showing well-developed tissue around scars.

The three sites were well-drained spruce stands >200 years old and >100 km apart. Site A (Fig. 1; 58°18′N, 65°40′W) was a black spruce krummholz stand with stunted trees 1–1.5 m high. It was located at a ford at the central portion of a long (10 km) lake. The other sites were open lichen–woodlands (height of dominant trees 8–10 m; conifer cover 15–25%), with black spruce as the dominant species at site B (Fig. 1; 57°17′N, 65°16′W) and white spruce at site C (Fig. 1; 56°02′N, 65°08′W). Some tamaracks were present at both sites. A network of caribou trails ran across both sites B and C.

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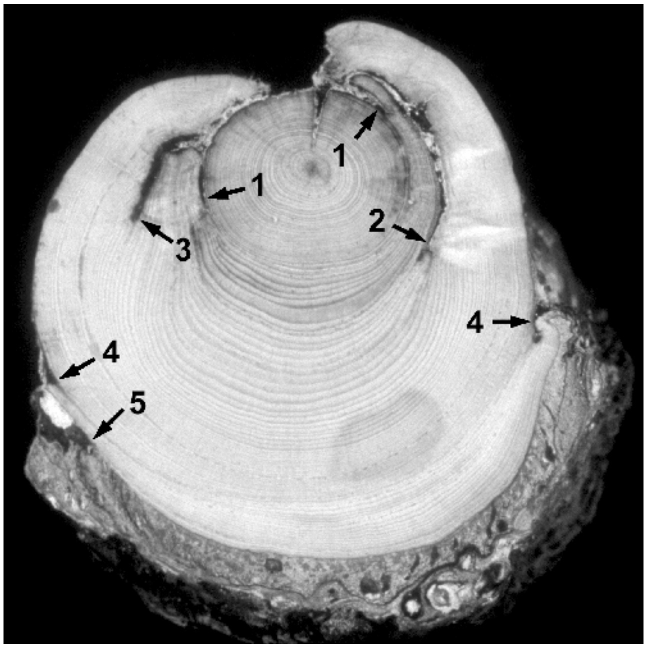
Fig. 2. Cross section of a black spruce root with trampling scars formed in 1904 (1), 1914 (2), 1931 (3), 1973 (4), and 1988 (5).



Sampling of trampling scars

Trampling scars represent a zone of cambial mortality induced by local debarking of a root or stem by caribou hooves (Morneau and Payette 1998). The scars are easily recognized from their shape and position on conifers. They are produced during the snow-free period (June to October) at the top or sides of exposed roots and low horizontal stems (branches and lying trunks) of stunted spruce. The scars left on xylem are rounded or elongated with neat margins. Cambial growth around damaged areas gradually overgrows the scars, but xylem may remain exposed for several years. The scars can occur at various places along the conifer parts and further scars may be superposed at the same location (Fig. 2). No other animal species produces similar damage to conifers in the area.

We collected trampling scars along an approximately 100 m long section of caribou trail (trail width 25–45 cm) at sites A and B and a few adjacent trail sections in a 30 × 70 m quadrat in site C. The trail section sampled at site A included stunted black spruce 200–300 years old, while that at site B contained large exposed roots belonging to several mature trees at the edge of the trail. The trail sections sampled at site C also were bordered by several old erect trees. We varied the surface area sampled in each stand to include areas where old scars were found to be relatively abundant and to ensure that a minimum of 500 scars per site were collected. We collected cross sections of all trampling scars encountered on living conifer parts that ran across the selected trail sections. When more than one scar occurred in the same location along a root or stem, we collected the cross section so that all the scars were included. We identified scars on the basis of externally visible features such as exposed xylem and resin accumulation on xylem. In the case of overgrown scars, we used resin accumulation on the bark and irregular shape on roots or stems due to uneven radial growth around the lesion to identify scars. We checked for overgrown scars by sampling sections of conifer parts showing any external growth anomalies in the locations usually affected by caribou trampling. We also exhumed roots buried under plant debris on trails to check for scar locations.

We finely sanded each cross section to enhance visual separation of annual growth rings. We determined year of scar formation by cross-dating, a procedure that allows the exact year of formation of each growth ring to be identified (Fritts 1976). Rings formed before and after the scar were cross-dated visually using patterns of ring width and diagnostic light rings (Filion et al. 1986). In our samples, diagnostic light rings were frequently produced on roots and stems in 1816–1817, 1853, 1904, 1936, 1956, 1969, 1972, and 1978. We also established a chronology of diagnostic narrow rings for each site. Cross-dating was facilitated because several scars in a site were located on the same tree. Because the seasonal dormant phase of cambium extends over 2 calendar years, the exact year of scar formation was determined only for scars formed during the period of ring growth. We attributed a scar on a complete annual ring to the most recent year (early-spring scar). Identification of the scar ring was uncertain at times because of the presence of wedging rings. In these cases, we dated scar formation within a time interval greater than 1 year. When cross-dating was unsuccessful, we counted the rings between the scar and the cambium to obtain a minimum age.

We determined the age of roots and stems bearing scars on each cross section. We calculated only a minimum age (number of rings) for the majority of conifer sections (85–90%) because cross-dating rings on roots from the period preceding root exposure on trails was often impossible. We grouped for analysis root- and stem-age data that we assumed to be exact and minimum-age data.

Data analysis

We constructed age-frequency distributions of trampling scars of the three sites by 5-year age-classes, using only scars assumed to be dated with certainty. For the first analysis, we assessed the influence of the age of roots and stems on scar data to identify fluctuations in scar frequency that are independent of the age of conifer parts. We proceeded in two ways. First, we weighted the age structures of scars in relation to the number of potential scar-bearing roots and stems according to age. Assuming that a scar first occurs on a conifer part at least 5 years old (Morneau and Payette 1998), we calculated the weighted frequency of scars by dividing the frequency of scars of a given age by the proportion of roots and stems that were at least 5 years older. Second, we computed age structures of trampling scars by using only scars located on conifer parts developed before 1870. Our second analysis took account of the increasing underestimation of caribou activity by scar frequencies as one goes back in time (Morneau and Payette 1998). For this analysis, we assumed a constant rate of loss of scars with time, which we addressed by removing an exponential trend from the age structures of scars using a log-linear regression. We log-transformed the number of scars after one scar was added to each age-class for the three sites. Two age-classes of scars (1913–1917 and 1918–1922) contained no scars at site B and therefore the addition of one scar was necessary because logarithmic transformation is inapplicable on value 0.

Results

Age structures of trampling scars and demographic trends of the RGCH

Among the scars collected at sites A, B, and C, we assumed that 88% (611/695), 91% (554/608), and 84% (464/555), respectively, were dated with certainty in the 5-year age-classes used to construct the three age distributions. The age structure of trampling scars covered the last 100–125 years at each site; it stopped in 1868 in site B and in 1893 in site C and became highly discontinuous before 1873 in site A (Fig. 3). Only 3 scars were formed before 1850 (≤1840, 1767, ≤1720), all at site A. The majority of scars were formed over the last 20–35 years, with a maximum in the mid-1980s (1983–1987 age-class). The recent increase in the number of scars started

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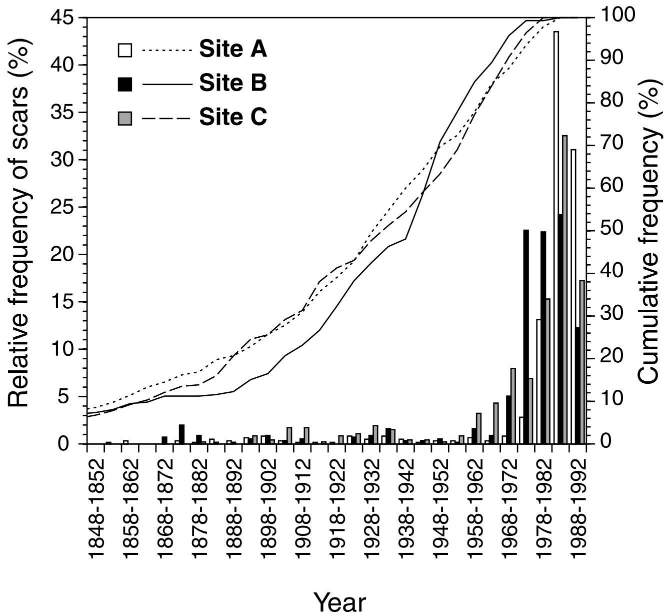
Fig. 3. Age structures of trampling scars (columns) and cumulative frequencies of ages of scar-bearing conifer parts (lines) from the three study sites.



around 1960 at sites B and C and in the 1970s at site A. Prior to 1958, the three distributions showed higher frequencies during the 1920–1930s and at the end of the 19th century and the beginning of the 20th century (i.e., during the period 1893–1912); at site B, high frequencies also occurred in the period 1868–1882. Lower frequencies occurred during the 1940–1950s and the 1910s (Fig. 3).

We used the mean age structure of trampling scars from the three sites to indicate general trends in scar age frequencies in the study area for comparison with caribou surveys (Fig. 4). An exponential increase in the mean age structure of the number of scars from 1953–1957 to 1983–1987 (log-linear regression, $R^2 = 0.98$) paralleled the recent numerical growth of the RGCH. The rate of increase (λ) in the number of caribou was 12–17% per year between 1954 and 1984 (Messier et al. 1988; Messier 1995). The number of scars in the mean age structure decreased between 1983–1987 and 1988–1992, while the size of the caribou herd was stable. Estimates of the number of caribou on the calving ground paralleled estimates of herd size (Fig. 4).

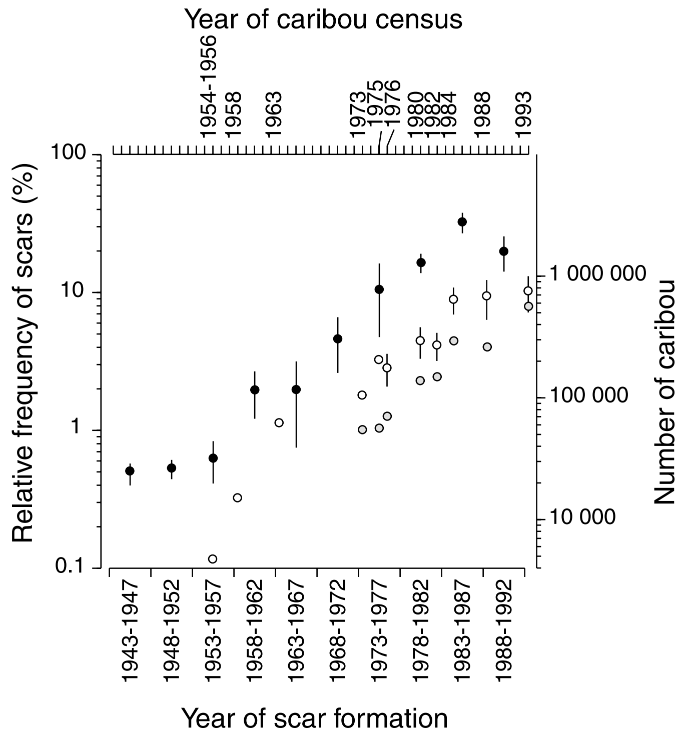
Influence of the age of conifer parts

All trampling scars were located on roots at sites B and C. At site A, 35% of scars were on low branches and main lying stems. The age-frequency distribution of scar-bearing roots at each site was characterized by low values for roots less than 10–20 years old, maximum values for roots 20–50 years old, and a gradual decreasing trend toward the oldest age-classes (roots 200–250 years old). The age-frequency distribution of scar-bearing stems at site A was similar in form to that of roots but with maximum values for stems 50–70 years old and stems up to 300–350 years old. At each site, >75% of scar-bearing conifer parts were present in 1960 and 10–15% were present in 1870 (Fig. 3).

The age of scar-bearing conifer parts had a strong influence on the age structures of trampling scars. Scar frequencies in each of the three distributions changed markedly when weighted in relation to the number of potential scar-bearing conifer parts according to age and when computed using only scars located on conifer parts developed before 1870, i.e., those parts that were present over the entire period covered by scar data (Fig. 5). However, the pattern of successive increase and decrease in scar frequencies in each of the three weighted age structures (Fig. 5*a*) remained similar to that of the corresponding nonweighted age structure (Fig. 3). Weighted or nonweighted, the three distributions showed a decrease in frequency around 1905–1915, 1940, and 1990 and an increase around 1920–1925 and between 1955 and 1985. The pattern of successive increase and decrease in scar frequencies in the age structures computed using only scars located on conifer parts developed before 1870 (Fig. 5*b*) was also similar to that of the corresponding distribution weighted or nonweighted according to the age of scar-bearing conifer parts. The exception was the most recent peak, which was 5–10 years older in each of the three distributions computed using only scars located on the oldest parts.

Analysis of the age of superposed scars on sections of old roots and stems indicated that trampling lesions can be

Fig. 4. Mean relative frequencies of trampling scars from the three sites between 1943 and 1992 and estimates of the size of the RGCH in 1954–1993. Solid circles show the mean relative proportion of scars (± 1 standard error). The open circles are estimates of the size of the RGCH (winter estimates for 1954–1975; June estimates without calves for 1976–1982; fall estimates for 1984–1993) with 90% confidence interval when available. Shaded circles are estimates of the number of caribou on the calving ground. Estimates are from Banfield and Tener (1958), Bergerud (1967), Messier et al. (1988), Crête et al. (1991), Couturier et al. (1996), and unpublished reports of the Quebec and Newfoundland–Labrador governments.



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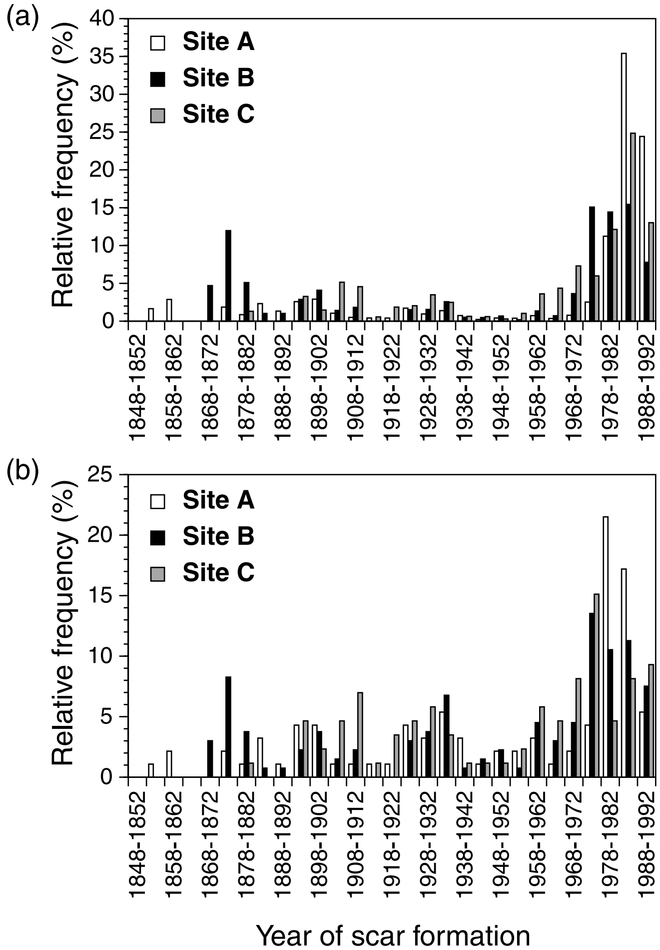

Fig. 5. Age structures of trampling scars weighted in relation to the number of potential scar-bearing conifer parts according to age (the number of parts more than 5 years old in each age-class) (*a*) and computed using only scars located on conifer parts developed before 1870 (*b*).

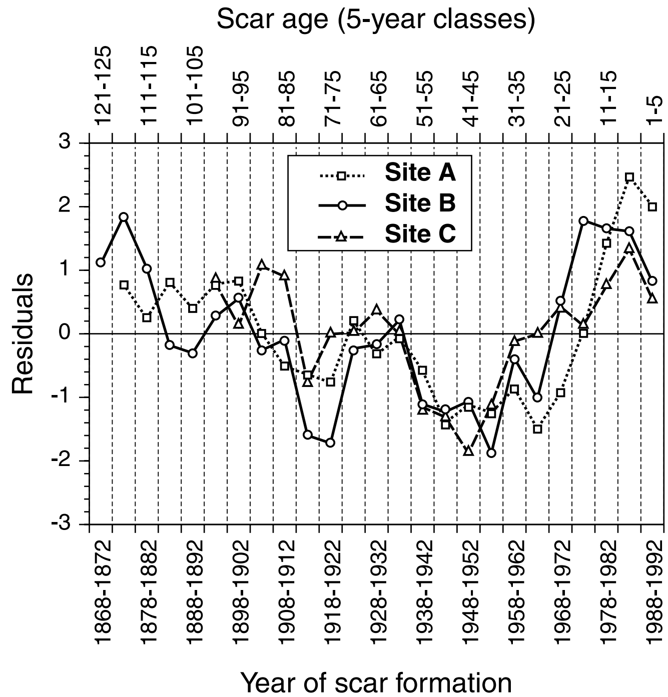

Fig. 6. Residuals of the log-linear regression on the age-frequency distributions of trampling scars at the three study sites.

produced over long periods at the same location along a root or stem. Considering only cross sections with scars formed before 1912, the mean number of scars per section was 2.3, 7.3, and 4.9, and maximum number of scars per section was 8, 13, and 10, for sites A, B, and C, respectively. For each site, between 20 and 40% of scars on these sections were produced during the period 1958–1992. For comparison, the mean number of scars per section when all cross sections were considered was 1.6 at site A, 2.1 at site B, and 2.0 at site C.

Long-term depletion pattern in the number of scars with age

Age-frequency distributions of trampling scars at the three sites were characterized by an exponential decreasing trend over the 100–125 years of records. The log-linear regression was significant for each distribution ($P < 0.001$ in each case) and there were no significant differences among the three regression lines (analysis of covariance on regression, $P < 0.05$). The large oscillations in number of scars around regression lines followed a pattern similar to that of the fluctuations in age structures of scars. We utilized residuals of the log-linear regressions to remove the long-term depletion pattern in the number of scars with age and to accentuate fluctuations in scar age frequencies (Fig. 6). The chronologies of residuals indicated the same trends in frequency of trampling scars over the last 100 years at the three sites. The three chronologies of residuals were all positively correlated with each other (Spearman's rank correlation, 0.70, 0.68, and 0.71 between sites A and B, A and C, and B and C, respectively; $P < 0.01$ for each comparison). The correlations remained significant ($P < 0.05$) when different starting years of the 5-year age-classes were used (i.e., moving the classes 5 times by 1 year), and the recent (0–50 years) and older (36–100 years) parts of the chronologies were considered separately.

Discussion

The age structure of trampling scars may provide a valuable index of changes in caribou activity if the capacity of conifers to produce scars remains constant with time. It is also important that fluctuations in age structure of trampling scars correspond to changes in the rate of scar formation rather than to changes in the rate of scar loss (Morneau and Payette 1998). Loss of scars is associated with the death of scar-bearing roots and stems, and destruction of xylem delineating the lesions by weather, decomposers, and repeated caribou trampling. The main characteristic of the age structures of trampling scars at the three study sites was a phase of sharp increase from the 1950–1960s to a maximum in the 1980s. This trend in scar frequency did not seem to be explained by factors that cause the loss of scars with time. Most scar-bearing roots and stems developed well before the recent period of high scar production, suggesting that the rate of scar loss due to death of roots and stems associated

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with the natural development of conifers was much lower than the rate of decrease in the number of scars from ages 6 to 40 years (1987–1953). Repeated caribou trampling contributes to scar loss by increasing mortality of roots and stems and abrading exposed wood, but this factor did not appear to modify fluctuating trends in the age structures of scars (Morneau and Payette 1998).

The phase of increase in trampling scar frequencies from the 1950–1960s to the 1980s likely reflects the formation of scars associated with the growth of the RGCH between the mid-1950s and the mid-1980s (Fig. 4). It appears that major changes in the population size of the RGCH were accompanied by parallel changes in the density of caribou in the Rivière George area between spring and fall (i.e., the snow-free period, June to October), which were reflected in the production of trampling scars. Trends in the caribou population before the 1950s may be reconstructed using common trends in age structures of trampling scars among sites. However, if a valuable index of caribou activity is to be developed, underestimation of past caribou activity by scar age frequencies because of the loss of the scar record with time must be considered.

One way to minimize underestimation of past caribou activity is to weight the age structure of trampling scars according to the age of scar-bearing conifer parts. However, this correction cannot be used to remove the effect of scar loss due to root and stem mortality. Scars on conifer parts developed before 1870 provided age structures of trampling scars not influenced by root and stem mortality. However, because the most recent peak was 5–10 years older in each of these distributions than in the corresponding distribution weighted or nonweighted according to the age of scar-bearing conifer parts, recent changes in caribou activity did not appear to be properly evaluated using age structures of scars located on the oldest conifer parts. Differences in the position of the most recent peak may be associated with a decrease in the susceptibility of conifer parts to scarring as they age. For instance, scars formed on old roots and stems are probably overgrown more slowly, owing to the reduction of secondary growth with age, which may lower the probability of subsequent scarring. Changes in the susceptibility of conifer parts to damage need to be investigated in relation to the age and size of roots and stems and size of lesions.

We used residuals of the log-linear regression on the age structures of trampling scars as an index of changes in caribou activity. This index assumed a constant rate of loss of scars with time, which we addressed by removing an exponential trend from the data. We consider this index to be valid for three reasons. First, it considers that the loss of the dendrochronological record increases with time. Second, residuals of the log-linear regression detect fluctuations in age structures of scars that were independent of the age of scar-bearing conifer parts. Third, similar trends in caribou abundance and age-frequency distributions of trampling scars since the 1950s suggested that fluctuations in scar frequency corresponded mainly to changes in the rate of scar formation. This indicated that variations in the rate of scar loss over time, which follow changes in caribou traffic and mortality of conifers, were probably minor compared with the changing rate of scar formation. For these reasons, we assumed that fluctuations in the chronologies of residuals adequately reflected fluctuations in the rate of scar formation and caribou activity.

Chronologies of residuals indicated that caribou activity at each of the three sites followed a general decreasing trend from the turn of the last century to around 1950, with two stages of rapid decline, around 1905–1915 and 1940, separated by a minor increase in the 1920–1930s. The period and rate of the recent increase in caribou activity varied according to site. Renewed caribou activity started in the late 1950s at sites B and C, while it increased sharply during the 1970s at the northern site A, to reach a maximum in the 1980s at the three sites. The common signal of synchronous changes in caribou activity at the three widely spaced sites indicated changes in the population dynamics of caribou inhabiting the Rivière George area. In addition to the general relationship between changing patterns of caribou activity and demographic trends of the RGCH, other trends in caribou activity deduced from trampling scars also coincided with population fluctuations identified from historical information. The decline of caribou activity around 1905–1915 in the Rivière George area detected from trampling scars is in accordance with the population decline at the beginning of the 20th century described by Elton (1942) for northeastern Quebec–Labrador. Also, the population low in the 1940–1950s (Banfield and Tener 1958; Audet 1979; Luttich 1983) was associated with lowest indices of caribou activity (trampling scars) for the last 100 years. The increase in caribou activity during the 1920–1930s detected from trampling scars reveals, however, a more complex changing pattern than that apparent in the historical data, which fail to reveal substantial population changes at that time (Elton 1942; Luttich 1983).

The sustained increase in caribou activity between the 1950s and 1980s is a unique phenomenon among the 100 years of records. Variations in the period and in the rate of the recent increase in scar frequency among sites are indicative of different spatiotemporal patterns of caribou activity associated with the recent expansion of the RGCH (Morneau 1999). Caribou activity increased first in the late 1950s in the southern part of the study area (site C), then increased sharply from the mid-1970s to the mid-1980s in the northern part (site A). The decline in caribou activity between 1983–1987 and 1988–1992 at each of the three sites may be due to greater caribou dispersion during summer (Vandal et al. 1989; Couturier et al. 1990; Crête and Huot 1993) and to a decrease in herd size, as suggested by demographic data (Crête et al. 1996).

The results of our study suggest that changes in caribou activity over periods that extend back to well before the first scientific surveys of caribou herds may be assessed by using trampling scars. Synchronous changes in scar frequency at the three sites appear to reveal a well-defined spatiotemporal pattern of caribou activity associated with caribou population fluctuations. However, our chronologies of trampling scar formation in the 19th century need to be refined; scar records are sparse before 1900 and they lack synchronism among sites. Sampling strategies to develop long chronologies of caribou trampling scars in the Rivière George area must account for the recent intensive use of the area. New trail systems have been developed and repeated caribou trampling has contributed to the loss of scars previously formed. Thus, old scars are very scarce compared with younger ones (<30 years old). Nevertheless, evaluation of patterns of

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caribou activity during the 19th century appears to be possible by making a thorough search for old-growth conifer stands with well-preserved old scars. Sampling should be more specifically directed toward old roots and stems to increase the chances of finding cohorts of old caribou trampling scars. This, together with collecting scars over a larger portion of northern Quebec and Labrador, may help in evaluating the natural dynamics of migratory caribou herds.

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