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Authors: Boudreau, Stéphane, Payette, Serge, Morneau, Claude, and Couturier, Serge

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Recent Decline of the George River Caribou Herd as Revealed by Tree-Ring Analysis

*Stéphane Boudreau,**
*Serge Payette,**
Claude Morneau,† and
Serge Couturier‡

*Centre d'études nordiques and Département de biologie, Université Laval, Sainte-Foy, Québec, G1K 7P4, Canada.
stephane.boudreau@bio.ulaval.ca
†Direction de l'environnement forestier, Ministère des ressources naturelles, 880, chemin Sainte-Foy, 5e étage, Québec, Québec, G1S 4X4, Canada.
‡Société de la faune et des parcs du Québec, Direction de la recherche sur la faune, 675, boul. René-Lévesque Est, 11e étage, Québec, Québec, G1R 5V7, Canada.

Abstract

Dendroecological analysis is often used in animal ecology to infer population fluctuations. In this study, we used scars produced by caribou hooves on superficial roots of conifers to evaluate the recent activity of the George River caribou herd (GRCH). In 1999 and 2000, we sampled a minimum of 300 trampling scars at each of 31 lichen woodland sites distributed over the summer habitat of the GRCH. Among the 31 selected sites, 18 had been previously sampled in 1992–1993 and showed a good agreement in trends inferred in caribou activity with the 1999–2000 data set at the same sites. We evaluated the recent activity pattern of the GRCH using mean values of pooled scar-age data from the 31 sites. We inferred two major trends from the tree-ring data: that the GRCH experienced an important increase from 1975 to the late 1980s, and that this growth was followed by a major decline that began in the early 1990s. Radio-collar data from 1991 to 1998 also support the decline as no major change was found in the geographical distribution of the GRCH during this period.

Introduction

Large herds of migratory caribou (*Rangifer tarandus* L.) are common in North America. These herds generally use the northern limit of the boreal forest as winter habitat before moving to the arctic tundra for the summer season. It is well known that these herds regularly experience important fluctuations of population size. Food limitation (Messier, 1995; Messier et al., 1988; Crête and Huot, 1993; Messier, 1995) and climate change (Klein, 1991; Caughley and Gunn, 1993) as well as hunting and predation (Banfield, 1954; Bergerud, 1974, 1980) have been proposed as explanations for such fluctuations. However, despite all the studies performed on the large herds of migratory caribou, herd dynamics is still poorly understood and there is no consensus regarding the causal factors of these fluctuations. Studies on caribou herd dynamics have been hampered by the vast area caribou cover throughout the year.

The George River caribou herd (GRCH) occupies most of the Québec-Labrador peninsula. This herd experienced rapid demographic growth from the early 1960s to the mid-1980s (Messier et al., 1988), when it reached a certain stability (Couturier et al., 1990, 1996; Hearn et al., 1990; Crête et al., 1991, 1996). Although census data collected since the 1970s are reliable, even if relatively unprecise (confidence interval generally over ±20%), earlier demographic changes are based on fragmentary information and superficial scientific surveys (Morneau and Payette, 2000).

Archival data, however, could be useful in identifying major demographic changes in the last century. Based on these sources, it is likely that the GRCH reached a population peak at the end of the 19th century (Low, 1896) before declining rapidly during the first decades of the 20th century (Elton, 1942). Thereafter, the GRCH remained at low levels until the 1960s, with some researchers even predicting local extinction of the species (Banfield and Tener, 1958; Bergerud, 1967; Audet, 1979). It appears that since the end of the 19th century, the GRCH has completed a demographic cycle. The animals' poor condition at the end of the 1980s (Couturier et al., 1988; Crête and Huot, 1993; Manseau, 1996), the decreasing survival rate of radio-tagged caribou (Crête et al., 1996), and the important degradation of the summer habitat (Crête and Doucet, 1998; Morneau, 1999) suggest a rapid decline of the herd.

Tree-ring analyses are often used in the study of mammal population dynamics, particularly for porcupine (Spencer, 1964; Payette, 1987), vole (Danell et al., 1981), beaver (Bordage and Filion, 1988), hare (Sinclair et al., 1993), moose (McLaren and Peterson, 1994), and lemming (Erlinge et al., 1999). For caribou, a dendroecological method using trampling scars (debarking lesions) produced by hooves on the superficial roots and low branches of conifers was recently developed by Morneau and Payette (1998, 2000) in order to evaluate the activity pattern of the GRCH across the summer habitat. This method allows the evaluation of demographic trends over the last 100 years (Morneau and Payette, 2000), evaluation of regional activity pattern (Morneau, 1999), and more precise assessment of the recent demographic trends revealed by aerial census. Using the age structure of these scars, Morneau (1999) identified a decreasing trend in the activity of caribou in the summer habitat (from 1988 to 1991–1992) that could potentially reflect the demographic decline of the GRCH.

In this paper, we examine the recent activity pattern of the GRCH over its summer habitat. The first objective was to verify whether the trends inferred in caribou activity by two different samplings in the same sites at different times were similar. To do so, we compared both the age structure and the trends inferred in caribou activity by the analysis of trampling scars sampled successively in 1992–1993 and 1999–2000 in 18 sites. The second objective was to evaluate the recent activity pattern of the GRCH between 1975 and 1999 in order to verify whether the herd is declining. We used scar-age data from 31 lichen woodlands distributed over the summer range of the GRCH, results of the aerial censuses done between 1976 and 1993 (Couturier et al., 1990, 1996; Crête et al., 1991), and radiotelemetry data of caribou spatial use from 1991 to 1998.

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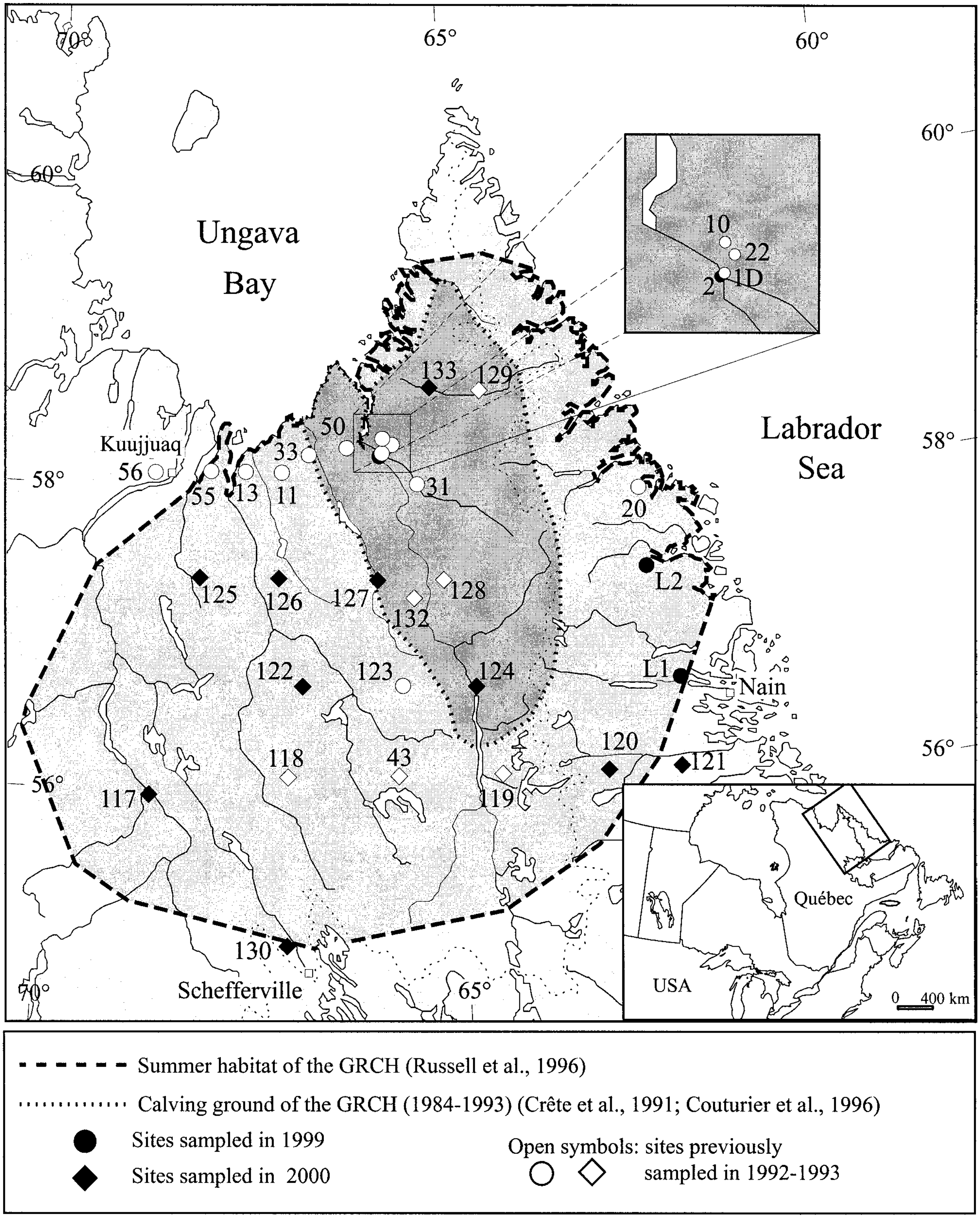

FIGURE 1. Study area. Fifteen sites were sampled in 1999 and 16 sites in 2000.

Material and Methods

STUDY AREA

The study area covers the Québec-Labrador peninsula (Fig. 1), from 69°W to the Labrador Sea and from 54°30′N to the Ungava Bay. We sampled trampling scars in 31 sites (15 in the 1999 field season, 16 in the 2000 field season). The sites were located along four east-west transects (at approximately 56°N, 56°40′N, 57°22′N, and 58°10′N), with a few others located in the vicinity of Schefferville and the Koroc River valley. All sites were composed of an old-growth conifer stand

TABLE 1

Kolmogorov-Smirnov test results on complete (left) and on 2-yr truncated age structures (right)

Site	*n* (92–93/99–00)	Max. Diff. Obs.	Crit. Value	Verdict	*n* (92–93/99–00)	Max. Diff. Obs.	Crit. Value	Verdict
1D	1898/202	0.162	0.101	Diff.	1802/159	0.092	0.112	N.-Diff.
10	315/204	0.251	0.122	Diff.	301/169	0.164	0.130	Diff.
11	343/70	0.169	0.178	N.-Diff.	303/50	0.145	0.207	N.-Diff.
13	399/151	0.147	0.130	Diff.	304/111	0.181	0.151	Diff.
129	373/205	0.059	0.118	N.-Diff.	350/186	0.062	0.123	N.-Diff.
20	267/106	0.134	0.156	N.-Diff.	246/88	0.074	0.169	N.-Diff.
22	464/170	0.280	0.122	Diff.	433/126	0.131	0.137	N.-Diff.
31	490/140	0.235	0.130	Diff.	460/112	0.131	0.143	N.-Diff.
33	416/231	0.069	0.111	N.-Diff.	344/188	0.079	0.123	N.-Diff.
119	215/200	0.187	0.133	Diff.	180/130	0.135	0.156	N.-Diff
43	440/222	0.206	0.111	Diff.	402/157	0.056	0.128	N.-Diff.
123	261/159	0.133	0.137	N.-Diff.	223/120	0.124	0.154	N.-Diff.
50	260/190	0.236	0.130	Diff.	220/136	0.223	0.148	Diff.
118	184/152	0.209	0.149	Diff.	135/198	0.217	0.180	Diff.
132	459/231	0.150	0.110	Diff.	400/186	0.116	0.121	N.-Diff.
128	405/262	0.204	0.108	Diff.	373/228	0.199	0.114	Diff.
55	288/147	0.104	0.138	N.-Diff.	221/111	0.125	0.158	N.-Diff.
56	183/220	0.122	0.136	N.-Diff.	172/180	0.138	0.145	N.-Diff.

Note: n = number of samples in 1992–1993 and 1999–2000 age structures, Max. Diff. Obs. = maximal difference observed in the cumulative frequencies, Crit. Value = critical value of the test at $\alpha = 0.05$, calculated with the following formula: $C.V. = [\ln(\alpha/2)]^{1/2} * [(n_1 + n_2)/(n_1 * n_2)]^{1/2}$, Diff. = different, N.-Diff. = not different.

of black spruce (*Picea mariana* [Mill.] BSP.), white spruce (*Picea glauca* [Moench] Voss), or eastern larch (*Larix laricina* [DuRoi] K. Koch) with tree cover of 10–40% and growing on well-drained soil, which at one time supported a dense lichen mat and showed evidence of caribou activity (trails). All study sites were selected at random along the transects. The geographical distribution of the sampling sites allowed an evaluation of caribou activity over the total summer habitat of the GRCH, including the least degraded areas (west, south, and extreme east) as well as the most degraded area (central area). Eighteen of the 31 sites were also sampled in 1992–1993 (Morneau, 1999).

SAMPLING OF TRAMPLING SCARS

Caribou trampling can produce considerable numbers of wood lesions (mainly debarking lesions) on superficial roots and low branches of conifers during the snow-free period. These trampling scars are dated by counting the number of annual rings added after scar formation. The age structure of the scars can then be used as an index of caribou activity at a particular site. For further information on the tree-ring techniques used, see Morneau and Payette (1998).

Trampling scars were sampled as follows. A central point was randomly determined at each site. Based on this point, the direction and distance of the corner of a 100-m^2 quadrat (10 m × 10 m) was randomly chosen. Once the quadrat was delimited, cross-sections of trampling scars were sampled from roots or, in a few instances, from low stems. If the number of scars was <300 in the first quadrat, a second quadrat was delineated 10 m from the first one. Trampling scars of the second quadrat were then sampled, and so on, until a total of 300 scars was collected.

The cross-sections were finely sanded for scar dating under a dissection microscope at 40×. The year of trampling-scars formation was determined by cross-dating, a technique allowing the precise identification of the year of formation of each growth ring (Fritts, 1976). Based on diagnostic light-rings (Filion et al., 1986) and ring-width patterns, rings preceding and following the year of scar formation were cross-dated visually (for more details, see Morneau and Payette, 1998, 2000). Samples were rejected when accurate dating at ±1 year could not be performed. The frequency distribution of the 31 sites was calculated using all dated scars.

DATA ANALYSIS

To verify the reproducibility of the results, we compared scar frequency distributions of the 18 sites sampled in 1992–1993 and 1999–2000 using a Kolmogorov-Smirnov (KS) test (Table 1). Similarity of the residuals of the semi-log regression of the two data sets were also compared using Pearson's correlation coefficient.

To determine the activity pattern of the GRCH for the period of 1975 to 1999, we applied a log-linear regression (using the number of scars on a logarithmic scale and the time on an arithmetic scale) to remove an exponential trend from the age structure of scars, assuming constant rates of production and loss (death of roots) of scars in absence of change in time and space of the GRCH. We used the residual values of the regression as an indicator of the activity of the GRCH all over the summer habitat (Morneau and Payette, 2000). We constructed an average curve of the activity of the GRCH using the mean value of the residuals for the 31 sites.

RADIOTELEMETRY DATA

The satellite radiotelemetry data (1991–1998, Service Argos Inc., Largo, Maryland, USA) were obtained from 69 caribou of the GRCH (49 females and 20 males). Radio collars were on a duty cycle to increase unit life expectancy, most of them operating 6 h every 5 d. After about 2 yr and before the end of the battery life, caribou were recaptured, when possible, to retrieve the old unit and deploy a new one. The satellite monitoring continued until the death of the animal or radio-transmitter malfunction. The number of active radio-collared caribou varied between 15 and 22 (1991–1998 period). Argos satellite radio collars usually provided between two and six locations per transmission period. Locations differ in quality, and Service Argos Inc. sorted them according to increasing accuracy order: B (worse, accuracy unknown) and A: 0, 1 (±1 km), 2 (±300 m), and 3 (best, ±150 meters). In the first step of data validation and selection, a Visual Basic macro program in Microsoft Excel 98 screened for the best available data per transmission period based on location quality provided by Service Argos Inc. Travel rate per day and per hour were also computed and later included in the database. These new variables provided a second level of validation, and

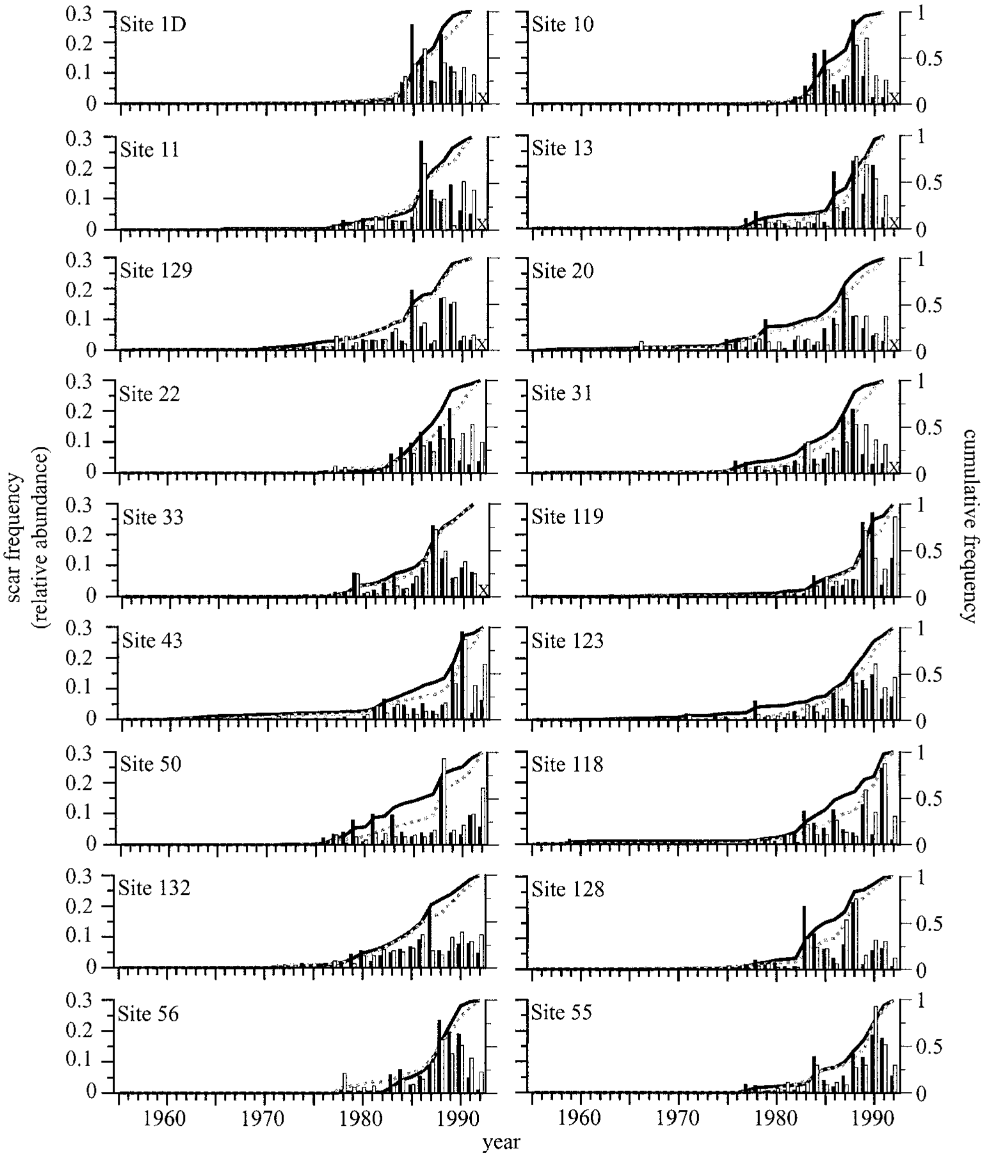

FIGURE 2. Frequency distribution and cumulative frequency of trampling scars sampled in 1992–1993 (black bars, solid line) and 1999–2000 (open bars, broken line). X = data unavailable since the 1992 scar-formation season was not over at the time of the sampling.

larger values (>50 km d^{-1}) were identified and individually checked for accuracy and likelihood. This second level of verification removed very few erroneous locations. A total of 9589 locations were kept following the Argos database validation (6638 female-locations, 2591 male-locations). Most of the locations used are from classes A1 to A3. Only the locations obtained during the snow-free period (31 May to 17 October) were considered, as trampling scars are produced only during this period. The snow-free period was then divided into 5-d classes, and only one location per collar per class was used to avoid an overestimation of collars with a high frequency of locations.

Results

COMPARISON BETWEEN SCARS SAMPLED IN 1992–1993 AND 1999–2000

For the 18 sites considered here, 61% of the trampling scars sampled in 1999–2000 were produced before 1992 (55%, 8 sites) or 1993 (65%, 10 sites) with a maximum of 87% in site 128 (262/300) and a minimum of 23% in site 11 (70/300). Fourteen of the 18 sites included >50% of trampling scars formed prior to 1992–1993.

For the sites sampled twice (in 1992–1993 and 1999–2000), there was a general agreement between all scar age structures, despite differences in the number of scars (Fig. 2). Both sampling periods showed that few scars were produced prior to 1975. The number of scars recorded after 1975 generally increased and culminated at the end of the 1980s, and then decreased. Significant differences (KS test) were found in 11 out of the 18 sites (Table 1). However, only four comparisons showed differences >10% between the critical value and the maximum observed difference. When removing the 2 yr preceding the 1992–1993 sampling, significant differences were found in only five sites (KS test).

The semi-log regression performed on the two data sets showed that the differences in the age structure have little impact on the residual values of the regression which are used to evaluate the activity of the GRCH (Fig. 3). Pearson's correlation coefficient was ≥0.48 for 15 of the 18 comparisons (Table 2).

ACTIVITY PATTERN OF THE GEORGE RIVER CARIBOU HERD

The age structure of trampling scars sampled in 1999–2000 indicated that most scars (99%) were produced after 1975 in the 31 sites sampled (Fig. 4). The semi-log regressions performed on age

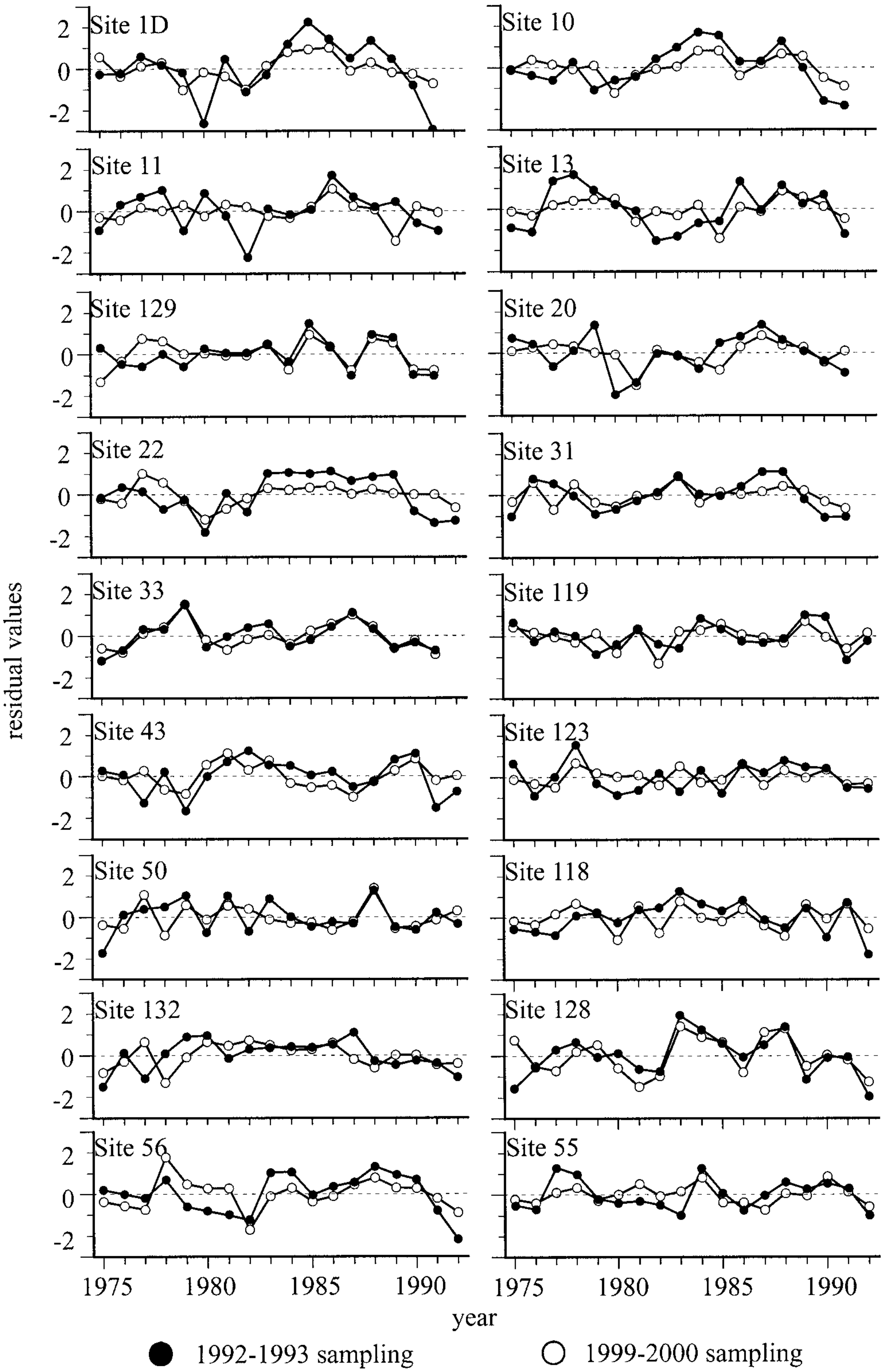

FIGURE 3. Residual values of the semi-log regression for the 18 sites sampled in 1992–1993 and 1999–2000.

structures showed R^2 varying between 0.01 and 0.74. Moreover, 22 of the 31 sites had $R^2 > 0.40$. The regression was significant in all cases except for four sites (sites 33, 120, 128, and 132).

The average curve of the yearly mean of the residual values of the 31 sites (Fig. 5) is divided into two components. The first half of the curve (1975–1989) indicates a sustained increase of the residual values of the regression, whereas there is an almost constant decrease of these values in the second half (1989–1999).

The compilation of radio-collar data indicated no major change in the distribution of the GRCH during the 1990s (Fig. 6), even if a higher proportion of locations was recorded in the study area between 1995 and 1998 (60%) compared to 1991 and 1994 (47%). When only fe-

TABLE 2

Pearson's correlation coefficient of the residuals values of the semi-log regression performed on the age structures of the 18 sites sampled in 1992–1993 and 1999–2000

Site	Pearson's Corr. Coeff.	Site	Pearson's Corr. Coeff.
1D	0.647	119	0.522
11	0.078	43	0.497
10	0.699	123	0.404
13	0.577	118	0.532
129	0.608	50	0.493
20	0.485	128	0.671
22	0.529	132	0.322
31	0.634	55	0.551
33	0.874	56	0.572

males are considered, this proportion is almost the same for the two periods, i.e., 56% in 1991–1994 and 57% in 1995–1998.

Discussion

The age structure of the trampling scars sampled in 1992–1993 and 1999–2000 are generally in good agreement, although the KS test indicated significant differences in 11 out of the 18 sites. A common feature when comparing both age structures from a given site was the smaller number of scars recorded in 1991 and 1992 in the first sampling, as shown by the cumulative frequency curves (Fig. 2). This seems to be due to an underestimation of the number of young scars (1 or 2 yr old), some of them likely having been missed during sampling in

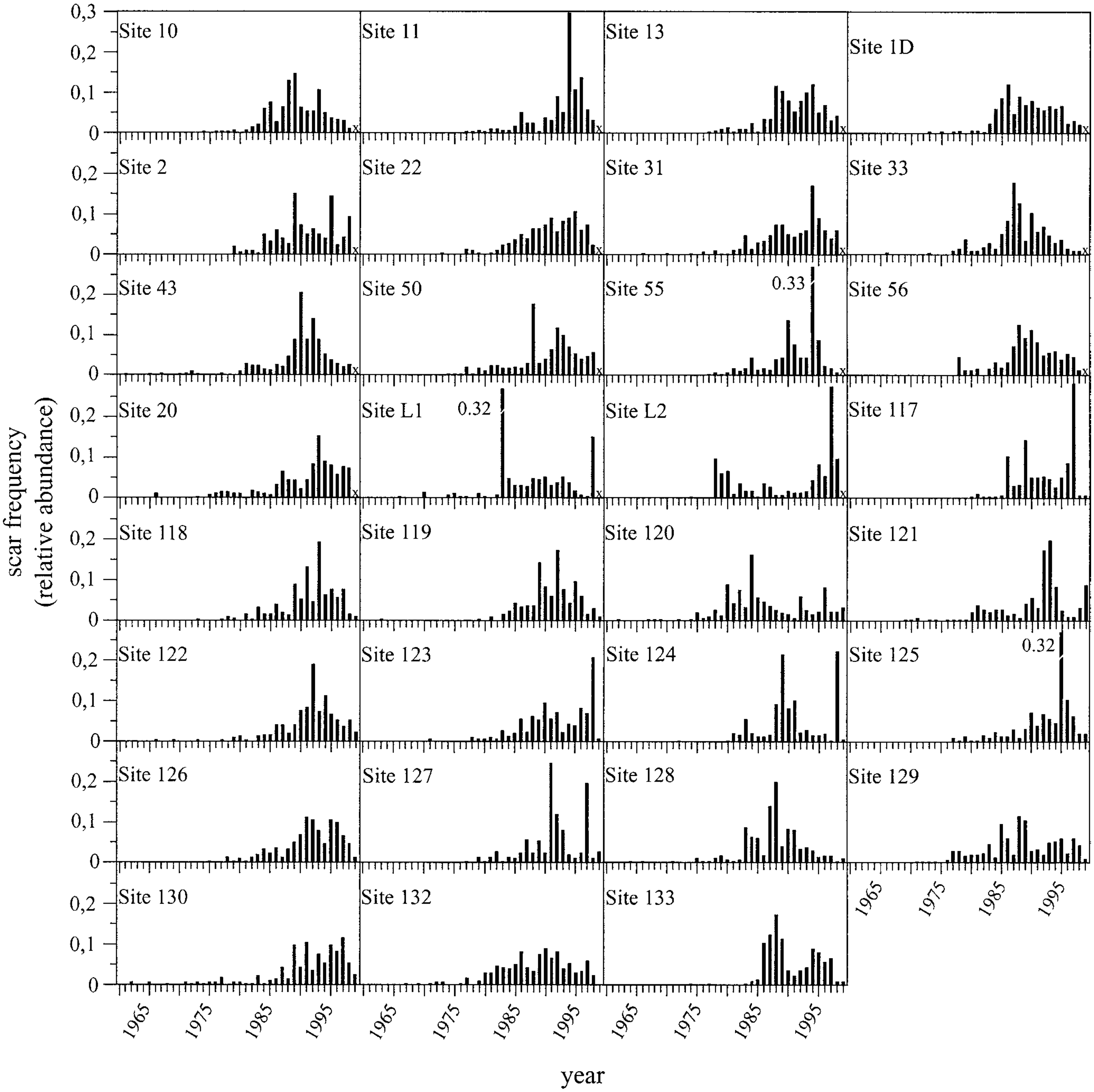

FIGURE 4. Age structure of the trampling scars sampled in 31 sites across the summer habitat of the GRCH in 1999–2000. X = data unavailable since the 1999 scar-formation season was not over at the time of the sampling.

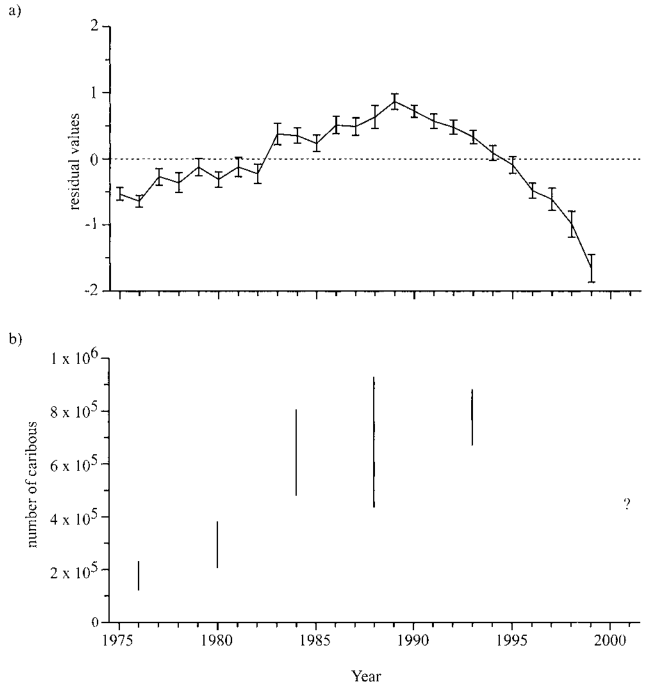

FIGURE 5. Demographic trends of the George River herd inferred with tree-ring data and the photo censuses. (a) Curve of the mean (±SE) of the residual values of the regression for the 31 sites sampled in summers 1999 and 2000. (b) 90% confidence intervals of the 1976, 1980, 1984, 1988, and 1993 photo census. The question mark shows the 2001 preliminary census result. (From Couturier et al., 1990, 1996; Crête et al., 1991.)

1992–1993. When deleting trampling scars produced the first year or the first 2 yr before sampling, only eight and five comparisons (KS test) between both data sets were significantly different. Natural variability inherent to this kind of sampling likely explains most of the differences observed between the two data sets. In addition, the 1999–2000 sampling was done at a site adjacent to the one sampled in 1992–1993. The KS test detected small differences between the two data sets, particularly when the number of samples was high (some age structures from Morneau [1999] were constructed using >450 scars).

Despite the results of the KS test, a similar trend of caribou activity is observed at each site when comparing the residual values of both age structures (Fig. 3). Results of the semi-log regression clearly show that for most sites the differences observed between the age structures are in most cases too small to influence the residual values of the regression (used as an index of caribou activity) as revealed by the Pearson's correlation coefficients. Based on these comparisons, the youngest part of an age structure of trampling scars may be truncated. The number of scars produced in 1998 and 1999 was likely underestimated. This phenomenon could be responsible, in part, for the sharper decline observed in the residual values of 1998 and 1999 (Fig. 5a).

Trends in caribou activity inferred from tree-ring data could reflect two potential phenomena: a change in the geographical distribution of the GRCH or fluctuations of population size. Since radio-collar locations of males and females of the GRCH between 1991 and 1998 revealed no major change in the distribution of the GRCH, the trends inferred in caribou activity in this study likely reflect important demographic changes. Moreover, if there was a change in the geographical distribution of the GRCH, it was toward a larger use of the study area after the mid-1990s.

Two major demographic trends are apparent (Fig. 5a). First, the GRCH experienced an important growth increase from the mid-1970s to the late 1980s. This expansion of the herd was well documented by several aerial surveys (1976, 1980, 1984, and 1988) and is thought to be the continuation of an important population growth trend that started in the late 1950s. The absence of old trampling scars is related to low caribou activity throughout the summer habitat since the beginning of the 20th century. Second, the herd experienced a major decline beginning at the end of the 1980s. Some studies using demographic parameters such as survival rate of radio-collared caribou (Crête et al., 1996; Bergerud, 2000) also estimated that the herd was declining between 1988 and 1993. Moreover, there is strong complementary evidence for the decline from data on the current recovery of the lichen cover in lichen woodlands over most of the summer habitat during the 1990s (Boudreau, S., unpubl. data). Finally, preliminary results of the 2001 aerial census revealed that the herd size was about 450,000 individuals (Couturier, S., unpubl. data).

The trends we inferred from the tree-ring data fitted well the herd demographic changes as described by census for the period 1976 to 1993 (Fig. 5). However, one should not attempt to infer direct relations between the rates of increase or decrease of the residual values and the number of individuals in the GRCH. Only general trends inferred by the two methods should be compared.

The 1976 and 1980 visual censuses were not supported by extensive radiotelemetry. These censuses have likely missed caribou aggregations and may have underestimated herd size. However, when comparing these numbers with tree-ring data, the trend observed is the same: the herd was definitely increasing during this period. Beginning in 1984, photo census and extensive use of VHF radiotelemetry were introduced, increasing the reliability of the herd size estimates. From the photo census done in June 1988, herd size was estimated at 682,000 ± 246,000 (Crête et al., 1991). In 1993, satellite radio tracking was also introduced to monitor caribou movements during the census. Two independent censuses done in June (Couturier et al., 1996) and July 1993 (Russell et al., 1996) confirmed that GRCH size was about 776,000 ± 104,000 caribou, including calves in the fall population (Couturier et al., 1996). However, Bergerud (2000) disagreed with this result, suggesting that groups from the neighboring Leaf River caribou herd may have moved into the photo census area and were included in the GRCH 1993 estimate.

The finite rate of increase of 1.03 computed from the 1988 and 1993 photo census results seems inconsistent with the trends inferred from demographic parameters (Crête et al., 1996; Bergerud, 2000) and trampling-scars analysis, which both showed that the herd was declining as early as the late 1980s. However, based on the extensive work done, the 1993 census seems to be the more precise estimate to describe GRCH demographic status because more sampling units were used (Couturier et al., 1996; Russell et al., 1996; Rivest et al., 1998). As a result, the most likely explanation for the discrepancy between the different methods is that the size of the herd was somewhat underestimated in 1988. Considering the confidence interval of ±246,000, the size of the herd could have been as high as 928,000 individuals in 1988 (Crête et al., 1991).

In conclusion, the results presented here suggest that tree-ring analysis can be a useful tool in the study of the dynamics of large herds of migratory caribou. The simultaneous use of aerial photo census and trampling scars gives a clearer picture of the demographic status of the George River caribou herd.

Acknowledgments

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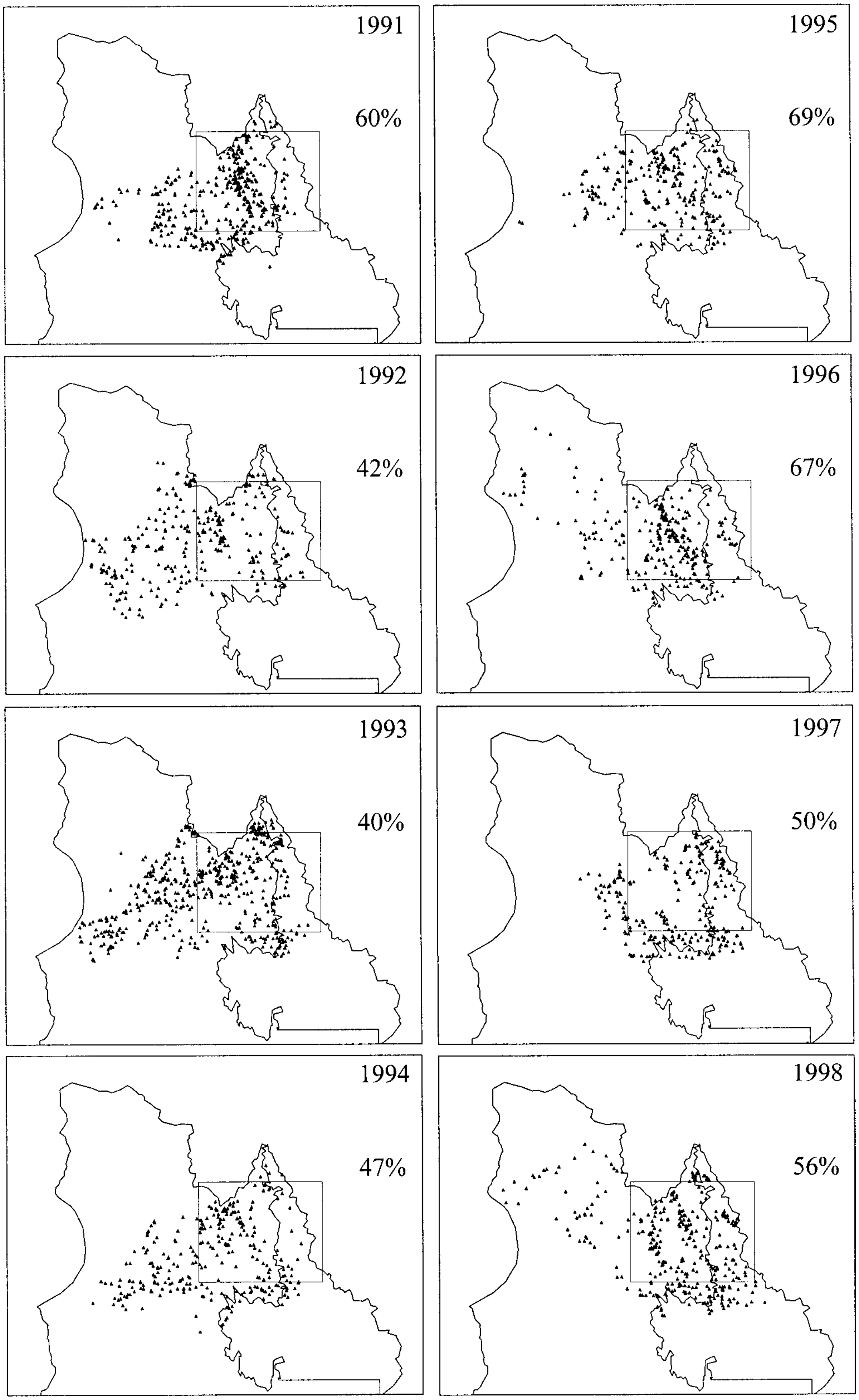

FIGURE 6. Radio-collared caribou locations of the George River herd during the snow-free period (31 May to 17 October) with the percentage of locations inside the study area (delimited).

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