The decline of the cyclic George River Caribou Herd

1989-2012

rabies, wolves and hunters

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Abstract: The George River caribou Herd in Ungava increased exponentially in a density dependent fashion from 5 000 animals in 1954 to 650 000 in 1988, expanding the lengths of its migrations and reaching a total range of 600 000 km² in 1989. Then the herd commenced to decrease in a inverse density dependent, anti-regulation mode. These two different demographics provided an opportunity to test the hypothesis that tundra caribou making long migrations have reduced predation risk compared to those herds making short migrations. Rabies epizootics occurred at intervals of 3.12±0.56 years, n=9, 1976, 81/82, 87/88, 92/93, 96, 01, 04, 09, 11/12. In the increasing years (1974-1988) there was no significant differences in the October recruitment (calves/100 females) in three rabies outbreaks 76,81/82,87/88 with the recruitment in the year prior in each epizootic, but in the spring recruitment (yearlings/100 females) 1976-92 there was increase recruitment in 4 rabies outbreaks compared to the year proceeding each outbreak. In the decreasing years 1989-2012 the October recruitment was higher in rabies years in 6 outbreaks then in the prior year but not in the most severe out break 2011-12. After 1988 range expansion ceased reducing mobility. This facilitated increased predation in October and in lieu of effective harvest management the herd went into exponential decay with enhanced recruitment in most rabies years. The large herd/long migration hypothesis to ameliorate predation was supported only in the years of normal fertility and range expansion and not in the years of decline.

The hypothesis that tundra caribou making long migrations have reduced prédation risk compared to herds making short migrations is **generally accepted**. However, once a population starts to decline—and any number of factors may initiate such a decline, including habitat dégradation (from human activity, volcano erutions or climate change for instance), excess hunting and/or eased access for hunters,

overgrazing/decreased fertility, and unregulated wolf populations—migrations and mobility also begin to shrink. This gives the edge to the wolves, whose numbers remain high even as the caribou numbers fall. The caribou are now doubly vulnérable to prédation: their ranges are smaller, and wolf populations are at their most robust. Wolf predation thus has a more intense impact on a declining population.

This study makes use of two different demographics to examine the relationship between prédation and long migrations: (1) the exponential increase of the George River herd in a density dependent (DD) fashion from 5,000 animals in 1954 to 650,000 in 1988, and the expansion in the length of its migrations, which reached an annual range of 600,000 km^2 in 1989; and (2) the subsequent decline of the same herd in an inverse density dependent (IDD), anti-regulation mode (1989-2001). The basic method for testing the relationship between predation and long migrations was to compare October calf recruitment (1974–2012) in years of rabies epizootics in wolves (*Canis lupus)* with the recruitment the year before the outbreak, when wolf populations would presumably have recovered from the previous outbreak and thus be at peak numbers. We also compared the spring (short yearlings) recruitment in a similar manner (1974–92). The rabies epizootics, whose impacts are thus crucial to the findings in this study, occurred at intervals of 3.12±0.56 years n=8 (1976, 81/82, 87/88, 91/92, 96, 01, 05, 09, 11/12.

Key Words: arctic hares, wolves, rabies, density dependent, Inverse density dependent, Western Arctic Herd, Leaf River Herd, 3-4 Arctic canid cycle

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The tundra caribou (Rangifer tarandus) of Ungava have fluctuated in numbers back through time and native peoples starved in the 1830-50s and late 1800s (Elton 1942). In 1883 Mount Krakatoa erupted cooling the Arctic for 5 years and the herd went into rapid decline the herd also also declined after the eruption of Mt. Tambora in 1815 (Bergerud et. al.2008, Fig 6.1,p.136) (Fig. 1).   A low was reached in the 1950s of less than 5,000 animals (Fig. 1) (Banfield and Tener 1958. The wolverine (Gulo gulo) went extinct and wolves (*Canis lupus)* became exceedingly rare (see Elton 1942, p. 254). Then the herd commenced to increase in the 1960s (Des Meules and Brassard 1964) and reached 100 000 by 1973 (Messier et al. 1988). Wolves reappeared and wolf harvests gradually increased in the 1970s (Novak et al.1987). By 1980 the herd had increased to 300 000 animals (Messier et al. 1988). Then wolves contacted rabies in 1981. The mean wolf pack size 1976-80 had been 4.8 animals/pack but declined with the epizootic to 1.7 by the winter of 1982 (Bergerud 1996), a decline of 65%, and the caribou herd increased to 537 000 by 1984, $\lambda=1.16$, (Crete et al. 1991) or based on a census in 1982 of 400 000, $\lambda=1.17$ (Berger and Luttich, 1983) and reached a herd size of 650 000 animals. At these numbers, greater than 10/ km² of summer range, the animals overgrazed their growing season range (Mansau et.al. 1996; fecundity was reduced from 89 calves per100 females (Parker 1981) to 67/100 females 1986-87 (Couturier et al. 1990) or based on autopsies or on udder counts in June 65±4.40/100 parous females (mean sample size 4,945±309, 1988-91 (Bergerud et al. 2008). Recruitment and adult mortality were nearly in balance in 1986 at 12 percent (Bergerud 1996) and the herd reached a peak of 650,000 caribou by 1988 **(**Bergerud et al. 2008). The reduced forage resulted in some summer mortality of adults, especially lactating females; 11 undernourished females were found and one lactating female with a calf swam a lake and laid down and died with our fat reserves. Despite the addition of high harvests 5% (25 000) and continued natural predation the herd

overcompensated (Grenfell et al. 1992) the forage carrying capacity resulting into an inverse density decline (IDD) after1988-89. An additional factor could have the cooling winter temperatures 1982-92 especially in 1992 when many calves died weighting only 4kg (normal weight 6-7kg (S. Couturier). With the cooling effect of the eruption of Pinatubo in the Philippines 1991, the ice in Knob Lake did not leave the lake until June 29, the latest on record (Bergerud et al. 2008. Fig.1.4, p.12, and Fig.6.2, p.136).

 A high census estimate in 1993 of 775 000 (Couturier et al. 1996) has been widely quoted as the peak population level by the media and some biologists but it included young calves. Recruitment is usually measured in the spring when the new generation reaches the age of yearlings that have mortality rates similar to those of adults (Hickey 1955, Caughley 1977).

The history of the rabies virus in arctic hares (Lepus arcticus} is sparsely known (Mørk and Prestud 2004). The rabies virus was first identified in Alaska by Williams 1949. The virus is transmitted to the northern canids: red fox (*Vulpes vulpes)*, arctic fox (*Vulpes lagopus)*, wolves and humans, by bites, saliva, even tiny scratches (MacInnes 1987). The folklore of the Canadian Inuits indicates these peoples knew of a rabies-like disease known as the sledge-dog disease transmitted to sled dogs and humans (Singleton 1969). In Greenland epidemics among sledge dogs have been described for close to 150 years (Lassen 1962).

Charles Elton in his classic manuscript Voles, Mice and Lemmings, (1942) documented the sledge-dog disease in Labrador as early as 1803 (Elton 1942) and described a 4.4±0.41 year cycle of outbreaks from 1858-9 to 1904. The first discussion of periodic fluctuations (cycles) in northern animals was published in 1924 (Elton 1924). The Canadian Arctic Wildlife Inquiry documented the synchrony of arctic foxes and lemmings cycles in Labrador and Quebec from 1933 to 1949 (Helen Chitty 1950). In the period 1931-83 arctic hares in

Québec showed 12, single year peaks (length 3.8±3.36 years) and the number of wolves harvested had 6 cyclic lows at 4.2±0.25 years, 1.4±0.20 years after the hare peaks (Fig. **2**) (data statistics from Novak et al.1987). After 1964 the wolves began to increase as the caribou numbers grew (data from Novak et al. 1987).

Krebs (2011) has recently reviewed the food web in the arctic; lemmings are a keystone herbivore and the primary food of foxes resulting in their cycling (Angerbjörn et al. 1995, Elmhagen et al. 2011). Krebs also reviewed and discussed the various hypotheses to explain lemming cycles: predation, food and or social interactions (the latter known as the Chitty hypothesis (Chitty 1960). However the future of cycles may be threatened—lemmings appear highly sensitive to a warming climate and increasing intervals of low-amplitude populations of small herbivores are expected impacting trophic webs across ecosystems (Schmidt et al. 2012, Cornulier et al. 2013, 21 authors).

The majority of the migratory herds in Canada reside in the North West Territories and Nunavut but the impact of rabies has not been investigated there my biologists. However the number of rabies cases processed from there each year by the Canadian Food Inspection Agency equals the combined cases in Quebec and Newfoundland/Labrador per year 1988-2012: Newfoundland/Labrador 3.0±1.24, Québec 5.2±1.00, vs. NWT. 8.9±1.32 (http:www.inspection.gc.ca.)

In Alaska biologists have been concerned about rabies relative to caribou for several decades (Williams 1949, Rausch 1958, Chapman 1978, Clough et al. 1987, Weiler et al. 1995, Ballard et al. 1997, Ballard and Gipson 2000. Ballard et al. studied a rabies out break from 1987-91. Eleven of 21 radio collared wolves died. Before the outbreak the finite-rate-of increase of wolves was 1.43, 1987-88, the next year, 1.05, third and fourth years, 0.62-64 the population went from 4.4 wolves/1000km² to 1.5/1000km²; 61% mortality similar to that in

Ungava 1981-82. Chapman (1978) was involved with a pack of 10 of which at least 6 died from rabies.

This paper is an evaluation of recruitment and behavioral causal factors including outbreaks of rabies in wolves in the inverse density dependent decline (IDD) of the George River Herd (GRH) 1989-2012. A contrast is made with that in the density dependent (DD) population increasing period. (1974-1988). The data for the increasing period has been published in the book The return of caribou to Ungava, McGill-Queen's University Press, 2008. The density dependent increase of the population is considered the population control phase and the inverse decline period of the herd the experimental phase. Inverse density dependent (depensatory) used in this paper can commence at high prey densities (Holling 1959), Messier and Crête 1985, Messier 1994) and is not equivalent with the Allee Effect that only occurs at low prey numbers and can lead to extinction (Courchamp et al. 1999, Stephens and Sutherland 1999). This paper evaluates the hypothesis that caribou moving long distances have less predation. Messier et al. 1988: said p.285: *"long-distance movements of caribou may prevent wolves from increasing because migrating caribou would become inaccessible during the 4-5 months of wolf pup sedentariness in summer. Thus, long-distance migration of caribou can be interpreted as an effective anti-predator strategy."* A major factor for this hypothesis was that there was only one ungulate prey in the Ungava system in those years. The George River Herd made longer movements in the increasing years than in the decreasing years allowing an evaluation of the hypothesis in a complete cycle of growth: low numbers, 1954-to a high in 1988, to a low again 2012 (59 years).

Methods

The number of positive cases of rabies in canids,: arctic foxes, red foxes (Vulpes vulpes), wolves, and dogs in Labrador 1974 to 2011 was provided by Dr. Hugh Whitney (Chief Veterinary Officer in

Newfoundland) (http://www.nr.gov.nl.ca/rabies). Dr. Christine Fehlner-Gardiner (Research Scientist, Center of Expertise for Rabies, Government of Canada) provided similar data for northern Quebec.

Wolves, the primary predator of caribou have never been censused in either Québec or Labrador. Wolf indices of abundance include harvest data 1920 to 1984 (Novak et al. 1987) and the registry of furs in northern Quebec by the Québec Ministry of Natural Resources and Wildlife. This latter index includes only harvests of native peoples north of 52 degrees of latitude for the years 1988-2011. Additional harvests figures were from Kuujjuaq and Nain 1974-93. (Bergerud et al. 2008, Fig. 1.11, p. 26.

The October recruitment of calves was measured by the Québec and Labrador wildlife departments 1973-2012. In the period 1973-1993 both departments did largely independent counts (Bergerud et al. 2008, Table 10.1, p.270). After 1993 the two departments often combined their flights in the October counts.   The Newfoundland and Labrador service also classified short yearlings in April- May 1974-93. Québec wildife tracked the October recruitment of the Leaf River herd 1994-2011 that inhabits the western half of the Ungava Peninsula and has in the past exchanged animals with the George River Herd (Couturier et al. 2004). The Leaf River Herd in these years was a large herd (500 000) moving in a large area of 400 000+ km² (Couturier et al 2004). similar to the George River Herd before its recent decline.

The recruitment considered to stabilize caribou numbers in October classifications was 39 calves/100 females (Couturier et al. 2004) and 25 calves/100 females in the spring classifications of short yearlings (Bergerud et al. 2008). This difference (39 vs. 25) acknowledges the likelihood that calves overwinter have higher predation mortality than adults.

To better understand the role of wolf predation on recruitment the annual recruitments were divided by the recruitment the prior year to establish a rate–of-gain statistic. The year before a rabies outbreak

was called the wolf year—the hypothesis was that it was the year that the wolves numbers should have recovered from the prior epizootic. If wolf predation is a major natural mortality factor of caribou this index (recruitment rabies year/wolf year) could result in high rates-of-gain compared to other years. Statistical t-tests were used to compare recruitment in: (1) rabies years vs other years, (2) wolf years vs rabies years, and (3) wolf years vs nonwolf years that excluded rabies years, an index where one can judge if wolves have recovered from the prior rabies by the magnitude of the negative recruitment (see Table 1).

　　The size of annual ranges in tundra caribou is an index to population size. (Bergerud 1980, Fig. 9, p.571) and might help explain changes in predation risk between the increase phase (1974-88) and the decrease phase (1989-2010). The size of total range and calving areas in the herd during the increasing years (1974-88) were from Bergerud et al 2008, Table 12.1, p.324). In the decreasing years. Boudreau et al. 2003 showed the distributions of satellite caribou in the snow-free period 1991-98 and the GRC caribou workshop, 2 Nov. 2011 mapped the size of the range in the winter period, November-April and also August-October. The size of the annual distributions and movement routes 1999-2001 of the Leaf River and George River were from Courturier et al 2004, Fig.1.

　　Another factor that could affect caribou mortality by predation and hunting mortality is the mobility of the herd. Kilometers traveled per day for the increasing years and high years (1987-90) were from satellite caribou Bergerud et al. 2008, pages 356-57, and for the decreasing years (2006,07,08,10) were estimated from maps of collared caribou (http:www.mrnf.gouv.qc.ca/english/wildlife/maps-caribou.), arrows connected weekly locations.

Findings

　　During the study 1973-2012 their were rabies epizootics of foxes and wolves occurring at mean intervals of 3.12±0.56 (n=9),

(Fig. 2). One year peaks are a common feature of arctic foxes populations elsewhere in the Holarctic (Angerbjörn et al. 1995, Elmhagen et al. 2011). There was a rabies outbreak in 1976 but neither provincial government quantified positive cases. The harvest of wolves (our index to population size) declined in 7 rabies outbreaks in 1975-2012 (Fig. 2). There was an overall increase in the wolf harvest statistics 1988-94 (λ=1.24, r=0.787, n=7, P<0.05) in the interval that the October recruitment changed from positive to negative (Figs.2, 3). A second increase in the wolf harvest occurred 2000 to 2010 (λ=1.25, r=0.958, n=10, P<0.01, (Fig. 2) at a time when the size of the range of the herd was rapidly declining (Table 2),

The declines in the wolf population based on harvest in the increasing period in rabies years (1976, 81/82, 87/88) did not result in significant increases in the survival of calves in the October recruitment (Table 1, Figs. 2, 3). In contrast to the lack of improvement in survival in October in the fall counts, the spring recruitment of short-yearlings showed increases in survival in all four of the rabies outbreaks (1976, 81/82, 87/88, and 91-92 (Table 1, Fig.4). In 1984 recruitment dipped below the stabilizing recruitment index: fall (39/100 females fall) and spring and (25/per 100 females (Figs.3, 4). In the decreasing, years in contrast to the increasing years, there were major improvements is calf survival in years of rabies outbreaks but a major decline in recruitment in 2011-12, both rabies years (Figs.2, 3). The difference between recruitment in wolf years and rabies year was magnified by the rate-of -gain technique which showed major changes in fluctuations after 1992 (Fig.3, bottom).

The annual changes in fertility that were measured, 1973-1993, n=16years (Bergerud et al. 2008, Table 10.1, p.270) affected the size of October and spring recruitments. From 1973 to 1983 fecundity was high: parous females 91.3±1.57%, n=5, CV. 3.9% (broken) and the mean October recruitment was 52.1±0.95%,calves.100 females, n=11, CV. Only 6.0%. From 1984 to 1990 fecundity fell to

67.5±3.73%, n=7, CV.=14.6% and recruitment declined to 35.8±1.965, n=7. In the last years that fecundity was measured, 1991-1993, fecundity increased to 73.8±1.00, n=3. CV. only 3.3% and recruitment was 32,9±1.00, n=3, CV,=21.4%; this latter large CV. was due to a wolf year 1992 and a rabies year 1993. In the decreasing years after 1993 the fecundity probably never returned to the high values in the increasing years when caribou were annually expanding to new lichen pastures west into the area of the Leaf River Leaf herd that was still relatively small (Belanger and Le Henaff 1985).

The mean October recruitment values in the increasing vs the decreasing periods were: increasing years 1974-88, 47.4±1.92, calves/100 females n=15, decreasing years, (1989-2012) 28.4±2.21, n=23, t=4.23.P.<0.001, percent decline 40%. Yearling count in increasing years, 1974-88, 28.5±2.49 yearlings/100 females, n=14, decreasing years 1989-92, 13.2±2.8, n=4, t=3.93, P.<0.01, percent decline 53%. There were major declines in recruitment between the increasing and decreasing periods and between measuring the recruitment in October and 6-7 months later in the spring (data were not corrected for adult female mortality)

In the decreasing period 1989-98 the herd continued to range widely, a mean of 366 000 km², n=10. r=-0.078 (ns) without significant range constrictions. Fall recruitment was below the isocline of 39 calves per 100 females in 8 of the 10 years (Fig. 3). The major decline in October recruitment occurred in 2005-12-- 40 calves/100 females declining to 7.4 calves/100 females in 2012, n=8, λ=0.78, r=0.905, P. <0.01. During this period the herd rutted in an area midway between it winter range and its calving range, and the only increase in recruitment was in 2009, a rabies year. This decline in recruitment occurred as the herd reduced its range as the population size decreased (Table 2),

The Leaf River data 1994-2012 showed major increases in October recruitment in 3 of the 5 years of epizootics (Fig 5) that .

exceeded the isocline >39 calves/100 females (Fig 5). The October recruitment in the Leaf River in wolf years was 26.6±3.30 and for the George River 17.2±2.92, (P<0.01,Table 1), in both herds the indices were below the recruitment isocline. However they were not significantly different considering all the declining years: Leaf 33.8±2.18, George River 27.8±2.76, n=18, 1999 missing, t=1.70. Both herd means were below the October isocline of 39 calves/100 females.

The-rate-of gain technique (recruitment year 2/year 1) provided graphic evidence of the lack of recognizable rabies influence in fall recruitment in the data in the increasing years 1974-88 but documented major fluctuations in gain in the deceasing years 1989-2010 for both the George River and Leaf River herds (Figs.3, 4, and 5). This resulted because in the wolf years caribou usually had the lower recruitments in the year prior to a rabies outbreak. Test of significance are tabulated in Table 1).

The George River Herd expanded its range in the increase phase 1974-88 at 0.74 km.² for each additional caribou, 1974-88 (Bergerud 2008 Fig 12.4, p. 327) reaching Hudson Bay Coast by 1983-84, 800 km. from the center if the calving ground, moving at 12-13 km. per day (Bergerud et al. 2008, Table 13.1 p.356). In the decreasing phase the George River Herd was estimated at 550 000 animals, 1990-91 in 500 000 km.² (Bergerud et al 2008, Table 10.5, p. 285, Table 12.1, p. 324); censused in 2001 at 300 000 adults (Couturier et, al 2004) in 300 000km², and censused in 2010 at 70 000 adults in 70 000 km.² (GRC workshop, 2 Nov. 2011). Thus the herd's range was reduced about 1 km² per caribou lost. After 2005 the herd stayed mostly east of 68º longitude, with reduced daily mobilities (Table 3). The herd in 2010 and 2012 wintered east and northeast of the Smallwood reservoir November to April. Thus the distance to the calving ground was approximate 400 km. and could be reached by mid- June at a mobility rate of 6.5 km/day, although spring migration did not commence until mid April .

The caribou in the decreasing years 2006-2011 used the same rutting area each year, an area of 35 000 km.² north of the Smallwood reservoir and within 40 km. of tree line (Caribou Workshop, 2 Nov. 2011). The general view is that wolves den most frequently in the vicinity of tree line and leave their summer areas in October-November (Heard and Williams 1992, Heard et al 1996, Walton et al. 2001. The concentration of the caribou in a predictable location near tree line plus reduced awareness in the breeding season should have resulted in a high numerical and functional predation responses .

In contrast to the restricted range and low mobility in October in the decreasing period, in the increasing years caribou in the George River Herd moved annually west and southwest hundreds of kilometers from the George River. They rutted in at least 21 locations over the years in an area of 210 000 km.² rotating to new pasture each year and splitting into breeding subunits (Bergerud et al. 2008. (Fig.12.7 p. 330). It would be expected that with this extensive movement of caribou wolves would have had to disperse over a wide area and may have attenuated their predation numerical response .

Discussion

The inverse density dependent decline in numbers and range was initially caused by by increase summer mortality of lactating females, heavy human harvests 1987-92, plus continued wolf predation in the early period when fecundity was still low from oe The wolves generally declined during rabies or just after outbreaks and increased in the interims. In the latter days of the decline after 2001 the reduced distribution of caribou facilitated the searching effort of the wolves as did the reduced movements of the herd. The forage partially recovered including lichens (Boudreau et al. 2003, Théau and Duquay 2004), Boudreau and Payette 2004). With some vegetative

recovery and a decline in caribou numbers, the occupied range contracted further concentrating predation pressure.

Walton et at. (2001) reported an annual mean range of radio collared male wolves in the Bathurst Caribou Herd,(NWT) of 63 000 km² and females 45 000 km². Wolves restricted to denning sites after the summer and denning period should be able to following the herd after the caribou move south of the tree line. By October 2011 the range of the George River Herd was less than 100 000 km². Recruitment of the George with its range greatly decreased was 16 calves/100 females in 2011 and 7.4 calves/100 in 2012 females. The much larger Leaf River Herd, with a much larger range, had a fall recruitment in those two rabies year of 34 calves/100 females In 2011 and 37 in 2012.

Sinclair 1979 showed that large predators in Serengeti had less influence on the demography of migratory ungulates than the sedentary phenotype. Fryxell et al. 1988 modeled the Serengeti system as to why migratory ungulates were more abundant than sedentary, three hypothesis were (1) migrants had access to more food, (2) migrants made more efficient use of resources, and (3) migrants were less vulnerable to predators, the result of modeling supported the predation hypothesis. In North America all the migratory caribou herds that have reached numbers greater than 300 000 km² have had herd distributions in excess of 300 000 km² and made long migrations (Bergerud 1996). The most significant behavior of the caribou in their expansion phase was the extensive movement 1977 to 1984 extending their range west and southwest gaining access to less trampled/grazed lichen phytomass.

During the years of increase 1974-83, years with positive October recruitment greater than 39 calves/100 females, the wolves with with young could not keep up with the herd moving west at 12-18 km/day. Possibly the wolves caught up with the caribou in November and December. The herd was classified 6 times in the winter of 1981-

82 and the greatest decline in calf survival occurred in those two months (Bergerud et al. 2008). Collared radio wolves in the NWT denning north of tree line did not follow the caribou south until late October/November; the median date of departure of wolves from summer denning ranges in 1997 was October 26, and in 1998 November 3, (Walton et al 2001). Such late departures by wolves in Ungava would minimize recruitment losses of caribou that were measured in mid-October during the years of increase. In mid October 1981-93 the monthly center of the George River herd was 350 km west of the Labrador tree line (Bergerud et al. 2009.Fig. 12.7 p,330) where wolves would be expected to den (Hearn and Williams 1992)

The harvest of wolves (the index of population in this study) increased rather than decreased 2000-2010. A possible explanation despite rabies is that the wolves' reproductive rate increased in the deceasing years with more access to caribou, I.e. larger litters, earlier estrus, multiple births (Boertje and Stephenson 1992, Ballard and Gipson 2000, Frame et al. 2008). The restrictions in space and mobility of caribou during the October rutting season should have enhanced both the numerical and functional predator responses (sensu of Holling 1959) and caribou recruitment did decline significantly 2005-2012, λ=0.78.

In the census of caribou March-April 1982, (a rabies year), 39 caribou killed by wolves were located and only 4 were above tree line (Bergerud et al. 2008. Fig. 15.4, p. 440). The wolves seen in that census were only in groups of 3 or less. Wolves are generally more common below tree line in winter than summer in the NWT (Heard et al. 1996). The constant movement in the herd in July to escape insects and the August dispersal of small groups to optimally forage before the end of the growing season may have also reduced predation risk from wolves that had restricted mobility in the vicinity of denning and rendezvous sites.

The finding that October recruitment in "rabies" years in the increasing phase showed no significant improvement over "non rabies" years but was detected in spring classification 6-7 months later supports the hypothesis that long migrations reduce risk. In this period the George River was annually extending their range 100-200 km/yr. west or southwest and the October breeding area by 1984 was 450 km. further west from the Labrador tree line (Bergerud et al. Fig.12.6, p. 329). The Leaf River also expanded its range 350+ km. south from its position in 1981 based its location in the early 1980s (Belanger and Le Henaff 1985). These large movements would hinder denning wolves keeping abreast of the herds as Messer et al. 1988 therorized.

However the finding in the decreasing years of major declines in recruitment in October in both the Leaf River Herd (still a large herd) and the George River Herd does not support the reduced risk hypothesis. In this decline period both the George River and the Leaf River were rutting in October near or at the tree line. Another factor that might help explain the reduced October recruitment as the herds declined could be that the wolves altered their denning sites locations to reach the reduced herd locations. In Alaska in 1985 an outbreak of rabies in the Brooks range killed collared wolves denning along three rivers; the survivors regrouped and moved to a forth river and denned (Clough et al. 1987). Wolves can move denning sites (Mech 1970). A third factor that could help explain the failure of the long-movement/less predation hypothesis is that the winter range of the George River herd, range, now with global warming, is no longer a single ungulate sysem and now supports a small moose popilation -0.019 moose/km² (LGL environmental associates 2008). Additionally the Red Wine woodland caribou herd is present (Brown 1986) on the winter range of George River was approxately 100 km southeast of the herd's in October range; the October recruitment of the Red Wine in 8 years 1981-2003 (broken) was 17.±1.92 calves/100 females

(Schmelzer et al, 2004) which suggests considerable wolf presence. Fall October calf counts are insufficient to measure population changes or to quantify the impact of rabies and the extent of predation—yearling counts are needed to accurately measure the size of new cohorts and are the standard method of measuring recruitment in Alaska and the Northwest Territories.

The George River had declined to 27 600 caribou by July 2012. (Nfld. Govt. news release, 16 August 2012). The high harvests in 2011 and 2012 were not appropriate for the size of the herd (the herd was only 40 km from a access road). Caribou recruitment was drastically reduced, despite the 2011-12 rabies outbreak (Fig.3). The outbreak of rabies was the most widespread on record, positive cases were reported from residents in 18 communities along the entire Ungava coast (west, east and north) spanning an area of 500 000 km². All the cases in both years were only in the first 5 months January to May. Rabies in March would have had an impact on wolf breeding, and in April and May would have adversely affected denning and reproduction. The surviving wolves free of denning activity in June would have been free to hunt without spatial restraint. In mid July 2012, two to three weeks after calving, the herd had only 12% calves reduced to 5% by October (Nfld. and Lab. news release 16 Aug. 2012). Wolves appear to have been more mobile in these years. There were comments from wildlife officers and trappers of more wolves on the coast in 2011 and 2012 hunting seals and also polar bears (Ursus arctos)-one observation of 9 wolves attacking an adult bear and another encounter seen from the air of 15 wolves following two bears. The surviving wolves could have moved in 2012 to their alternate coastal food supply (Andriashek et al. 1985) after visiting the calving ground adjacent to the coast and instigated surplus killing of newly born calves. Surplus killing of young caribou calves has been extensively documented in the NWT (Miller et al. 1985) and was observed in the George River Herd: in 1989 2 wolves killed 5 calves in

15 min. and in 1991 3 wolves killed 11 calves in 83 min. (Bergerud et al. 2008, table 11.7, p.310)

Long cycles of abundance and scarcity of individual arctic caribou herds have occurred for millennia and the decades of scarcity well remembered in traditional knowledge (Beaulieu 2012). Recently the Bluenose-west Herd, and the Bathurst Herd in the NWT have declined with reduced distributions and with low spring counts of yearlings and increased mortality of collared adult females 2000-10 (Adamczewski et al, 2009, Boulanger et al. 2011) ,

Perhaps the best example of predation and over harvest resulting in inverse density dependence in tundra caribou was the decline of the Western Arctic Herd (WAH) in Alaska declining from 242 000 animals 1970 to 75 000 by 1976 (Davis et al. 1980). Wolves were managed and the harvest drastically reduced from 25 000 per year to a license quota of 3000 males and the Inuit cooperated (Davis et al. 1980). The herd turned around and reached 490 000 by 2003, $\lambda=1.07$ (Ballard et al. 1997). Then the herd was censused at 3 year intervals and went into IDD in 2004 decreasing to 325 000 by 2011, $\lambda=0.96$. Annual satellite cow mortality in the WAH in the DD years 1985-2003 was $\overline{x}$ =15.1±0.81%, n=19, CV.=23% and in the declining years 2004-13 was $\overline{x}$= 22.5±2.22%, n=10, CV.=31%, t=3.14, P<0.01. The mean short yearling/100 adults ratio in the increasing years was $\overline{x}$=22.7± 0.32%, n=23, CV.=24%, and in the declining period $\overline{x}$=15.9±1.67%, n=10, t=3.48, P.<0.02, CV.=33%. The **mortality** rate of the collared females was negatively correlated with the **survival** rate of the yearlings, r=- 0.5303, n=29 years (DD+IDD) P.<0.02 (data were calculated from Dau 2009 and pers. comm. A factor in the large CVs. was due to rabies outbreaks.

Prichard, 2009, modeled the decline of the WAH; there was no discernible decline in parturition rates, body condition nor harvest levels, He postulated the decline was due to changes in weather or predation. Deep snows in the past have played a role in increase wolf

predation on calves and females in Alaska (Valkenburg et al. 1996, Mech et al. 1998, J. Dau pers. Comm.). Alaska, unlike the NWT, has few lakes for caribou to seek low snow depths on ice to reduce risk.

These data suggest that population cycles of tundra caribou result largely from predator prey interactions plus high human harvest but also includes a positive role in cyclic increases during rabies epizootics. In the increase years 1984-88 overgrazing reduced fecundity in the George River taking recruitment below the prey isocline; this reduced fecundity of caribou was *only* recognized because udder counts were made in June. In the past other large herds in Canada may have overgrazed their growing season range but it went unrecognized in the absence of udder counts. Possibly inverse density dependence–anti regulation could also be initiated by longer intervals between rabies out breaks, however epizootics have not been monitored in NWT or Nunavut.

Barren ground caribou are a herd species aggregating in both the breeding season and the winter. In the winter large cow/calf aggregations form, in open habitats with low snow profiles; normally wolves are also presence (Parker 1973, Miller 1975). In such habitats the caribou can compact the snow and use their cursorial speed, as well as reducing risk by early flight and dilution. When mortality from predation and hunting exceeds recruitment in this gregarious species individuals remain together reducing the herd's distribution and movements. This in turn enhances the searching and hunting efforts of the predators and instigates a further decline. This continuous decline sequence once started can continue for years en lieu of our intervention.

In the years of ***increasing*** caribou numbers (1974–1988), there were no significant differences in the October recruitment (calves/100 females) in three rabies outbreaks 76, 80/81, 87/88 with the recruitment in the year prior to each epizootic. There *was* increased

recruitment, however, of spring yearlings (yearlings/100 females) 1976-92 in four rabies outbreaks compared to the year prior to each outbreak. **In other words, the présence of fewer wolves in rabies years resulted, predictably, in less prédation over the winter, but had little impact on fall recruitments since the expanded ranges (combined with normal rates of fertility) had already reduced prédation and kept recruitment numbers high.**

However, in the years of ***decreasing*** caribou numbers (1989-2012), the rabies outbreaks made a significant différence in October recruitment, which was higher in rabies years than in the year prior to the outbreak in six instances. This supports **the hypothesis that calves in these less-mobile (and presumably less-fertile) herds were more vulnérable to prédation.** (This was *not* the case in the period of the most severe outbreak 2011-12, but reasons for this will be discussed later.)   The inverse density dependent decline in numbers and range was initially caused by heavy human harvests 1987–92 combined with continued wolf predation in the early period when fecundity was still low from overgrazing. After 1988, range expansion ceased, reducing mobility. This facilitated **increased predation in October—albeit with** enhanced recruitment in most rabies years—and the herd went into exponential decay.

Large herds with long migrations do indeed experience less predation in years of normal fertility and range expansion. The strategy of moving further and faster works as long as there is ample food and normal fecundity. **However, once a herd begins to decline, for whatever reason, that strategy is no longer enough.** To compound matters, when mortality from predation and hunting exceeds recruitment in this gregarious species, individuals remain together, further reducing the herd's distribution and movements. This in turn enhances the hunting efforts of the predators and instigates even further decline. Without effective

harvest management, the impact of predation on a declining herd's population can be devastating.

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Table 1 Tests of significance of recruitment calves and yearlings

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1.October recruitment, 1973-88, (George R./) density dependent , calves/100 females, rabies years, $\bar{X}$=48.0, n=4, *wolf years, $\bar{X}$=48.4,* n=3, not significant.

2.October recruitment, 1989-2010,(George R.) inverse density dependent, calves/100 females, rabies years, $\bar{X}$=33.4, n=6, vs *wolf years, $\bar{X}$=20.4* n=6, t=4.23, P<0.01,

3.October recruitment, 1989-2010, (George R.), Inverse density dependent, calves/100females, w*olf year, $\bar{X}$=20.4,* n=6,vs other years (excluding rabies yrs.) $\bar{X}$=32.5, n=9, t=3.89, P<0.01.

4.October recruitment, 1994- 2011 (Leaf River Herd), inverse density dependent,, rabies year, $\bar{X}$=39.4, n=6 vs *wolf year $\bar{X}$=19.8,* n=5, t=3.90, P,<0.01.

5.October recruitment, 1994-2011, (Leaf River Herd), inverse density dependent, *wolf year $\bar{X}$=19.8,* n=5,vs other years (not rabies) $\bar{X}$=40.8, n=7, t=3.80, P<0.01.

 6. October recruitment 1994-2011 (Leaf River Herd), inverse density dependent *wolf years, $\bar{X}$= 26.6,* n=5, (George R.) $\bar{X}$=17.2, n=5 paired t= 5.35, P.<0.01.

7. October recruitment, 1994-2011 , inverse density dependent, rabies yr. (Leaf R.), $\bar{X}$= 40.8, n=5, George R $\bar{X}$=33.4, n=6, not sign.

8. October recruitment, (George R + Leaf R), Inverse density dependent, years after rabies. $\bar{X}$=37.4, n=8, next *wolf yr. $\bar{X}$=24.8±3* n=11, t=2.90,P<0.02.

9.Spring recruitment, 1974-92 (George R.), Increasing and high years yearlings /100 females, rabies years, $\bar{X}$=28.0, n=7 vs *wolf years$\bar{X}$=15.5%,* n=4,t=3.98 P<0.02.

10.Spring recruitment, 1974-92 (George R), Increasing and high years, (yearlings/100 females, wolf years and other years excluding rabies, *wolf years $\bar{X}$= 17.6,* n=11, rabies years $\bar{X}$= 25.8%, n=7, t =1.56, not significant. The October rabies years not include in the Table

Table 2 The total range of satellite females (1000km²) compared between years of increasing and high populations 1986-90 (DD)[1] and decreasing populations 2006-08 and 2010

Total Range	Increasing (DD) Mean Area km²	Decreasing (IDD) 06	07	08	10	Mean km²	Mean Probability
January	16.2±2.98	15	6	14	14	12.3±2.00	ns.
February	14,6±3.98	16	6	16	5	10.8±3.03	ns.
March	17.2±4.22	7	11	12	5	11.5±2.25	ns.
April	17.8±0.92	16	13	15	4	14.6±0.76	ns.
May	30,0±4.42	8	7	10	6	7.8±0.85	P<0.05
June	24.1±5,25	3	5	3	6	4.3±0.75	P<0.02
July	36.8±12.76	13	8	6	4	7.8±1.93	P<0.02
August	43.6±10.00	31	46	16	4	24.3±9.11	P<0.05
September	55.2±16,77	35	21	19	10	21.3±5.17	NS
October	74.6±8.19	39	15	11	5	17,5±14,9	P<0.01
November	62.0±9.65	20	6	3	6	8.75±3,82	P<0.01
December	31.0±5.89	11	18	3	--	10.6±4.35	P<0/01
Total km²	797²	203	162	128	70		

[1] Increasing and high periods (Bergerud et al. 2008 table 13.8,p.379,

[2] The large total range In DD period is due to the constant enlargement of range as the herd increased.   The correlation coefficient between total range size 2006, 2007, 2008,and 2010 and calves/100 females in October was r=0.989, P<0.01

Table 3. Comparison of the km traveled per day in the increase phase and high density phase 1987- to 1990 (DD) n=4[1] vs the inverse density dependent phase (IDD) 2006,2007,2008 and 2010 (IDD)

Yearly Month	1987-90 Mean±SE	06	IDD Km/Day 07	08	10	Mean ±SE	Probability Difference
Jan,	8.0±1.99	1,8	1,2	1,6	2,3	1.7±0.22	P<0.02
Feb,	6,0±1.04	1.1	0.8	0.9	1.8	1.2±0.23	P<0.01
Mar.	7.7±1.08	1.0	1,0	1.5	1.5	1.3±0.14	P<.001
Apr.	10.4±1.69	2.0	4,3	4.5	5.3	4.0±0.71	P<0.02
May	14.4±2.37	25	17	23	24	18.2±3.45	ns.
Jun.	10.7±2.53	---	3,7	6,8	3.2	4.6±0.98	P<0.05
Jul.	16.7±0.90	9.9	8.7	10.8	9.4	9.7±0.44	P<0.001
Aug	19.8±1,72	2.7	5.5	5.6	1.3	3.7±1.09	P<0.001
Sep.	15.4±0.74	4.0	11.5	5.5	6,6	8.2±1,33	P<0.05
Oct.	17.8±0.51	5.0	7.0	7.7	9.7	7.4±0.97	P<0.001
Dec.	10.8±0.56	3.7	8.3	5.1	---	5.7±1.36	P<0.05
Means	13.0±1.35	5.4	5.8	6.8	6.8	6.3±1.37	

[1]Increase+high phase from Bergerud et al. 2008, Table 13.1 p.356-357
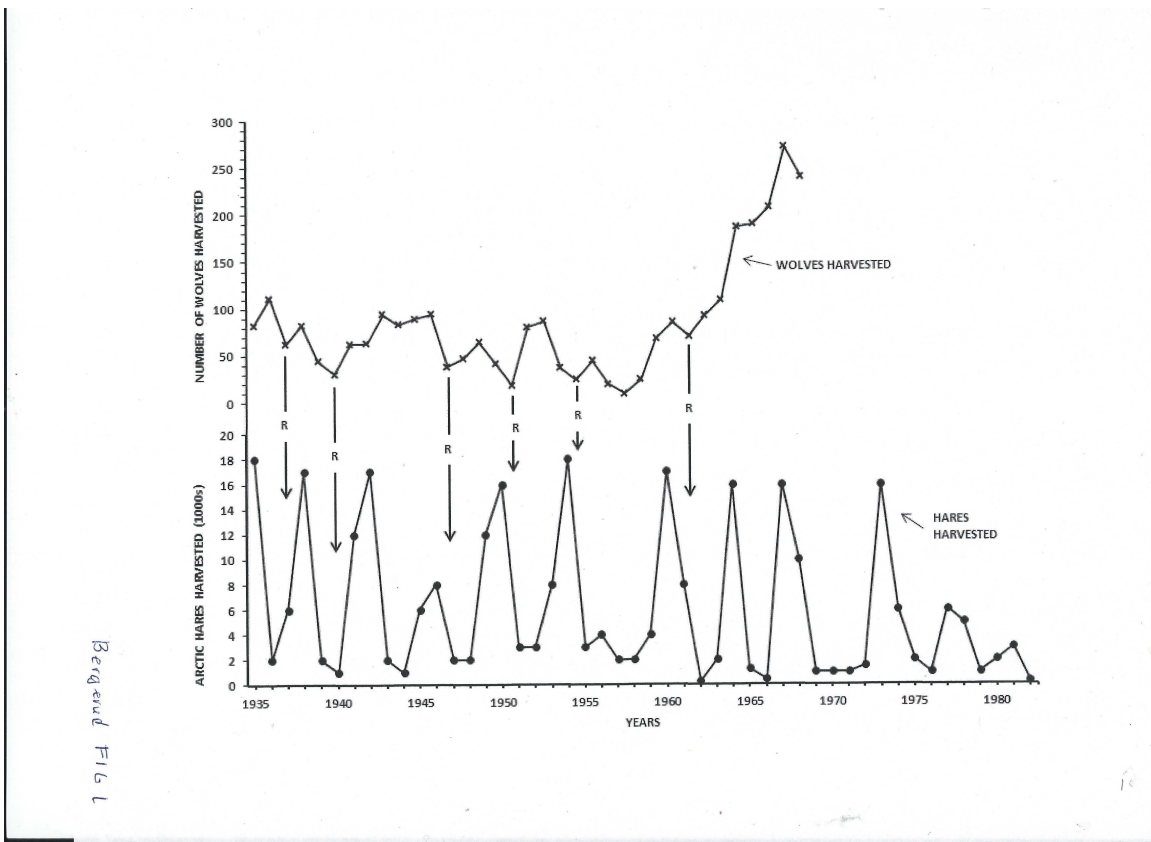
Fig. 1. (above) The number of wolves harvested 1935-1968. mostly in northern Quebec in the years of caribou scarcity and when moose were still farther south. The harvest increased as the caribou increased. (below) The harvest of arctic hares 1935 to 1982. Wolves commonly declined following arctic hares highs. Arctic hare numbers rounded to the nearest 1000. (Data from Novak et al. 1988, Furbearer Harvests in North America).

Bergerud FIG 2
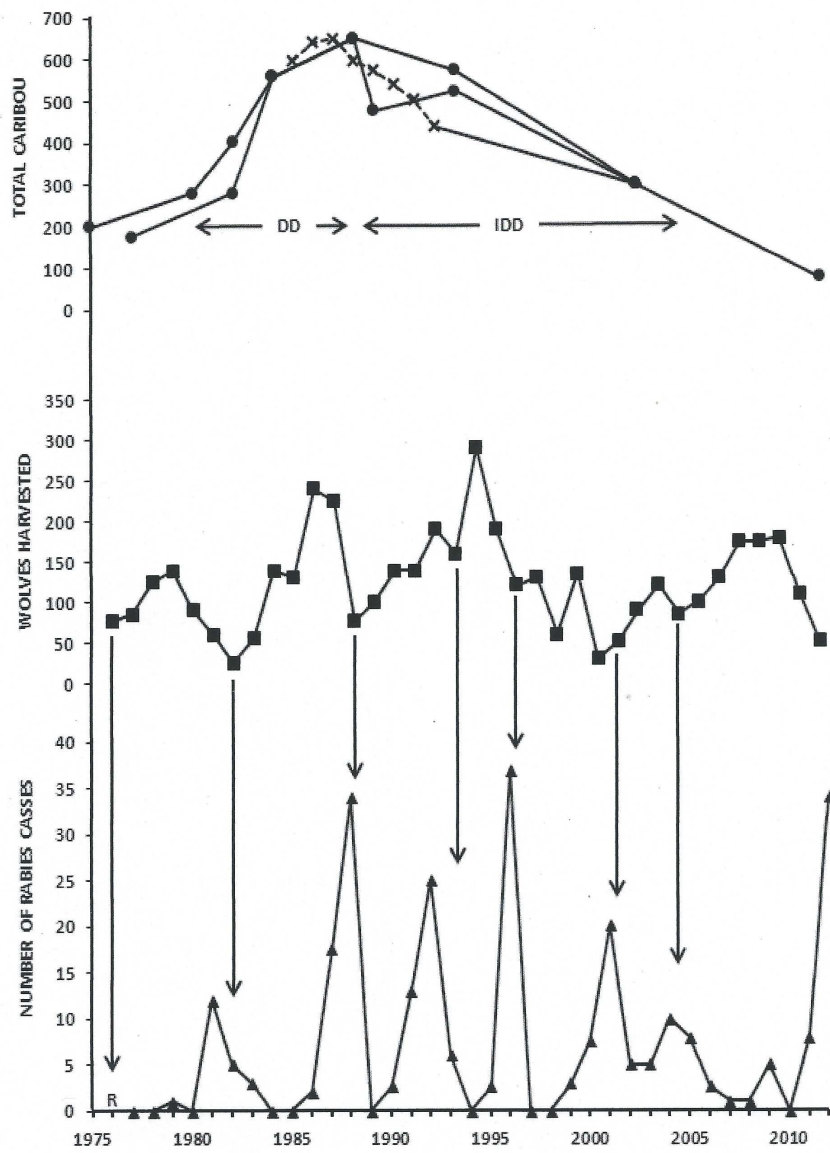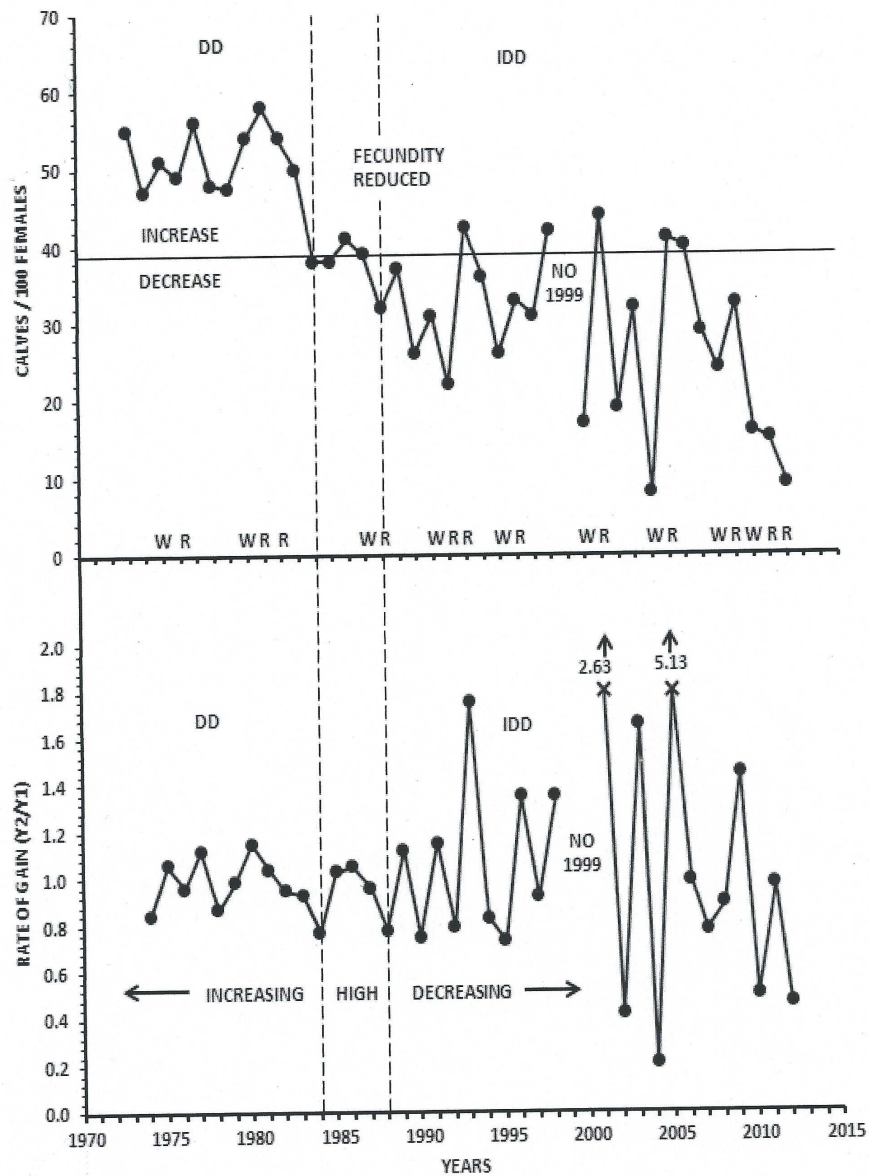
Figure 3 (above) The fall recruitment of the George River Herd from 1973-2012. Years of rabies are shown and the year prior to rabies is termed the wolf year. (below) The rate of gain analysis (Y2/Y1) plot

commenced to fluctuate widely in the decreasing years. (below)   The rate of gain analysis (Y2/Y/1) plot commenced to fluctuate widely in the decreasing years . These large fluctuations did not occur in the increasing phase 1974-88 (DD) when the herd was large with less contact with wolves. The recruitment in year before epizootics were usually lower than other years suggesting a positive recovery in the abundance of wolves between outbreaks.
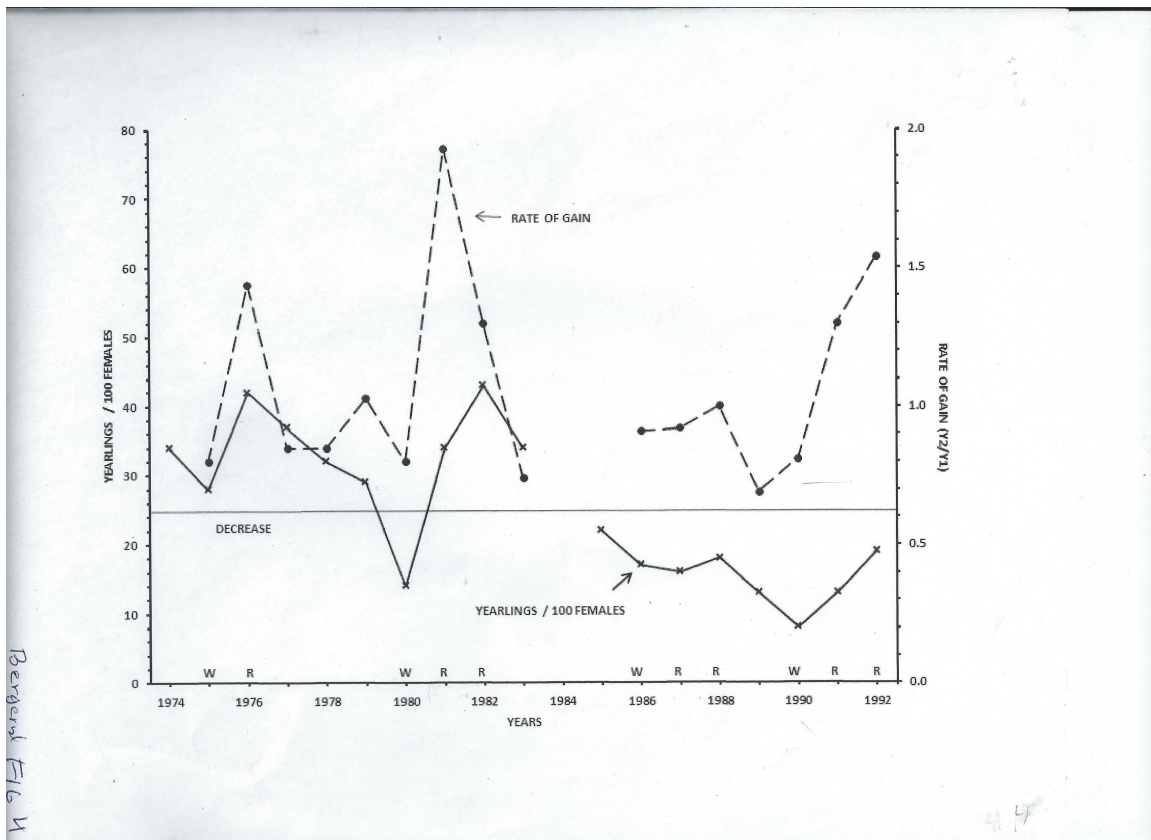
Fig. 4.The recruitment in short yearlings 1974-92. Recruitment increased in all 4 rabies outbreaks but only exceed the isocline of 25 yearlings /100 females in two outbreaks.
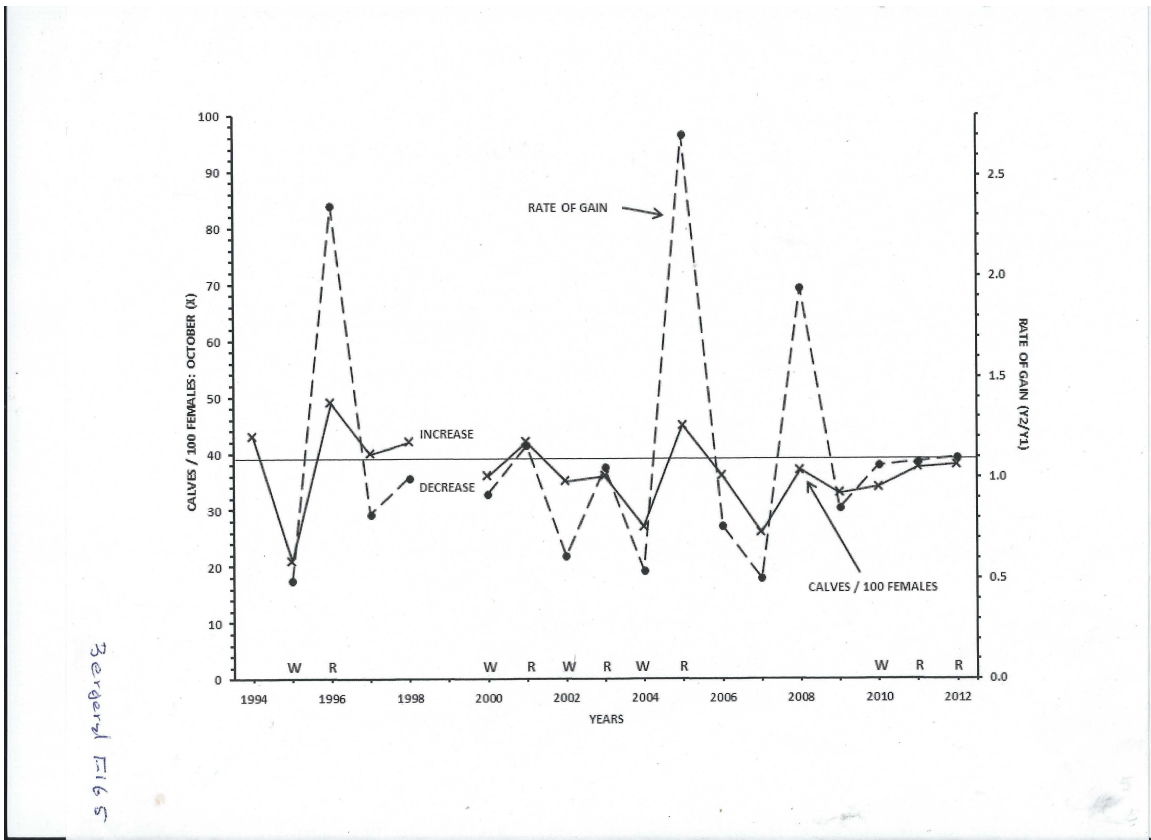
Fig. 5. The figure shows the spread between recruitment and rate of gain. statistics for the Leaf River Herd 1994-2012. In 2008 the rate-of-gain suggests a rabies year but no positive cases were reported that year.
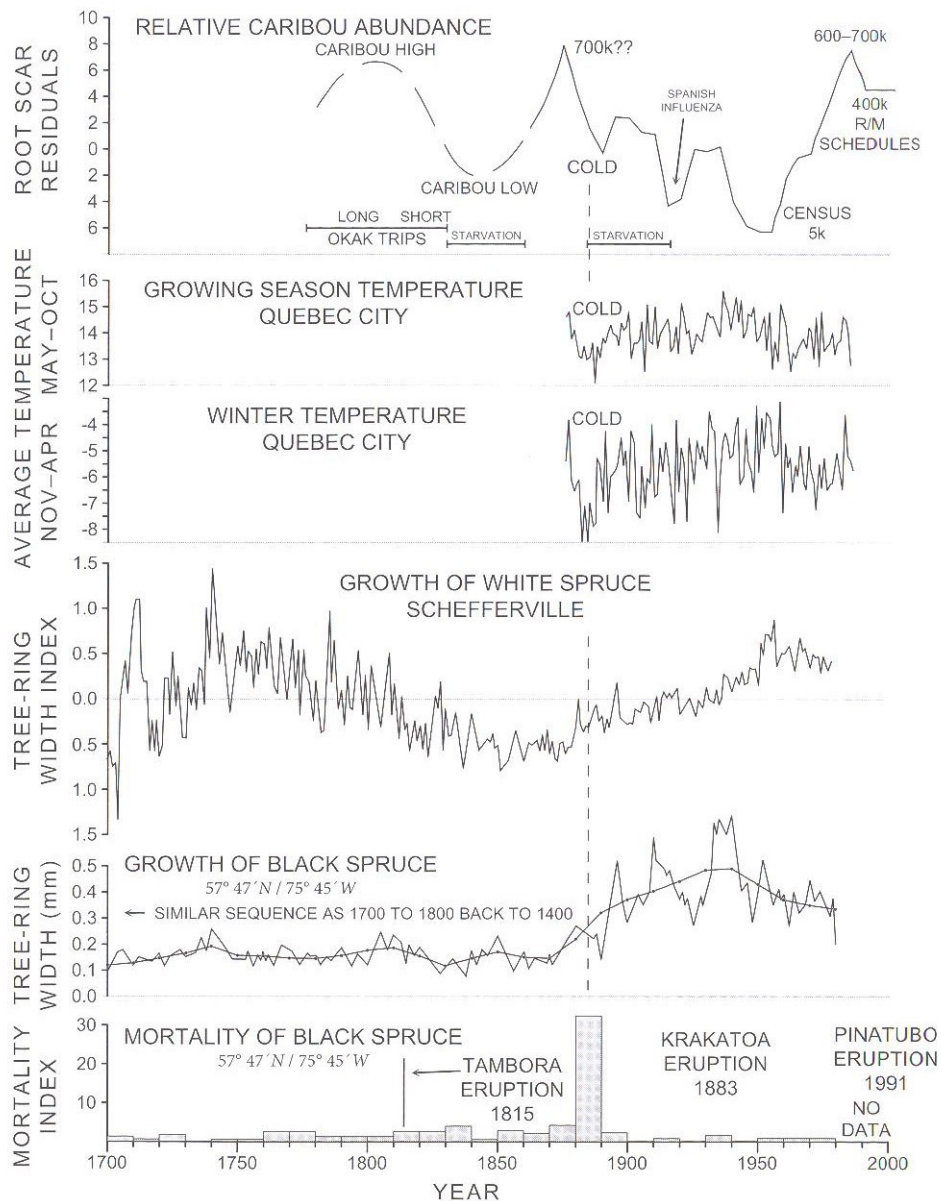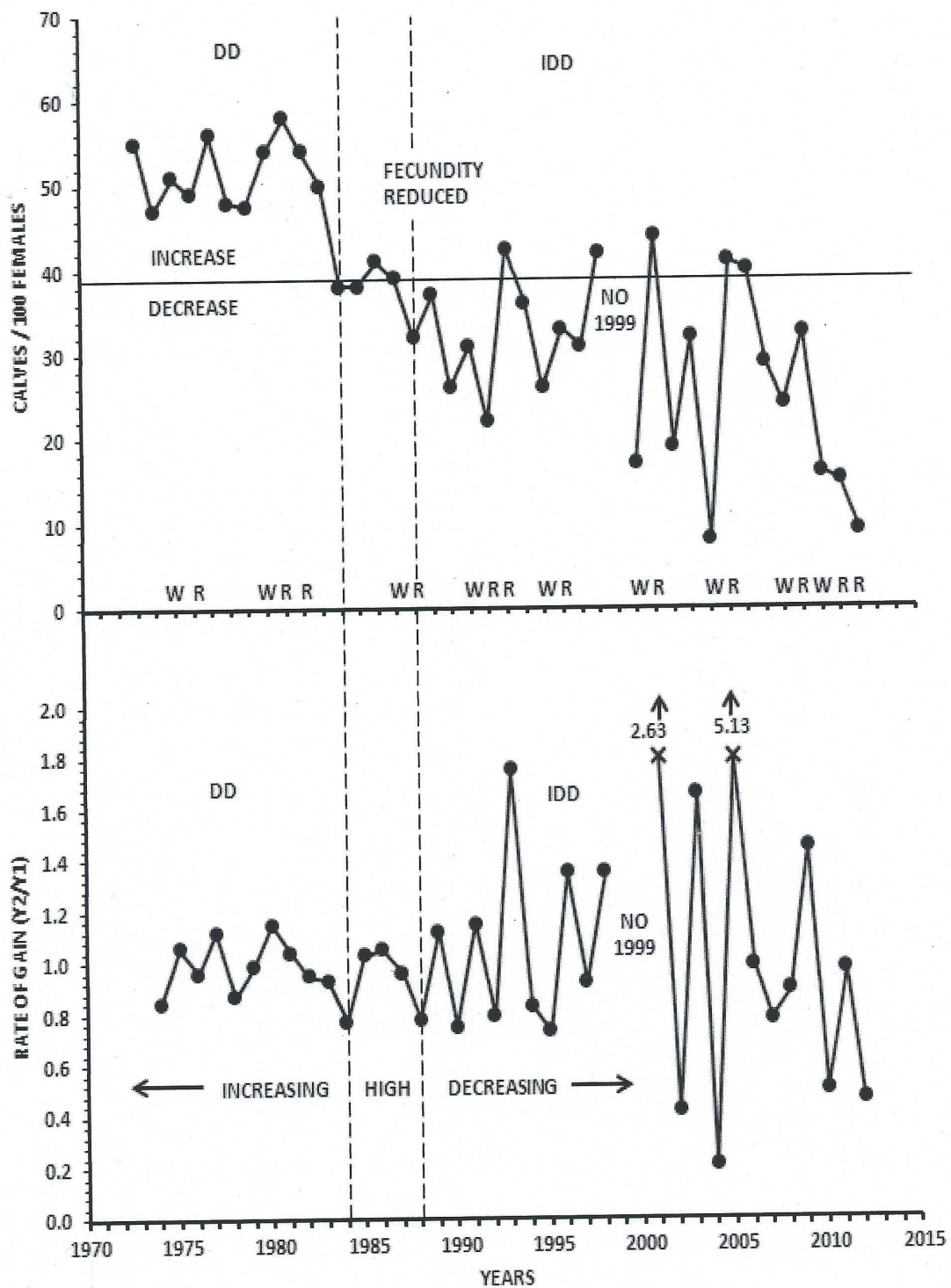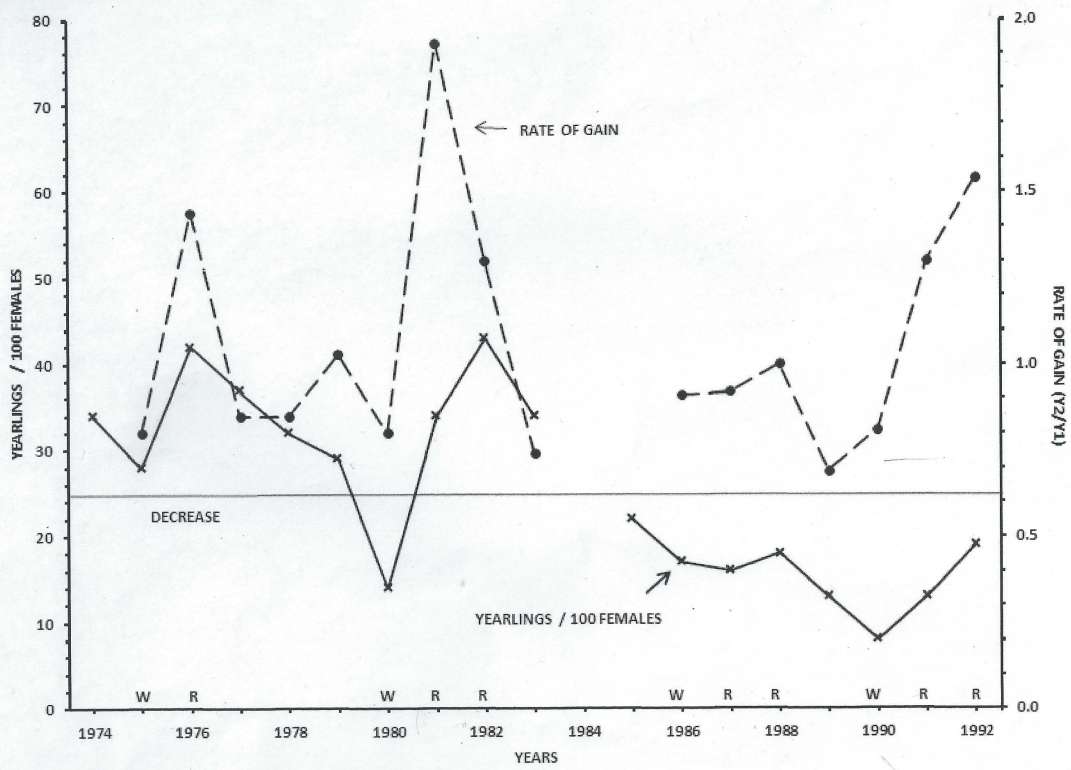
Fig. 6 The relative abundance of the George River Herd 1800 to 1993 compared to long-term factors. The root-scarring index adapted from Morneau and Payette (2000); the Quebec city temperatures from Crete and Payette (1990); the growth of white spruce from Enright (1984); the growth of black spruce from Payette et al. (1985) as well as the graph of the mortality of black spruce in the 1880s (bottom). Note the failure of spruce occurred in the decade 1880-1890 in the same decade that the volcano Krakotoa, lying between Sumatra and Java in

the East Indies, had a huge explosive eruption in 1883. "The dust veil in the atmosphere cooled the planet, which didn't warm back to normal for five years" (Quammen 1996, p. 142). This story was repeated 100 years later in 1991 when Mount Pinatubo in the Philippines erupted, polluting the George River herd and other herds across the Arctic in 1992 (Bergrud et al. 2008). Earlier in 1815 Mount Tambora erupted. Harington (1992) called the following year 1816, the year without summer.
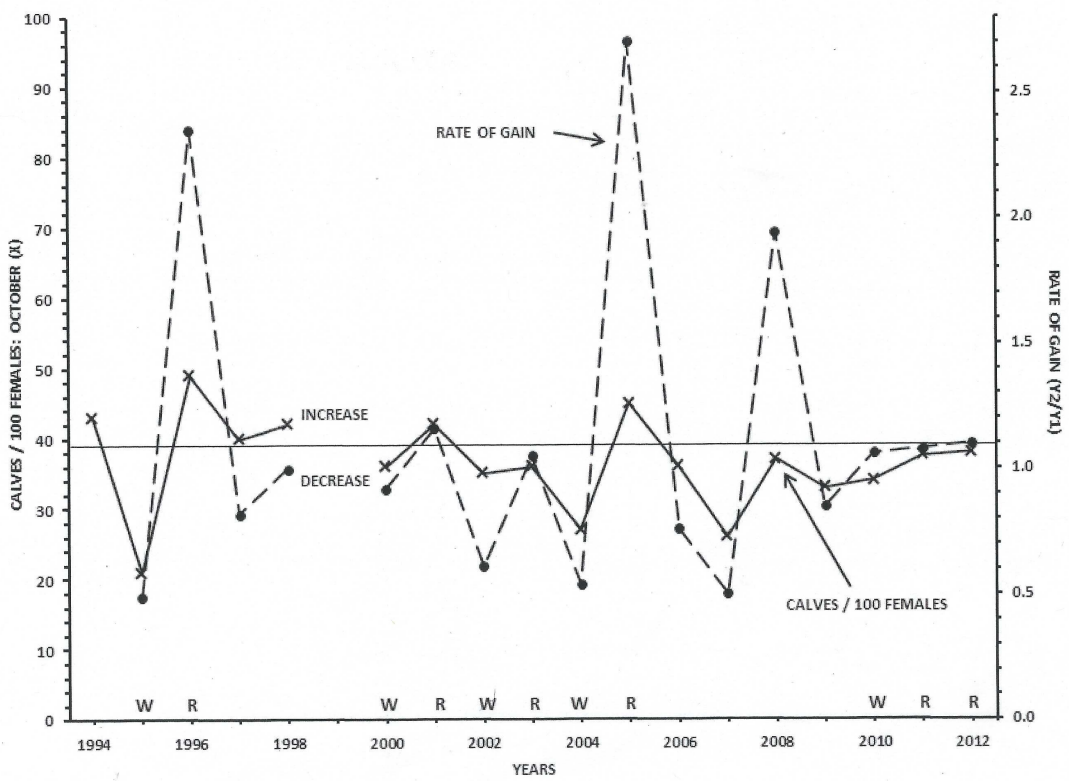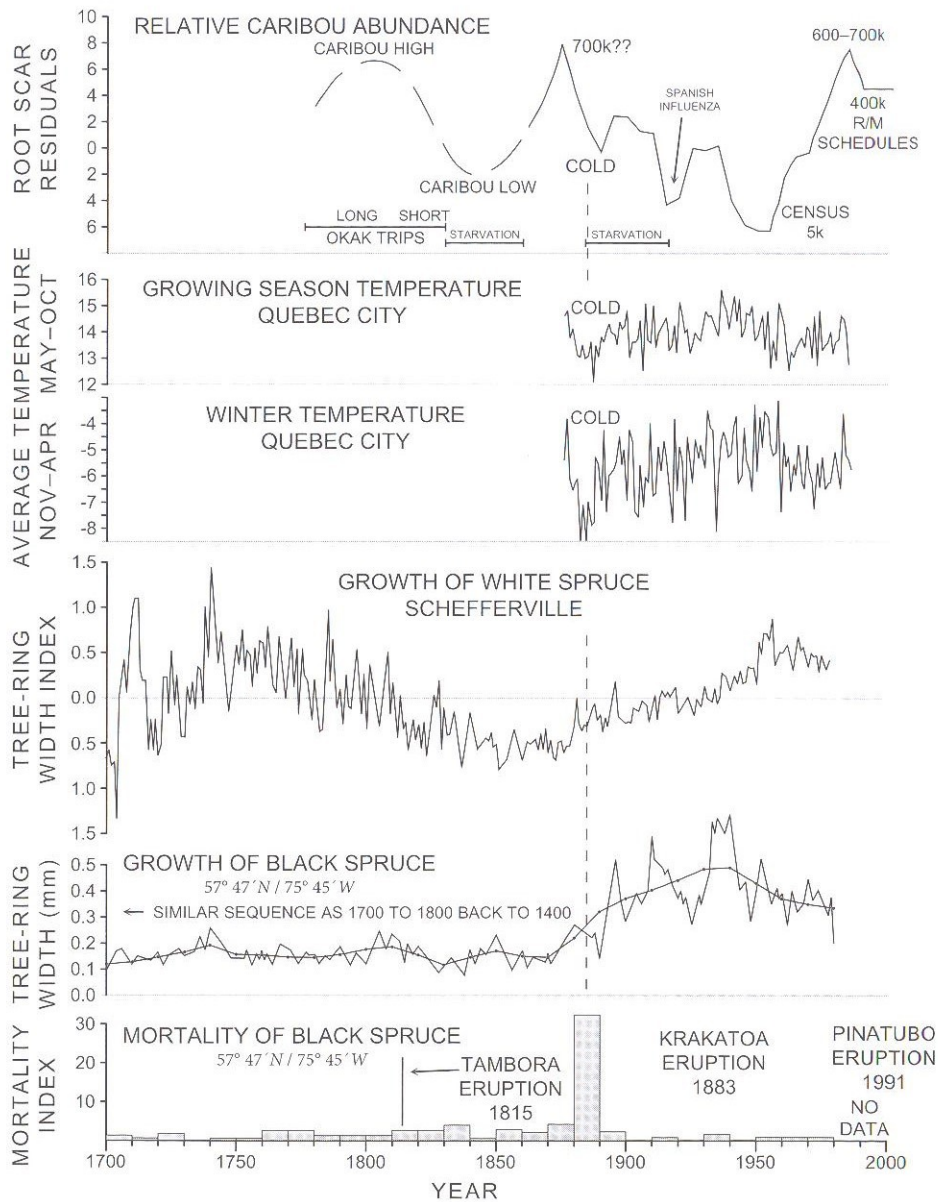
Bergerud F16

RELATIVE CARIBOU ABUNDANCE
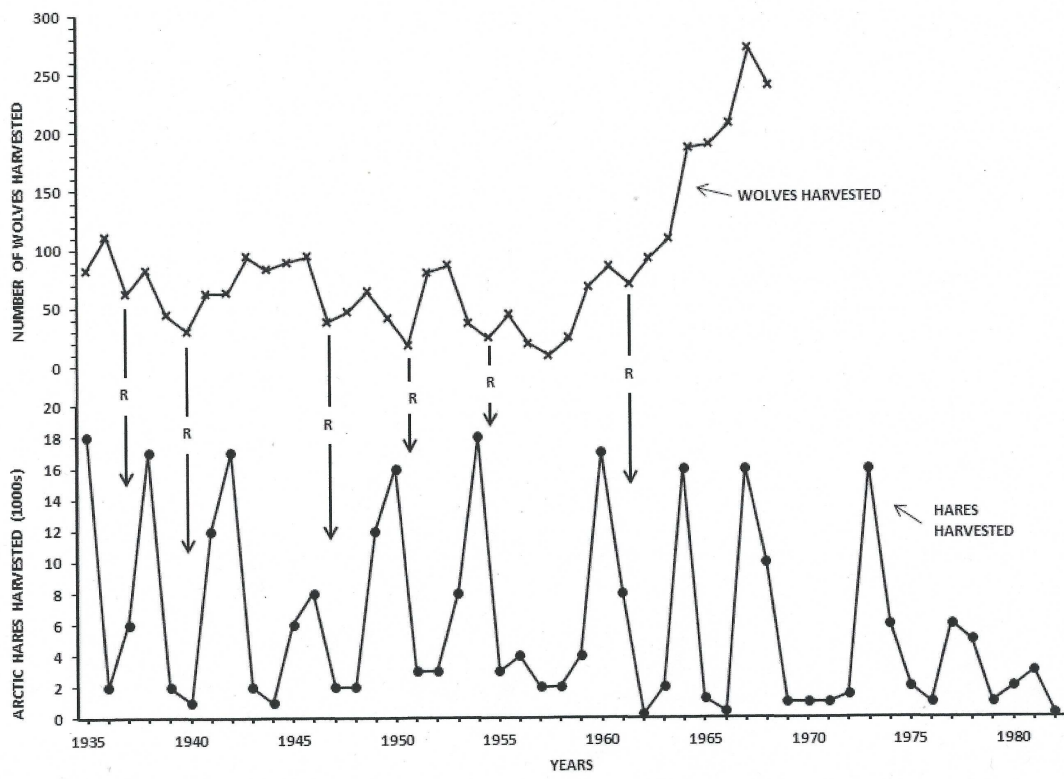
ROOT SCAR RESIDUALS

CARIBOU HIGH

700k??

600–700k

SPANISH INFLUENZA

400k R/M SCHEDULES

COLD

CARIBOU LOW

LONG   SHORT
OKAK TRIPS   STARVATION

STARVATION

CENSUS 5k

GROWING SEASON TEMPERATURE
QUEBEC CITY

AVERAGE TEMPERATURE MAY–OCT

COLD

WINTER TEMPERATURE
QUEBEC CITY

AVERAGE TEMPERATURE NOV–APR

COLD

GROWTH OF WHITE SPRUCE
SCHEFFERVILLE

TREE-RING WIDTH INDEX

GROWTH OF BLACK SPRUCE
57° 47′N / 75° 45′W

← SIMILAR SEQUENCE AS 1700 TO 1800 BACK TO 1400

TREE-RING WIDTH (mm)

MORTALITY OF BLACK SPRUCE
57° 47′N / 75° 45′W

MORTALITY INDEX

TAMBORA ERUPTION 1815

KRAKATOA ERUPTION 1883

PINATUBO ERUPTION 1991 NO DATA

1700   1750   1800   1850   1900   1950   2000

YEAR

Bergerud FIG 1

Bergerud FIG 2