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Evolving perspectives on caribou population dynamics, have we got it right yet?

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Abstract: The roles of food, weather and predation are compared between sedentary and migratory caribou herds. Sedentary herds disperse (space out) at calving time while the cows of migratory herds move in masse (space away) to calving grounds to reduce predation risk. The sedentary ecotype calves on ranges near open water if tree cover is present or in rugged topography in the absence of tree cover. The migratory ecotype aggregates on calving grounds located on alpine mountain plateaus or on the tundra north of the Arctic tree line. The two herds with the greatest densities in North America, the sedentary Slate Islands Herd and the migratory George River Herd both had changes in abundance that followed summer food problems. The hypothesis that winter lichen supplies determine abundance and set the carrying capacity is rejected. Lichens are not a necessary food for caribou. A review of the mortality of young calves documented in the past 30 years provides no support for the hypothesis that hypothermia is a common mortality problem. Young calves documented can be born inviable at birth if their dams are severely malnourished. The migratory caribou in North America reached peak numbers in the 1980's after wolf populations were heavily harvested in the 1970's. The sedentary ecotype is frequently regulated by wolf predation that affects both recruitment (R) and the mortality of adults (M). The balance between R/M schedules commonly occurs when R (calves) represents, about 15% of the herd and when numbers (prorated to the area of the dispersed annual range) approximate 0.06 caribou/km^2. Population limitation of migratory herds by predation has occurred in the NWT and in several herds in Alaska but only when wolf densities were > 6.5/1000 km^2. Wolf predation halted the growth of the George River Herd in 1980 but then wolves contracted rabies and the herd again increased and degraded spring/summer ranges. The reduced summer phytomass resulted in lower birth rates and increased the vulnerability of calves and possibly adults to wolf predation. Stabilizing mechanisms for migratory herds include movements between herds above tree line and range contractions/expansions with resultant changes in demography. It is hypothesized that the most important ecological variable in all seasonal distributions of caribou is predation risk rather than to maximize forage supplies.

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Introduction

In this paper I will review the literature on the classical limiting factors for caribou of food supplies (both winter and summer), weather, and predation. To give the paper more life I will include some unpublished results from the three long terms studies I have been involved with: (1) the Slate Islands Herd on Lake Superior where there are no predators (the experimental herd), 1974 to present, (2) the Pukaskwa National Park Herd also adjacent to Lake Superior where wolves are present (the control herd), 1974-1988, and the George River Herd in Ungava where wolves are also present, 1974-1993.

Migratory/Sedentary ecotypes

In 1988 I proposed that we drop the woodland/barren ground nomenclature and recognize two ecotypes, sedentary and migratory (Bergerud, 1988a). Sedentary animals are those who stay south of the Arctic tree line and disperse or space out from each other at calving. The migratory mode pertains to those animals where females move to calving grounds north of the tree line (Arctic or alpine) and space away from higher densities of wolves in forested habitats (Bergerud *et al.,* 1984; Bergerud, 1985; Bergerud *et al.,* 1990; Bergerud, 1990). These cows aggregate at calving locations at maximum distances from tree line but where calves can remain cryptic on brown substrates (≤ 75% snow cover at calving) (Bergerud & Page, 1987; Bergerud, 1990). The key factor in distinguishing the two ecotypes is not the length of their migration, nearly all non-insular caribou move locations between winter and calving habitats, but whether the animals are dispersed (spaced out) or aggregated (spaced away) when the young are born.

The migration of cows to calving grounds in April-May cannot be explained by the hypothesis that they are seeking nutritious forage at calving or post-calving. These spring migrations back into winter result in a negative energy balance and weight loss for migratory cows compared to cows that might choose the option of remaining with the bulls farther south following the green phenology north (Russell *et al.,* 1993). The diet quality of cows at parturition is less than that of bulls remaining further south or at lower elevations (Table 1). The weight of calves at birth reflects the condition and weight of their dam (Bergerud, 1975; Cameron *et al.,* 1993) and calf weights are in turn a measure of viability at birth. (Bergerud, 1975; Skogland, 1984; review Cameron *et al.,* 1993). Whitten *et al.* (1992) reported that in the Porcupine Herd 59-74% of the calves that died in three springs within a month of birth (May 27-June 24) did so within 48 hours of birth. These calves that died within 48 hours weighed less than calves that survived this critical period. Thus it is disadvantageous for cows to return to calving grounds prior to green-up on the basis of the intrinsic viability of their neonates. Such a disadvantage can only be compensated by reduced mortality from predation because of a reduced presence of predators on calving grounds (abundance of wolves see Heard & Calef, 1986 and Fig. 1). If the main limiting factor for cows and calves in springtime was nutrition rather than predation risk they could avoid the cost of these long migrations on a winter diet by calving further south and benefiting from an early green phenology. Both the Leaf River and the George

Table 1. Percent nitrogen of caribou at calving compared between males and females on the Slate Islands, Ontario, sharing the same range in spring, and between males and females in migratory herds, segregated at calving by the migration of females to calving grounds. (values in parantheses are sample sizes).

Herd & Collection	Location (Lat°/Long°) and Elevation (m)		km[a] M to F	Percent Fecal Nitrogen[b]		Prob. of No. Diff.
Dates	Females	Males		Females	Males	
Control (Nonmigratory):						
Slate Islands, ONT.						
May 13 - June 7 1985	49/87	49/87	0	3.30 ± 0.165	3.37 ± 0.133	0.7356
	183-212 m	182-212 m		(18)	(26)	
May 20 - June 20 1986	49/87	49/87	0	3.61 ± 0.291	3.74 ± 0.233	0.3574
	183-212 m	183-212 m		(6)	(8)	
June 3 - June 17 1987	49/87	49/87	0	3.23 ± 0.122	3.47 ± 0.133	0.3185
	183-212 m	183-212 m		(21)	(5)	
Experimental (Migratory):						
Delta, AK.	64/147	64/148	50	1.78 ± 0.056	2.32 ± 0.109	0.0001
May 17 - May 26 1984	1200 m	600 m		(20)	(18)	
Fortymile, AK.	65/144	64/143	75	1.99 ± 0.036	2.18 ± 0.079	0.0174
May 27 - June 2 1984	1050 m	725 m		(22)	(10)	
Western Arctic, AK.	69/160	68/159	150	1.98 ± 0.037	2.18 ± 0.027	0.0001
June 6 - June 12 1984	250 m	300 m		(25)	(29)	
Penn Island, ONT.	57/89	57/90	110	1.71 ± 0.034	2.35 ± 0.030	0.0001
May 25 - May 28 1987	< 10 m	< 10 m		(34)	(29)	
George River, QUE.	57/65	56/67	130	1.58 ± 0.032	1.97 ± 0.042	0.0001
June 13 - June 19 1988	1200 m	400 m		(17)	(11)	

[a] Kilometres between locations of Males and Females.

[b] Protein (nitrogen) content is generally acknowledged to determine the nutritive value of forage for ruminants. Caribou select species high in protein in the spring and fecal crude protein has been used to quantify range quality for a variety of ungulates as well as lagomorphs. However, secondary compounds can reduce the digestibility of protein thereby biasing fecal nitrogen determinations. This problem is minimized at the start of the growing season (this study period), because phenols and tannins are at low concentrations.

River herds calved farther south when they were low in numbers and were less conspicuous to predators (personal files, Le Henaff, 1975).

The evidence is now overwhelming that wolf numbers are less on tundra landscapes where there is less alternative prey than in forested habitats (for reviews of wolf numbers see Ballard *et al.*, 1987; Hayes *et al.*, 1989; Fuller, 1989). Wolves that depend heavily on migratory caribou frequently den near the tree line (Kuyt, 1972; Jacobson, 1979; James; 1983; Heard & Williams, 1992; Fig. 1). At such an interface they can maximize their contact with migratory caribou and also find more alternative prey than on the tundra. Caribou cows with young calves should want to maximize their distance from wolves; several of the calving grounds of migratory herds are on the Arctic Coast (Porcupine, Bluenose, Bathurst herds) at the maximum distance that cows could space away from denning wolves and forested habitats.

I propose that the northern boundary of the calving distribution of the sedentary ecotype using forested habitats east of the Rocky Mountains is the presence of muskegs with open water at calving. The open water is needed to reduce predation risk. In Ungava the northern boundary of 505 calving locations of dispersed cows was distributed between the June 1 and June 15 isotherms for the spring breakup of large lakes (Fig. 2). The small muskegs ponds in Ungava where caribou calve are free of ice about two weeks before the large lakes; hence the

Table 2. Correlation matrix of possible parameters that might relate to winter starvation on the Slate Islands (First figure is correlation coefficient, then the probalitity and number of years as n).

	(1) Dead caribou	(2) Fall weights	(3) Spring weights	(4) March snow	(5) Fall density	(6) Start growing[a]	(7) Days growing[b]	(8) Lichen g/m^2	(9) Blowdown trees/Km
(1) Spring dead		-0.0727	-0.580	-0.064	0.609	0.590	-0.580	0.023	-0.076
caribou/Km^2	--	0.002	0.172	0.844	0.009	0.056	0.062	0.938	0.797
(Y_2)		15	7	12	17	11	11	14	14
(2) Fall weight			0.464	-0.379	-0.480	-0.764	0.713	-0.038	-0.129
females		--	0.354	0.281	0.082	0.006	0.014	0.911	0.723
(Y_1)			6	10	14	11	11	11	10
(3) Spring weight				-0.680	-0.821	-0.337	-0.255	0.806	0.689
females			--	0.207	0.024	0.781	0.836	0.100	-.198
(Y_2)				5	7	3	3	5	5
(4) March snow					-0.086	-0.258	-0.035	0.192	0.105
depth				--	0.791	0.576	0.941	0.595	0.787
(Y_2)					12	7	7	10	9
(5) Fall density						0.400	-0.191	-0.023	-0.0007
/Km^2					--	0.252	0.599	0.941	0.998
(Y_1)						10	10	13	13
(6) Start growing							-0.858	-0.190	0.356
season						--	0.0007	0.653	0.433
(Y_1)							11	8	7
(7) Total days								-0.143	-0.685
growing season							--	0.736	0.892
(Y_1)								8	7
(8) Spring lichen									0.767
litter g/m^2								--	0.002
(Y_2)									13
(9) Spring blowdown									
trees/Km									
(Y_2)									

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[a] The start of the growing seasons was based on the date the mean temperature on the Slate Island $\geq$ 6.11 °C. Growing seasons have not been determined at this time for years after 1985.

[b] The lenght of the growing season was the total days after temperatures averaged $\geq$ 6.11 °C until leaf fall of the major deciduous trees.

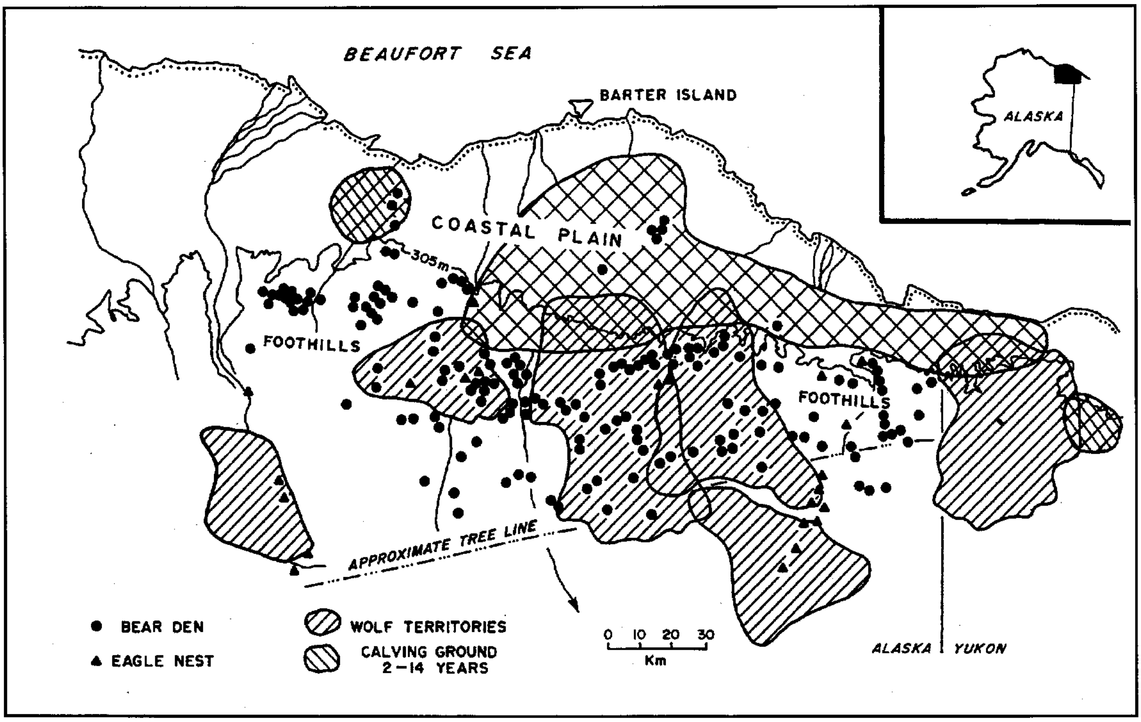

Fig. 1. The composite distribution of the calving grounds of the Porcupine Herd 1972-85. Also shown are indexes to the distribution of the 3 primary predators, wolves, golden eagles (*Aquila chrysaetas*) and grizzly bears (*Ursus arctos*)1982-85. The territories of the wolves in 1985 was mostly near tree line and in the foothills (92%) and the territories overlapped only 17% of the area of concentrated calving. The actual den sites or areas of concentrated summer activity were > 25 km from the southern edge of the calving distribution. The density of the wolves in 1984 and 1985 was very low, 1.4/1000km^2. Adapted from Garner & Reynolds (1986.)

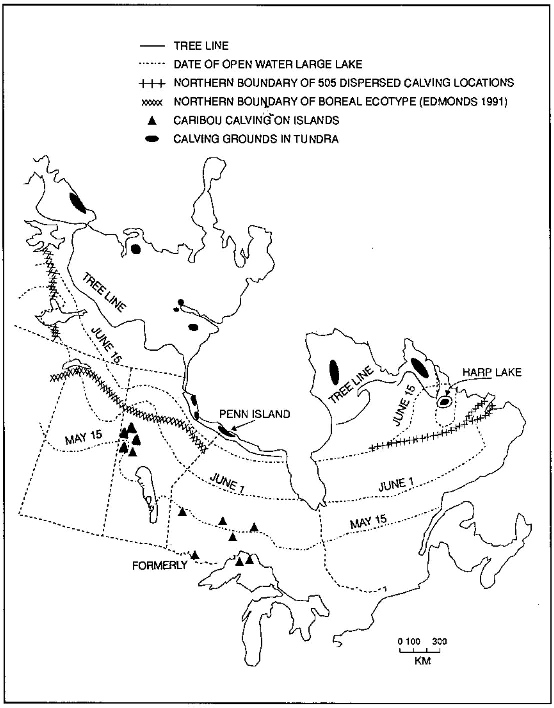

Fig. 2. The northern limit of the sedentary ecotype coincides with the presence of open water in small water bodies at calving. Winter aggregations may be found north of this line. Note there are three distinct tundra areas in Ungava and there are three calving grounds. The open water hypothesis was tested by flying lines north and south from Goose Bay across the Red Wine Herd (sedentary - open water present) and across the Harp Lake calving grounds (migratory - lakes frozen). The Penn Island is a herd that winters in Manitoba and migrates to a calving ground on the coastal tundra in Ontario, north of open waters. Migratory herds when they are high in numbers come south to the northern limit of the sedentary calving distribution.

northern limit of open water in small ponds coincides with the northern limit of calving. The northern boundary of the boreal ecotype (sedentary) in Manitoba and Saskatchewan based on Edmonds (1991) also coincides with the presence of open water in small ponds at calving time (Fig. 2). Since the migratory ecotype only calves north of tree line, there is a broad belt of 400-500 km in central and eastern Canada without calving animals. When the migratory herds are low in numbers they only come south in the winter to within 150-200 km of this northern limit of dispersed calving (see maps in Parker, 1972; and Messier *et al.*, 1988). The common characteristics of the area between tree line and the dispersed ecotype that I believe makes this region unsuitable for calving are the lack of escape water, the lack of mountains and the lack of extensive tundra.

In Newfoundland animals aggregate on calving grounds despite the fact that open water is present. Dispersed calving (spacing out) is a hiding tactic which reduces encounter rates with predators that cannot be left behind by long migrations. However if the animals are easily found because of level open habitats and reduced migration space then they should use tactics of grouping to reduce risk after being detected (Bergerud & Page, 1987). The selection of small water habitats is predicted only within the context of being lost in space; first reduce encounter rates but if this doesn't work have water available as escape habitat.

West of the Rocky Mountains habitats with open water at calving are rare and the animals either disperse to rugged terrain (sedentary ecotype) or aggregate at calving grounds on level plateaus above a alpine tree line or migrate to calving grounds north of the Arctic tree line. If flat treeless plateaus are interspaced with rugged topography both ecotypes should occur and this has been documented for the Denali and Nelchina herds in Alaska (Pitcher, 1983; Adams *et al.*, in press). The Yanert Herd in Alaska is dispersed adjacent to the aggregated Delta Herd (pers. obs.). Predation risk as determined by the habitat options is the precursor to the choice of strategies (ecotypes) .

Limiting factors

Food Supplies

Leopold & Darling (1953), Edwards (1954) and later Scotter (1964, 1967) argued that an increase in forest fires could have caused caribou declines through reduced food supplies and Scotter further felt the reduced lichen pastures would prevent caribou in the Northwest Territories from increasing in the late 1960's. These authors never presented any statistics showing that reduced lichen supplies had adversely affected either birth or survival rates. In fact forest fires had not increased in Alaska and the N.W.T. 1940-70 (Bergerud, 1983a) nor were rates-of-burning correlated with fluctuations in caribou numbers (Bergerud, 1983a) and the herds increased in the 1970's reaching high numbers in the 1980's (Bergerud, 1988a). Skoog (1968) and Bergerud (1974b) argued that winter lichens were not necessary nor did they drive population dynamics.

If the density-dependent or absolute abundance of lichens can regulate numbers then it should be apparent in the starvation of animals in the two herds in North America with the highest densities. The highest density of the sedentary ecotype in North America is on the Slate Islands, Ontario (36 km^2); densities there have exceeded 5/km^2 since 1974 and probably much earlier (see Cringan, 1956). This herd lives under a closed canopy and the primary winter foods are lichen supplies on rocks, on the bark of trees such as paper birch (*Betula papyrifera*) and arboreal lichens that blow down in winter from above the 2 meter browse line. Caribou in this herd commonly die from falling off cliffs when reaching for lichen supplies and also from hanging themselves in birch trees when

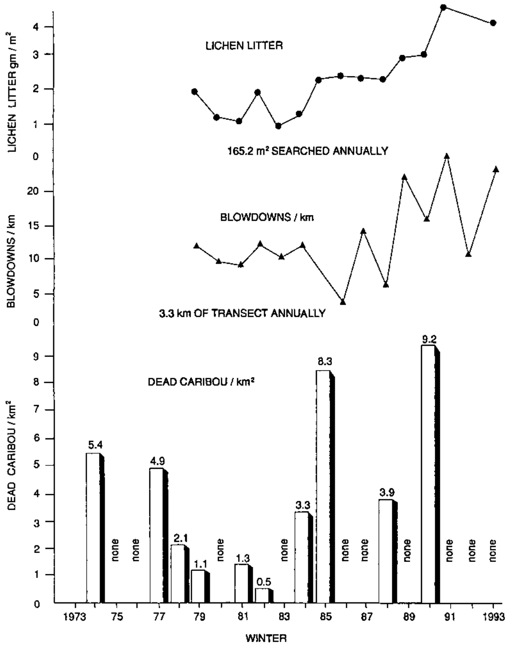

Fig. 3. The caribou that died/km^2 found on the Slate Islands by strip censuses in May-June (below) was not correlated with the number of trees that blew down with lichen loads counted the following spring (middle) nor with the lichen litter found in exclosures in the spring. More lichens are blowing down annually as the forests get older.

reaching and jumping for lichens. Lichen supplies for this herd are extremely meagre (Fig. 3, Bergerud, 1983a). The winter die-offs of this herd, as many as 9 dead caribou/km^2, were not correlated with the variations in winter lichen supplies, as indexed by measuring lichen litter fall (lichens that fell into exclosures) nor the abundance of trees with arboreal lichens uprooted or broken-off in winter storms (Fig. 3, Table 2). Nor were the die-offs correlated with winter snow depths (Table 2. Snow depths in 12 winters in March averaged only 61 ± 4.45cm and were usually similar between winters (CV was 25%). The severity of the winter starvation losses were correlated with the number of animals that entered the winter period (Table 2), but this correlation could reflect forage problems in the summer predisposing animals to winter losses quite independent of winter density interactions or lichens supplies in the winter.

The summer forage on the Slate Islands has also been greatly reduced; we have been unable to find a number of herbaceous species reported by Cringan in 1949 (Cringan, 1956). There has been no successful regeneration in the past 20 years of the four dominant deciduous tree species {paper birch, mountain maple (*Acer spicatum)* mountain ash (*Sorbus americana*), and aspen (*Populus tremuloides*)} except on cliff exclosures.. We have measured the green phytomass (leaves of shrubs and herb of utilized species) several times since 1974. The most recent tabulations were: May 17-23 1994 --31.1 g dry weight in exclosures (total phytomass in 20 m^2) and 3.8 g (12%) outside (20 m^2), May 26-June 1--13.6 g in exclosures (20 m^2) and 2.2 g (16%) outside (20 m^2), and June 10-14--22.9 g in exclosures (20 m^2) and 3.5 g/m^2 (15%) outside (20 m^2). The shrub and herb stratas have been severely depleted on the islands and this was most noticeable in summers of high numbers (> 10 animals/km^2)

The extent of the winter die-offs on the Slate Islands was correlated with the fall density of animals, the fall weight of adult females, and the length of the growing season preceding the winter die-off (Table 2). These correlations indicate that the density regulating factor for this population living without predators was the abundance of summer foods.

The highest density of the migratory ecotype in North America was the George River Herd 1984-88 (Crete *et al.*, 1991) (Table 3) where winter densities prorated to the annual winter ranges ≥ 2/km. I measured the lichen stands on the winter range in the summer of 1988 (Bergerud, 1988b) by recording the percent lichen cover disturbed (thalli lying horizontally or shattered) and undisturbed, and recording lichen heights between disturbed and undisturbed and also on rock exclosures. Only 11 ± 1.53 % (*n*=39 stations) of the lichen cover had been disturbed or shattered on winter ranges below tree line and 32 ± 3.29% (*n*=19) on ranges used in fall migration and early winter. The percent lichen phytomass removed from the cryptogam was 9 ± 2.31% (*n*=24) for winter ranges and 26 ± % 4.43 (*n*=18) for migration ranges. Thus major lichen supplies remained.

The animals in this herd were not malnourished in the spring. The percent bone marrow fat in the leg bones for this herd following migration from winter ranges in April (1976 to 1992) has averaged

Table 3. A comparison of the densities above and below treeline[a] for the major migratory herds in North America.

	Recent Maximum Population estimate	Kilometres (1000)		Density caribou/km^2 [b]	
		below treeline	above treeline	below treeline	above treeline
George River	650,000	429	47[c]	1.5	13.8
Leaf River	250,000	179[d]	246	1.4	1.0
Kaminuriak	236,000	314	103	0.8	2.3
Beverly	335,000	362	152	0.9	2.2
Bathurst	385,000	232	208	1.7	1.9
Blue Nose	120,000	90	130	1.3	0.9
Porcupine	178,000	259	44	0.7	4.4
Western Arctic	500,000	117	206	4.3	2.4

[a] Treeline in Canada based on Rowe 1959 and in Alaska on map National Geographic June 1956 Vol CIX, No. 6.

[b] The densities are based on the use of the entire range at maximum numbers . Actual densities would be much higher.

[c] Includes only the tundra used in the summer in Eastern Labrador and excludes much of the Torngat Mountains that were not visited. George River animals also used the western tundra north of the Leaf River (129,000 km^2) but only in the winter (mostly March).

[d] The extend of the range below treeline should increase as the herd continues to increase.

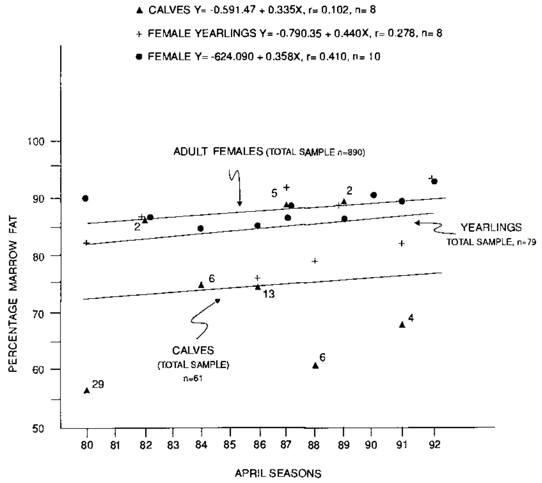

Fig. 4. The percentage of bone marrow fat in leg bones of caribou in the George River Herd from 1980 to 1992 showed no trend as the herd increased. Collections were in April (generally west of Nain) after the animals had migrated back to the tundra. The 1980 figures are from Parker (1981).

annually 87% for adult females, 84% for female yearlings and 74% for female and male calves (Fig. 4). These percentages showed no trend as the herd increased from 176,000 animals to 600,000 (Fig. 4). Animals in this herd have not starved in the winter despite the fact that this herd faces the greatest snow depths of any migratory herd in Canada (Thomas, 1953). And certainly the burning rate on the herd's winter range has not been atypical for the boreal forest; Payette *et al.* (1989) reported 19.7 % of the area below tree line burned, 1944-84, and Couturier & St. Martin (1990), 16.5%, 1972-89.

On the other hand the summer foods for the George River herd above tree line in 1988 had been decimated. The percentage of birch (*Betula glandulosa*) dead was 34 ±3.67 (n=23), and the percentage of the ground covered in turf created by caribou was 20 ± 2.23 (n=23). A comparison of plant abundance along the George River in 1975 vs 1993 showed that tundra shrubs had declined by 70.5 ± 5.10% (n=8 species) at one station and had declined by 57.4 ± 9.60% (n=10 species) at another location. In 1975 24 species of forbs were found and in 1993 only 11. The density of the animals in this herd on the calving ground, along the George River, and in the insect relief habitat on the coast has been in the order of > 12 animals per km^2 1984-88. Our results indicated that 37,000km^2 had been degraded and landsat imagery showed a thrashed June/July range of 46,000 km^2 (Anonymous, 1992).

This degradation of summer range should not be extrapolated to other herds since the George River has the smallest summer area north of tree line of any of the large migratory herds in North America except the Porcupine Herd (Table 3). However the Nelchina Herd probably had similar high summer densities (> 10/km^2) at peak numbers in 1962 and the mandible lengths in this herd, similarly to the George River (Couturier *et al.*, 1989), were reduced in length from when there were fewer animals (Valkenburg *et al.*, 1991)

Overwinter Weight Loss and Starvation

Consider that there is a threshold weight that results in starvation. The mean spring weight of females on the Slate Islands in 5 years when animals died the previous winter was 78.1 ± 0.63 kg and in three springs following good winter survival was 87.2 ± 0.81 kg. These animals needed to maintain weights greater than 75-80 kg to successfully overwinter. In the fall of 1989 the females averaged only 79.5 ± 0.78 kg already at the threshold starvation weight, and the meagre lichen supplies latter would not matter. The higher the weights are in the fall the less likely the animals will reach the starvation level. Hence winter lichen supplies may affect the slope of the overwinter weight change but their availability could still be density independent.

The July-August weight of females on the George River in high density years commonly reached lows of 70 kg and some females died in the summer. But animals in this herd left the degraded June-July range in August and crossed the tree line where they were able to gain weight prior to deep snows. This weight gain plus adequate winter lichen supplies resulted in weights higher in April than October (Huot & Goudreault, 1985) and above the starvation threshold.

Adult caribou on Coats Island, N.W.T. starved in the winters of 1974-75 and 1979-80 (Gates *et al.*, 1986). Gates *et al.*, felt this starvation was density independent but Ouellet *et al.*, (in press) implied it was density dependent and Heard & Ouellet (1992) stated for the Coats population that the effect of weather in causing starvation was not independent of density.

I think the animals on Coats had some forage problems similar to the Slate Islands. Originally the Coats animals in the 1970's had large body sizes and antlers (Parker, 1975); this sequence also occurred on the Slate Islands (Butler & Bergerud, 1978). Both islands had no predators and also few insects. Conditions for summer growth and reproduction must have been excellent. Further both populations had substandard lichen stands prior to high densities (Cringan, 1956; Parker, 1975). Ultimately high densities in both situations reduced these stands even further. Summer foods were reduced on the

Slate Islands and I hypothesize also on Coats Island; caribou on Coats Island weighed less than animals on nearby Southhampton Island in the fall of 1983 (Gates, pers. comm.). Animals in both populations died in the winter when summer numbers where high and the already meagre lichen supplies were generally unavailable because of snow cover on Coats Island and lack of winter storms on the Slate Islands.

But my argument is that starvation in both cases is density independent of winter forage abundance and nonregulatory. Lichens grow so slowly that once they are reduced by high numbers they cannot show annual responses to rapidly changing animal numbers. However summer vascular foods can respond rapidly and their annual abundances are not masked as is the case for lichens by snow cover. Note that all the authors reported that the Coats population made major summer recoveries following density reductions after the die-offs. On the Slate Island the highest fall weights occurred after the two greatest die-offs; females in the fall of 1985 weighed 106.4 ± 5.82 kg and in 1990 101.1 ± 0.87 kg. The mean weight of females in 15 autumns was 93.8 ± 1.86 kg and was significantly correlated with spring numbers (r=-0.571, P = 0.026).

Thomas (1980) said "most biologists agree that available forage on winter ranges is the key factor governing the potential upper limit of population size (Klein, 1970)". We have had it wrong for the past 30 years. The annual abundances of winter lichens are density independent and do not determine carrying capacity. We must finally reject the critical winter range hypothesis.

But summer forage resources can have serious density-dependent consequences on demography contrary to my earlier view (Bergerud, 1980), if densities in June-July exceed 10 animals/km^2. In the George River herd pregnancy/parous percentages for 15 years were negatively correlated with July densities (r=-0.861, P<0.01) (pers files) also Messier *et al.*, 1988; Couturier *et al.*, 1990). Annual mortality rates of adult females have increased from 10-11% in 1984 to 17-19% in 1992-93 (Messier *et al.*, 1988; Hearn *et al.*, 1990; Crête *et al.*, in press). These consequences are compounded because the migratory ecotype is prepared, similar to the sedentary ecotype, to sacrifice high quality foraging, to remain in habitats above tree line with low predation risk. Forage selection will occur in the summer but only within the options provided by the low risk habitats (see Ferguson *et al.*, 1988).

Table 4. Percentage of calves in the Northwest Territories herds in late winter between years when there was light precipitation in the spring vs heavy precipitation.

Low Precipitation < 12 mm			High Precipitation > 12 mm		
Year	Precipitation (mm)	Percent[a] Calves	Year	Precipitation (mm)	Percent Calves
1949	6.9	16.4	1950	12.5	7.6[b]
1953	2.0	15.4	1951	31.2	11.0[b]
1954	8.1	12.2	1952	17.0	26.6
1956	1.5	8.0	1955	44.5	6.9
1957	7.1	11.3	1958	14.7	20.0[b]
1959	10.8	25.0	1967	22.9	10.0[b]
1960	2.3	21.5	1971	15.0	19.0
1966	0.3	10.5	1977	20.3	23.0[b]
1968	2.5	11.4	1978	17.5	13.5[b]
1972	9.9	10.3	1979	37.9	28.0
1980	6.9	18.5	1981	20.3	25.5[b]
1982	2.8	21.0			
1983	10.7	21.0			
Mean	5.5±1.04	15.6±1.50		23.7±3.13	17.4±2.38

[a] Average percent calves for Kaminuriak and Beverly herds; no corrections made for unrepresentative proportions of male and female adults.

[b] Cold years when mean minimum temp. < -2.0 °C (mean cold wet years = 15.7 ± 2.59).

Weather/climate hypotheses

Hypothermia

Another population limitation hypothesis that dates back to the 1960's and is apparently still supported (Klein, 1991) is that inclement weather can cause hypothermia of newborn calves resulting in major mortalities (de Vos, 1960; Pruitt, 1961; Kelsall, 1968). The original evidence was the finding of the intact remains of young calves often in clumps. In one case the remains were not located until the following year. Miller *et al.* (1988) studied the early mortality of 287 calves in 3 years on the Beverly Herd and found calves were not dying from hypothermia but instead the chief cause was wolf predation. They stated that not a single calfs death during the 3 years of this study could be linked directly or indirectly to exposure to adverse weather. The wolves often killed several calves on one occasion and frequently consumed none or little of the carcass. These workers felt that surplus killing was the explanation for the majority of the deaths formerly attributed to hypothermia (Miller *et al.*, 1985).

I have been with caribou during 25 calving seasons which includes herds in Newfoundland in the freeze/thaw zone and herds in the Arctic (Western Arctic, Kaminuriak, Bathurst and George River) where snowstorms and high winds are common. I have not found calves that died from exposure. Skogland (1989) watched caribou calving in 17 springs in Norway and Svalbard and reported no exposure deaths with the possible exception of one calf in Svalbard. The calves in Svalbard weigh only 3-4 kg at birth (Tyler, 1987). Radio collars have been placed on 615 newborn calves in 4 herds with only one reported weather related death (Page, 1985; Mahoney *et al.*, 1990; Adams *et al.*, (in press) and Whitten *et al.*, 1992). A comparison of the percentage calves in the N.W.T. in the winter following cold/wet springs vs moderate springs for 25 cohorts showed no correlations with weather (Table 4): the correlation with mean min. Temp June 1-20 $r = 0.299$, $n = 25$, and total precipitation $r = 0.084$, $n = 24$. In years when there was heavy precipitation (> 10.7 mm) and it was cold < -2.0 °C) the calf percentages were 15.7 ± 2.59 ($n = 7$) not significantly different from the mean of all years 16.4 ± 1.34 ($n = 24$) (Table 4) .

Possibly wolves may be more successful killing young calves during snowstorms with reduced visibility (Kelsall, 1968). Still wolves have no difficulty, killing large numbers of calves on calving grounds at any time. Lo Camps (biologist) observed 3 wolves as they killed 11 2-week old calves in 84 minutes on the George River, July 2,1991. As with the case of density-dependent winter starvation, we must discard the hypothermia hypothesis; a hypothesis that once was exciting but has not stood the test of time. Miller & Gunn (1986) stated that caribou biologists have no sound basis for assuming that adverse weather frequently causes major loss of newborn barren-ground caribou.

Weather Cycles

Klein (1991) proposed that the synchrony of population fluctuations in the past two decades is most parsimoniously explained on the basis of continental wide weather patterns. He provided no mechanism on how weather could drive demography.

Table 5. The mean annual harvests of wolves by 5 year winter intervals.

Time	Mean Annual Harvest [a, b]				
Period	N.W.T.	Manitoba	Saskatchewan	Alaska	Yukon
1940-45	579	too high	619	455	285
1945-50	671	359	241	389	42
1950-55	479	284	53	898	40
1955-60	267[c]	131	27	595	21
1960-65	186	143	50	632	56
1965-70	400	155	107	1486	55
1970-75	807	314	234	1020	136
1975-80	805	397	257	934	123
1980-84[d]	537	415	227	589	132

[a] Source: Novak *et al.*, 1987.

[b] Ontario and Quebec not included because of recent northern and eastern extension of coyotes (*Canis latrans*) and confusion with wolves in harvest statistics.

[c] Many more taken with control (see Heard, 1983).

[d] 1984-85 not available.

All the large migratory herds in the world were increasing in the 1980's and peak numbers were probably reached in that decade (Bergerud, 1988a). At the same time the sedentary populations were declining world-wide. But synchrony in growth phases in other decades has not been the case for the migratory herds in the past (Skoog, 1968; Thomas, 1980) nor does it now prevail, since several major herds are now out-of-step in Alaska, N.W.T., and Ungava.

An alternate explanation for the increase in the migratory herds in the 1980's is Man's influence on predator-prey interactions. First in the 1950's we had synchronous wolf reduction programs in Alaska and Canada; then control ceased coincidentally. Then the skidoo was introduced into the North in the late 1960's profoundly increasing the harvest of wolves above tree line. Now we have a worldwide boycott of wild furs. Peak caribou numbers in the 1980's followed the increased harvest of northern wolves (Table 5).

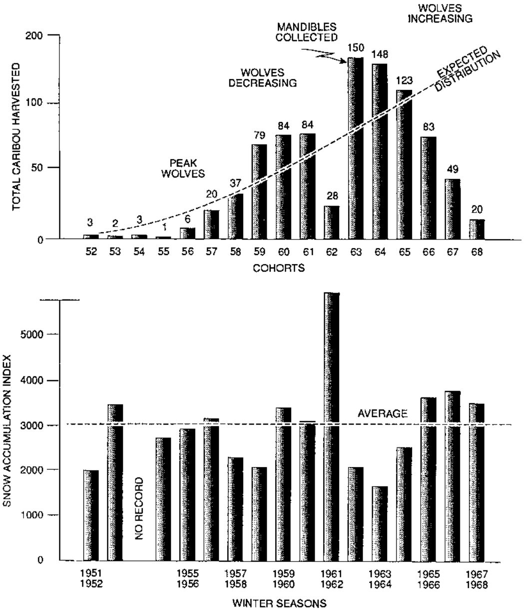

Fig. 5. The size of the 1952 to 1968 cohorts of the Kaminuriak Herd taken from Miller, 1974:Fig. 21. The 1967 and 1968 cohorts are under represented by the collection schedule. The 1962 cohort is far less than expected and follows the worst winter in 16 years (below) when dead animals were observed (Kelsall, 1968). Also shown above is the expected age distribution based on animals collected by Thomas & Barry (1980) from the adjacent Beverly Herd (age array smoothed by Taylor, 1991). Wolf numbers decreased for the Beverly Herd 1955 to 1961 from control (Kelsall, 1968) and then increased.

Weather and Fetal Malnutrition

Calves may be inviable at birth if their dams are severely malnourished during gestation. Such mortalities could be confounded with deaths from hypothermia or surplus killing. Calves of low viability were probably born in the N.W.T. in 1962. The winter snowfall in 1961-62 was by far the most severe in 16 years (Fig. 5, Dauphine, 1976). Kelsall (1968) reported that adults starved. The 1962 cohort had the lowest survival of 12 cohorts analyzed by Miller (1974) (Fig. 5) and males were more common than females for that cohort. Yet spring temperatures and precipitation were favorable in June 1962 and wolves were probably at an all time low following 11 years of control (See Heard, 1983: p.44). The loss of this cohort just when calf survival was expected to be highest may have confounded an evaluation of the importance of the wolf reduction programs on herd growth. In Alaska the Nelchina Herd declined after 1962 when three cohorts (1964, 1965, and 1966) had low survival (Bergerud & Ballard, 1988). These three cohorts were born at lower elevations than in other years and nearer to predators, but these calves may also have had low birth weights because of their dam's winter nutrition and been more vulnerable to predation.

A relationship between female malnutrition and calf viability is also suggested from our Slate Island work. In the spring of 1985 after a very extensive die-off (Fig. 3) we found the legs of extremely small calves that had no wear on their hooves at fox (*Vulpes vulpes*) dens; these calves may never have stood and nursed. Calf recruitment in the fall of 1985 was 10.7% calves (*n* = 291) compared to a mean of 14.4 ± 1.28 % in 10 other autumns.

A fourth example of calves of low viability is from the George River Herd in 1992. Calves born in 1992 were very small, a mean birth weight of 4.7kg (*n* = 80) (S. Couturier, pers. comm.) 2 kg less than that recorded in 5 other years. Couturier noted many dead calves. We estimated calf mortality in 1992 at about 2 weeks of age at 20%, based on cows with regressing udders not followed by calves (*n* = 308 cows) (udder counts corrected for cows with small udders still nursing yearlings); the mean mortality of calves of this age in 8 other years was 6.6 ±1.24% (mean sample size of females 2,406 ± 578). The growing season in 1992 was the latest on record in 37 years; the ice did not go out of Knob Lake, Schefferville until June 29, the mean date of breakup from 1955 to 1993 was June 13 (the previous extremes were May 28, 1959 and June 25, 1972 (McGill Research Station records). Cows in 1992 did not switch to new birch growth until July 8 about 2 weeks later than in the four previous years.

In this spring we actually had a cow with a calf swim a river in front of the crew and then fall down and die.

Weather is not Regulatory

At this conference it has been shown that winters with deep snow have played a role in the recent declines of caribou of the Alaska Range 1991-94. Reduced nutrition from a relative food shortage has lowered conception rates and increased winter and summer mortality rates of adults and calves (Boertje *et al.,* 1993; Valkenburg, 1994; Adams *et al.,* in press). Both caribou at high densities as in the Delta Herd (0.9/km^2) and at low densities as in the Denali Herd (0.4/km^2) have been affected.

Winter snow depths are not an ultimate explanation in the *sensu* of Lack (1954). Ultimate factors are those that drive survival in an evolutionary sense whereas proximate factors are behaviour and physiological influences that modify ultimate factors. For example the ultimate regulatory factor for wolves is their prey biomass (Keith, 1983; Fuller, 1989). But the proximate adaptation that influences how the ultimate factor operates is territorial behaviour (see Packard & Mech, 1983).

Weather is density independent hence not regulatory. Weather can only cause death as an interaction since animals don't die directly from exposure, if in good nutrition (and or in the absence of predation). Both starvation and predation may be density dependent and regulatory; weather alone cannot. Hence weather is not a sufficient mortality factor, either nutrition or predation are necessary interactions to bring death and influence population dynamics. Caribou and wolves are in a predator x prey adaptive race with the extrinsic environment the arena. At times weather favors the prey and at other times the predator in this dynamic competition.

We should distinguish between climate and weather. There have been long term climatic trends such as the Little Ice Age that have modified the distribution and abundance of caribou. I am sure we are all concerned about the potential for disaster if there is a global warming trend. Deer (*Odocoileus virginianus*) and moose (*Alces alces*) would expand north bringing increased disease and predation to sedentary herds and increased freezing/thawing patterns would cause high mortality to Arctic Island herds. However such major changes are the pages of time.

Natural predation

I proposed in 1967 that wolf predation might regulate the numbers of the George River Herd (Bergerud, 1967) and later expanded this hypothesis to other herds but was more cautious by using the words limiting factor rather than regulation (Bergerud, 1974b). To make the hypothesis more specific and testable Bergerud & Elliot (1986) predicted that wolves would halt herd increases if wolf numbers exceeded 6.5/1000 km^2. The recruitment needed to stabilize numbers (R_S) in the 1986 paper was 12 % calves (sedentary and migratory ecotypes). A later analysis indicated that R_S for only sedentary herds was closer to 15% (25 calves/100 females) the finite-rate-of-increase regressed on percentage of calves was $Y = 0.757 + 0.016X$, $r = 0.737$, $n=32$ (Bergerud, 1992).

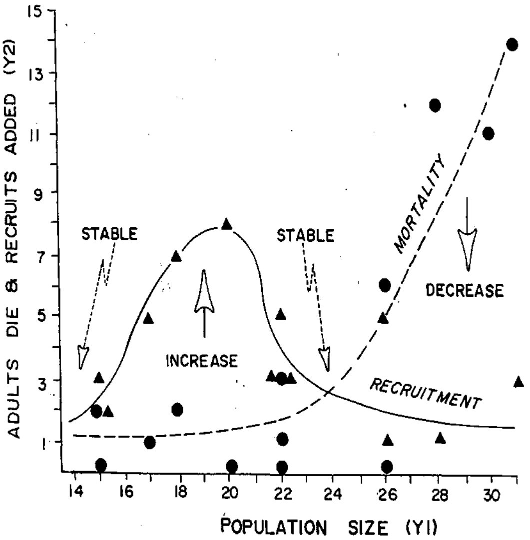

Fig. 6. The upper and lower stabilizing numbers (R = M) for the Pukaskwa National Park (1974-87) a herd of < 35 animals that lives along the coast of Lake Superior, Ontario. The major cause of adult mortality was wolf predation. The cause of calf mortality is not known but calf survival has been high on Otter Island in the presence of lynx, and bears are rare along the coast.

The predicted density of 6.5 wolves/1000 km^2 postulated to halt growth has been useful. Herds when faced with < 6.5 wolves/1000 km^2 have generally increased in recent years (Western Arctic, Central Arctic, Porcupine, Blue Nose, Leaf River and George River herds). Herds when they were exposed to ≥ 6.5/1000 km^2 wolves have remained stable or declined (Finlayson, Denali, Quesnel, Pukaskwa, Tweedsmuir). For example wolves in the Denali Herd reached 7.0-8.0/1000 km^2 in 1989 and 1990 and the herd declined from 1990 to 1991 (Adams *et al.,* in press). A major exception to the 6.5/1000 km^2 yardstick was the Delta Herd where wolves reached ≥ 10/km^2 but caribou still increased and the wolves may have continued to hunt mostly moose.

Sedentary Herds

The sedentary herd that I have examined (1974-87) relative to predation regulation is in Pukaskwa Park, Ontario (Bergerud, 1985; Bergerud, 1989). This herd of less than 35 animals resides in a 2 km strip along the coast (or at density of about 0.06/km^2) near water escape habitat whereas moose and wolves are more common inland (Bergerud *et al.*, 1983). The percentage of calves in the herd in late winter (Y_2) declined as total numbers increased in Y_1, $r = -0.681$, ($n = 11$) or $r = -0.828$ ($n = 12$) . The annual percent mortality of adults was also density dependent on total numbers ($r = 0.757$ $P < 0.05$ ($n = 13$) . In the winter of 1993-94, 3 of the 4 tagged cows in the herd were killed by wolves. Recruitment in this herd equalled adult mortality at a lower stabilizing number of 14 animals and at a upper stabilizing herd size of 24 (Fig. 6). When we modeled this system by reducing the wolves the caribou went extinct because with less wolves the moose increased beyond 0.2-0.3/km^2 which ultimately permitted many more wolves in the system (wolf biomass modelled after Fuller, 1989).

This predator x prey system was complexed by snow and ice, density independent processes, that changed the distribution of moose. The wolves in the Park hunted mostly moose inland (Bergerud *et al.,* 1983) but even when on the coast they still spent more time searching for moose rather than caribou; the correlations in the distributions of moose, caribou, and wolves on the coast in 15 years in 26 4km^2 blocks adjacent to the shore were: moose and caribou $r = -0.0702$ ($P = 0.734$), caribou and wolves $r = -0.1042$, ($P = 0.613$), and moose and wolves $r = 0.4257$, ($P = 0.032$). But when the moose moved towards the coast with deep snows the wolves did likewise (the regressions of mean annual km from shoreline of aggregations or tracks seen vs snow depths were for moose, $Y = 85.28/(12.49 + X)$, $r = 0.666$, $n = 13$; and for wolves $Y = 1.783 - 0.021X$, $r = 0.578$, $n = 13$. This shift of moose and wolves compromised the displacement of the caribou. Additionally there was generally more landfast ice in winters with deep snows; this landfast ice in Lake Superior reduced the opportunity for caribou to escape to water and further facilitated the searching of wolves along the coast.

The majority of the other sedentary herds in North America have similar low densities as those in Pukaskwa (Bergerud, 1992). Generally when herds in North America had densities greater than 0.06/km^2 they were decreasing and when less increasing (27 herds graphed in Bergerud, 1992, page 1011). A regression of the annual recruitments from 9 herds on herd densities that ranged from 0.03 to 0.15/km^2 was $r = -0.646$ ($n = 29$) and a recruitment of 15% (R_S) intersected densities at 0.06/km^2 ($Y = 30/[1 + (1.350X*10^{(0.8565)}$ (Bergerud, 1992) . I termed the density of 0.06/km^2 the stablizing density (D_S)

There now seems to be a consensus by many biologists that predation is the greatest and most consistent cause of natural deaths in these sedentary herds. The concern now is how to preserve sufficient space for these caribou in the face of habitat alienation (primarily logging) so the predators will not be more successful in finding the animals (Bergerud, 1990). The older hypothesis that logging reduced lichens as a necessary food directly precipitating declines is no longer a viable alternative. In fact the thinking has changed so strikingly that when you mention increased forest fires to biologists now, instead of relating fires to reduced lichen supplies, as in the past, these workers may assume you are speaking of how burning drives changes in forest succession and could result in more moose in the system thus more wolves and more predation of caribou (D. Seip, pers.comm.) .

Migratory Herds

However in the case of migratory caribou the role of wolf predation in regulating numbers has been questioned (Kelsall, 1968; Messier *et al.*, 1988; and Klein, 1991). The fluctuations in these herds are of such long duration that density dependant interactions are hard to visualize. And also wolf predation has not halted the growth of several large herds in Alaska in recent times (Davis & Valkenburg, 1991) and in Ungava the George River Herd, overgrazed its summer range.

Back in the 1950's wolves exceeded 7/1000 km^2 in N.W.T. (Kelsall, 1968) and did take sufficient calves at least in the Beverly and Bathurst herds to halt population growth. Late winter calf percentages were less than 12% needed for stability for the 1950, 1951, 1955, 1956, and 1957 cohorts (Kelsall, 1968). The correlation of calf percentages with wolf harvest statistics was $r = -0.633$ ($n = 10$) $P < 0.05$ (Fig.7). The wolf population declined from control after 1955-56 (Fig. 7, Kelsall, 1968). Thomas, (1980) stated, "Kelsall's, (1968) data and subsequent data suggest that the population of the central mainland declined until about 1957 when a pronounced upsurge began."

Parker (1972) concluded for the Kaminuriak Herd that wolf predation was the chief natural limiting factor 1966-68 and the 1966, 1967, and 1968 cohorts were all less than 12% needed to maintain numbers and indeed the herd continued to decline until 1980 (Heard & Calef, 1986). A cohort analysis of this herd from collections 1966-68 compared to the age structure of the Beverly Herd 1980-87,

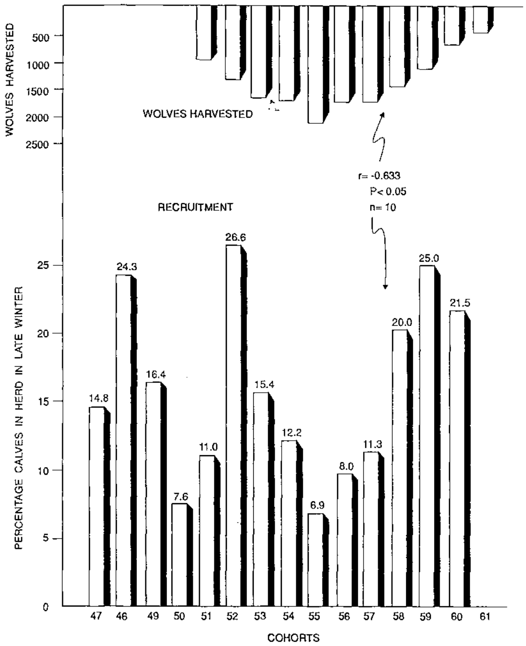

Fig. 7. The late winter recruitment of the caribou in the western herds in the N.W.T. (Kelsall, 1968:Table 18) compared to the estimated harvest of wolves from control (Kelsall, 1968:Fig. 14).

when there was no wolf control (Thomas & Barry, 1990; Taylor, 1991), showed that the 1959, 1960, 1961, 1963, 1964 and 1965 cohorts had more calves than expected and the 1955, 1956, 1957 and 1966 cohorts less than expected (1962 cohort reduced from inviable calves) (Fig. 5). These results are consistent with the changes in the abundance of wolves from the reduction program. If in the future the harvest of wolves in the N.W.T. declines we should again see the limiting effects of predation on these herds.

In Alaska it has not been shown for the herds on the North Slope that wolf predation is regulatory. Wolves there have not exceeded 6.5/1000km^2. These wolves are now heavily hunted from skidoos and there is some history of rabies (Rausch, 1958; James, 1983; Garner & Reynolds, 1986). But for the herds farther south, the Denali, 40-mile, and Nelchina, previous studies have shown that when wolf numbers exceeded 6.5/1000 km^2 recruitment was less than needed to maintain numbers and in the case of the Delta, 40-mile and Nelchina Herds the experimental removal of wolves was followed by sufficient recruitment that allowed the herds to increase.

In Newfoundland the migratory herds have not been regulated by density-dependent predation. The wolves on the Island went extinct in the early 1900's. In their place lynx (*Lynx canadensis*) became the main predator. Lynx reached extremely high numbers following the introduction of snowshoe hares (*Lepus americanus*) into the Province in the late 1800's. Millais (1907:249) said about lynx "Doubtless they were very scarce until recent years, but now are the most abundant of all carnivora... Everywhere one sees their tracks. A good trapper will kill 50-100 in a season." At the same time he said bears had been reduced in numbers. When the hares crashed in their cycles the lynx switched to caribou (Bergerud, 1971) and caused long cycles in calf survival (Bergerud, 1983b). Three cycles documented were 8-9 years duration (Bergerud, 1983b). Lynx predation and overhunting may have caused the decline of the caribou herds in the early 1900's (Bergerud, 1971) but since the 1950's caribou have increased despite this predation, probably because hare numbers drive lynx abundance rather than caribou. By the 1970's lynx had been reduced from trapping (Bergerud, 1983b; Mahoney *et al.*, 1990) and bears (*Ursus americanus*) and lynx were taking similar numbers of calves (Mahoney *et al.*, 1990). Bears had been rare on the calving grounds in the 1950-60's (Bergerud, 1971); I saw two bears in 11 calving seasons and little bear sign. Now bears are a major predator of caribou, perhaps in response to major increases in caribou and moose. But still the herds have had positive growth. The numerical and functional predator responses of bears to caribou prey has not been documented, but bear predation elsewhere has been described as density independent (Boertje *et al.*, 1988). Perhaps the new predator in Newfoundland, the coyote (*Canis latrans*) will regulate numbers, but both lynx and bears while being major limiting factors have not shown density dependence in their predation.

The George River Herd in Ungava increased from 1958 to 1984 at a finite-rate-of-increase of 1.11 (Messier *et al.*, 1988) . Wolf predation did not regulate numbers as the herd grew to > 2/km^2 contrary to what I had hypothesized (Bergerud, 1967). However wolf predation was the most important limiting factor in the growth of the herd 1974-84. The size of the annual cohorts declined each year 1976 to 1980, and adult mortality and calf recruitment were about balanced in 1980 (Fig. 8). Wolf predation in 1980 I argue temporarily halted the growth of the herd while forage was still abundant. The wolves developed rabies in 1980-82 and wolf numbers dropped drastically. No wolves were seen in 6 caribou classification surveys (each flight > 7 days) 1982-84. The mean number seen per survey 1976-80 was 4.8 ± 0.83 and 1984-87 3.3 ± 1.48. The mean pack size 1976-79 prior to the outbreak was 4.4 ± 1.18 (18), during the outbreak 1.7 ± 0.17

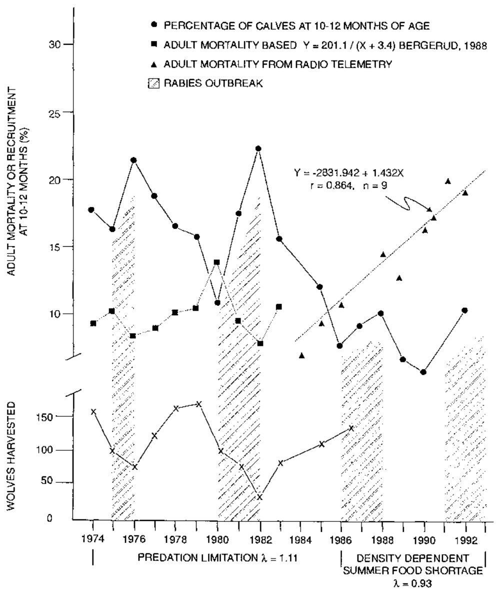

Fig. 8. The recruitment of calves at 10-12 months of age for the George River Herd (1974 to 1992 cohorts) compared to the mortality of adults. Adult mortality 1974 to 1983 is based on Y=201/(X + 3.4), Bergerud, 1988) and is not independent of adult mortality. Adult female mortality 1984-1992 based on Hearn *et al.,* 1990 and Nfld files. Adult male mortality based on $M_m = 1 - [(1-M_f + \beta r)(M_2/F_2 - \alpha r)](F_1/M_1)$ where: M_m= male mortality, M_f = female mortality, r= ratio calves/females, α = fraction of male calves, β= fraction of female calves, F_1 = number of females 1st year, F_2= number of females 2nd year, M_1 = number of males 1st year, M_2 =number of males 2nd year. Formula can be reduced because of constant adult sex ratio to $M_m = M_f + (\alpha F/M - \beta)r$. Wolf harvest figures (below) from Kuujjuaq and Nain. Rabies outbreak based on confirmed (positive) cases in northern canids by government health officials.

(27) and after in 1984-86 4.2 ± 0.67 (10). The harvest of wolves from Nain and Kuujjuaq declined to a low of 30 animals in 1982-83 (Fig. 8). With such a major reduction in wolves the herd escaped the predation limitation and with the addition of the very large 1981 and 1982 cohorts (see age structure in Messier *et al.,* 1988) went on to degrade its June/July habitat and start to decline from unfavorable R/M schedules (Fig.8).

One further comment on the interaction of forage and predation in this herd. The winter mortality of calves from October-November to April-June was positively correlated with July densities (*r* = 0.574, *n*= 18 years, *P* = 0.0127) yet the calves that died overwinter did not starve (Fig. 4). The calves (1984-89) were smaller in body size (Couturier *et al.,* 1989) and should have been more vulnerable to predation. But if the wolves had not been in the system this increased mortality would not have resulted. In cause/effect argument the reduced nutrition is not sufficient for the increased mortality, predation was necessary.

Stabilizing space and mobility

Andrewartha & Birch (1954) told us at the beginning that abundance and distribution were two sides of the same coin, and I have argued in the past that caribou use their mobility and space to successfully cope with wolves. For sedentary caribou the stabilizing mechanisms are easier to visualize; cows seek safe sites alone for calving, show philopatry and dispersion from predators and altemative prey. Spacing strategies of migratory caribou are harder to quantify with the confounding effects of group interactions. For these herds we need to view the herd as the individual that successfully interacts with predators. The calving locations of individually tagged cows in the George River Herd were farther apart between consecutive years than were the centers of the entire calving distributions in the same adjacent years (see also Fancy & Whitten, 1991) Some of the shifts between years depended on snow cover, but it is not clear whether these movements related to maintaining young calves on brown cryptic landscapes or related to locating forage. The herd did continue to show a philopatry to a relatively safe range. I believe that if the abundance of predators changes we should expect changes in calving distributions. The Leaf River herd once calved at 58° N but by 1991 the center was 320 km farther north (60°30′) . (S.Couturier, pers. comm.) .

Movement Between Herd Areas

There can be major movements between caribou herds (Kelsall, 1968; Skoog, 1968). The Kaminuriak Herd was censused at 149,000 animals in 1955 but the herd had declined to 40,000 animals three years later (1957-58) (See review in Parker, 1972). Coincident with this decline Kelsall (1968) noted thousands of caribou migrating west from Dubawnt Lake in July 1956; the animals moved across the range of the Beverly Herd and the Bathurst Herd; some animals continued to the range of the Bluenose Herd. Twenty-five years later the Kaminuriak Herd showed another unexpected change in numbers; it increased from 39,000 in 1980 to 180,000 in 1982; additional counts in 1983 gave > 120,000 animals, 1985 > 200,000 and 1985 > 148,000 caribou (see Heard & Calef, 1986) These two unexpected major changes in the Kaminuriak Herd cannot be wished away by faulting census techniques. Nor could they have come about by internal R/M changes (see Heard & Calef, 1986). If we understand why females calve where they do, we can predict when these traditions should be abandoned and major range shifts within the tundra will result. If in fact these shifts are influenced by the abundance of wolves they could have important stabilizing results.

Range Expansion/Contraction

When caribou numbers are low migratory herds become more sedentary and often remain throughout the year above tree line in their most constant range (the center of habitation, Skoog, 1968; also see Kelsall, 1968). Reproductive performance is enhanced because of a high green phytomass and reduced energy expenditure in travelling. Furthermore animals are spaced away from many wolves near tree line. The great advantage caribou have over wolves is their precocial progeny allowing them to be mobile soon after parturition whereas wolves have helpless young and are tied to dens sites for the spring-early summer. If wolves denned on calving grounds they would be satiated for two weeks and then left stranded when the caribou left, especially if the calving ground had few alternative prey. In winter an advantage to caribou in staying north is the reduced snow depths. With less snow, less energy is spent cratering and the caribou are less impeded in their displacements from wolves. With caribou on the tundra in the winter we could expect the wolves to have a decreasing demography. Difficulties for the wolves could include: (1) the problems in finding caribou (less predictable patterns), (2) choosing between caribou and alternative prey that are near the tree line, (3) and the increased mobility of caribou that would minimize contact time. The predator functional response should be reduced on the tundra compared to that south of the tree line. In the tundra ambush is more difficult, lead-times are enhanced and caribou can group together more quickly and evaluate the predators threat relative to the appropriate evasive action.

The Western Arctic herd in the 1970's an example of a large migratory herd in which a proportion of the herd shifted to a more northern distribution above tree line on the North Slope when its numbers were low. In such a location the herd relied more on shrubs for forage rather than lichens (Davis *et al.*, 1982). Kelsall (1968) provides other examples where large numbers of caribou remained on the tundra in the winter on ranges where shrubs were more common than lichens. Lichens are not necessary even for a relatively large migratory herd.

However the major shortcoming that most ranges above tree line have is a reduced phytomass after leaf fall. Moderate numbers of caribou can successfully cope with this but when numbers grow the reduced phytomass will not hold the herd. When caribou herd numbers expand, the animals spend more time south of tree line and less nutritious lichens dominate the diet. This range expansion south of tree line and nearer to wolves occurs between the end of the insect season and the period of deep snow and is a density dependent food interaction, not social facilitation (pers. files).

The densities of caribou south of tree line for the 8 major migratory herds in the 1980's ranged from 0.7 to 4.3 animals/km^2, mean 1.6 ± 0.41 (densities based on total maximum numbers divided by the maximum range) (Table 3). Within this density range R/M schedules should turn sour, primarily from increased wolf predation. The physical condition of the animals will be reduced resulting from the longer migrations, cratering in deeper snows, possibly summer forage problems, and the less satisfactory winter diet of lichens. Animals should not starve from a density dependent absolute food shortage, but their reduced physical status may increase their vulnerablity to predation. Wolves on these winter ranges can affect both numerical and functional responses when caribou mobility is reduced by cratering for lichens through deep snow. In forested habitats lead times are reduced and ambush is more feasible. The large caribou aggregations provide a highway of trails for wolves (Kelsall, 1968) and the demographic equation moves $R < M$ and retraction begins.

Thus I believe that two major stabilizing mechanisms in migratory caribou fluctuations are (1) major movements between herds especially relative to above tree line distributions and predation pressures and (2) range contractions to above tree line optimum habitats when numbers are low and range expansions when numbers are high into more marginal lichen habitats below tree line. Involved in these stabilizing mechanisms are elements of density dependent regulation by wolves but also a density dependent caribou x food interaction. The important insight is Skoog's (1968) center of habitation hypothesis. These stabilizing mechanisms are final solutions that help buffer major fluctuations. Many other limiting factors can occur at lower numbers so that these processes do not result.

The periodicity and amplitude between these range contractions / expansions hence fluctuations for migratory herds would be in the order of decades. There would be lags because of the caribou x food interaction, the continuum of increasing contact with wolves and lags in wolf demography. For the sedentary caribou there are no lags due to food and total ranges remain stationary as populations rise and decline as the spacing between preparturient females increases and decreases. The time interval between peak numbers in the Pukaskwa herd was 3.5 ± 0.28 years (n = 4) amplitude 1.8. Interestingly the periodicity on the Slate Islands with its caribou x food rather than caribou x wolf interaction was 3.3 ± 0.48 years (n = 4) and the amplitude also about 2 times. In contrast the George River Herd decreased from a high in the 1880's to another one 100 years later with an amplitude of 100 times (Bergerud, 1988b).

Recent census results of the Beverly and the George River herds (N.W.T. news release, Russell, in press) do not agree with predictions from R/M schedules. The Beverly herd should have remained stable (R taken from Williams *et al.*, 1989; and M from Thomas & Barry, 1990; Taylor, 1991) rather than declined and the George River Herd should have had a major decline rather than remained stable. We need to consider that there could have been major lateral movements. In June 1988 4 of 22 (18%) of the radio cows from the Leaf River Herd were found on the George River calving ground and in 1993 2 of 5 (40%) Leaf River cows were with the George River cows (Couturier, *et al.,* in press). My understanding is that wolves are now more common on the range above tree line of the Leaf River Herd than the George River range (S. Luttich, pers comm.); again the Beverly Herd has a history of more wolves on the calving grounds than either of the two adjacent herds (Fleck & Gunn, 1982; Heard & Calef, 1986) and this could have been a factor in the unexpected changes in the size of the Kaminuriak discussed earlier. We should consider reinstituting winter censuses, when the herds may have less interchange. At this time the George River winters in the east whereas the Leaf River winters farther west in Quebec. We need to give these caribou more credit than we usually do; fitness theory would predict that animals should displace from situations when the risk to neonates has increased. There is nothing unique about the habitat quality of calving locations (Fleck & Gunn, 1982; Fancy & Whitten, 1991) except the low risk character.

Habitat selection

The conventional wisdom that we've all been indoctrinated with is that the resources of the habitat best describe and delimit where an animal will be found – intraspecific food and cover rather than interspecific risk and relief considerations. With caribou, biologists first questioned this view when they found animals standing on barren mountains even on snowfields to find relief from insects. Then we found calving females on mountains, islands, and calving grounds with low phytomass. Then we realized that males and females had different fitness requirements and they could be expected to chose different habitats. The next step in this evolution is to question the view that caribou select habitats in the fall and winter primarily on the basis of food resources. By fall calves are no longer excessively at risk from predators but then too the season of protein and growth is ending. Thus survival vs nutritive needs are both more muted and distinguishing the first-order priorities requires finer measurements.

At the 3rd caribou workshop in 1988 H. Butler evaluated 3 hypotheses for habitat selection in the breeding season for 22 sedentary herds: (1) caribou chose rutting areas with the best prospects for forage, (2) caribou chose breeding areas that minimized the risk of predation, and (3) they chose areas that facilitated sexual aggregation and display for breeding. For each herd forage was segregated as to whether it was best where they rutted or better elsewhere and predation risk was classified as low (bears only), medium (bears and 5-10 wolves/1000 km^2) or high, wolves > 10 /1000 km^2). The third hypothesis was evaluated on the visibility of the habitat (open/closed canopies).

Butler reported the following: with no predators 2 herds selected sites of optimal forage, with low predators 4 herds optimally foraged and 6 herds selected safety first, with medium predators all 4 herds rutted in suboptimal forage sites, and with high predators all 6 herds selected more safe sites over forage considerations. Relative to H_3 she stated most herds had traditional open sites to breed. However such openness was not needed and tradition could be perpetuated at closed canopy sites and further males would disperse to find females if the cows were not at the traditional sites.

From my experience the clearest example of animals selecting low risk sites over forage for breeding was on Otter Island (1.3 km^2) in Pukaskwa National Park. Every year males and females met on this island (Bergerud, 1989). The island was mostly closed canopy with few lichens and was heavily grazed; food was certainly better elsewhere but the island was safe as long as landfast ice did not form (Fig. 9).

Another herd that rutted in a degraded food habitat but where predation risk was low was on Pic Island (11.1 km^2), Ontario, an island only 1 km from the undisturbed mainland that had unutilized food supplies. But even on the island a female with a calf further restricted herself to the shoreline of the island; but the males on the island foraged in a central valley where they optimized the available island forage but where their location meant wolves would find them first when they occasionally visited (Fig. 9) (Ferguson *et al.*, 1988).

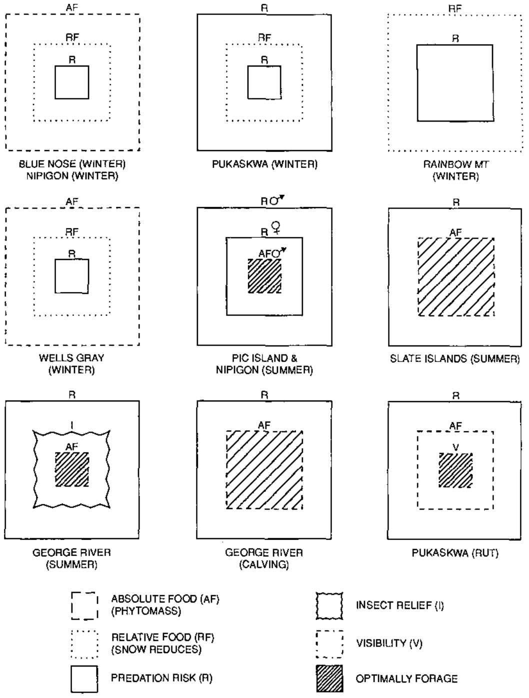

Fig. 9. The habitat niche is visualized as decreasing space areas as selection requirements increase. Ecological factors considered are food resources, snow depths, insect relief and predation risk. For example the winter distribution of the Bluenose Herd (Carruthers *et al.*, 1986) is first determined by the absolute abundance of winter foods (animals will not winter where there is no food), within this area animals select areas of reduced snow cover (relative abundance of food) and within this area they select areas with reduced risk. The other niche presentations in the figure are based on my personal observations.

Both males and females used the islands in Lake Nipigon, Ontario but only during the open water season. Here too animals further restricted themselves to shorelines with reduced food supplies. The animals remained during the rut breeding under closed canopies (Fig. 9) (Bergerud *et al.*, 1990).

Turning to the winter the sedentary ecotype may be dispersed or aggregated in the winter and we need more information in most situations to decide between risk and forage options. The real problem is that biologists seldom radio track both predator and prey simultaneously to understand how wolves search and caribou space relative to risk.

The animals in Pukaskwa National Park are dispersed along the shore of Lake Superior in winter, water escape was available if landfast ice did not develop. The shore is an area of low snow fall and lichens are available on exposed bedrock shoulders. But the caribou show preference for islands and peninsulas. Caribou are probably so rare along the shore that they don't attract much searching time from wolves, but still the caribou are in the safest locations available (Fig. 9).

In the Rainbow Mountains of British Columbia I observed that a herd in 1974 that was separated from wolves hunting moose at lower elevations by deep snows but when I visited the herd the wolves used my snowshoe tracks to make contact with the herd. Seip (1992) has reported how the mountain caribou he studied were seldom hunted by wolves who distributed themselves relative to the moose abundance. In Wells Gray Park I have noted caribou in small islands of old growth surrounded by soft snows too deep for wolves (> 40 cm). Is this solely a snow lift to reach more arboreal lichens and or are they there to avoid wolves?. Given that predators are absent we can assume caribou in winter optimally forage; with wolves present we can not make this assumption in the absence of data.

The distribution of migratory caribou in the winter is more a product of snow cover than phytomass (relative not absolute abundance). This sequence applies to populations with and without predators (Bergerud, 1974c; Skogland, 1978; and Russell *et al.*, 1993). There is a niche of reduced snow cover within the wider food niche (Fig. 9). But is there a further reduction in the snow cover niche to occupy ranges with less risk? Carruthers *et al.* (1986) argued that caribou in the Bluenose Herd selected areas with smaller lakes that increased the searching time for wolves and possibly improved escape opportunities for caribou. We also know that males with their longer legs are commonly in deeper snows than females (Kelsall, 1968) and more dispersed than females. If wolves are selecting calves (Miller, 1975) then males being apart and dispersed should attract less predator attention. It is unlikely that forage is better where males locate and males certainly are not displacing to draw predation pressure from females or reduce food competition with females. Wolves show a numerical response to large winter aggregations (Miller, 1975; Fleck & Gunn, 1982). But the habitat components that affect the functional response have not been documented.

Where to live relative to food and risk should be viewed in a fitness sense. In the past 20 years caribou from the Slate Islands have been introduced twice to the mainland. Both colonizations failed from predation whereas two introductions to islands without wolves succeeded. In a fifth instance a radio tagged male was released on the mainland after the rutting season in 1983. This male (No 169) left the land of milk and honey on the mainland (all that untouched food) and swam 11.3 km back to the degraded barnyard of the Slates where he died from malnutrition in the winter of 1984-85. He faced certain and swift death on the mainland from wolves. By returning he probably increased his fitness by breeding females in the fall of 1984 (he had good antler development). Survival will always take precedent over where to find the next meal. Give these caribou some credit for understanding their priorities and environment better than we do. They've made it this far.

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