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Predation risk and optimal foraging trade-off in the demography and spacing of the George River Herd, 1958 to 1993

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Abstract: The behavior options of feeding animals lie on a continuum between energy maximization and minimization of predation risk. We studied the distribution, mobility, and energy budgets of the George River herd, Ungava from 1974 to 1993. We arranged the annual cycle into 6 phases where we argue that the importance between the priorities of optimal foraging and predation risk change between periods. At calving, risk is more important than foraging for females but males take more risk to optimally forage. During the mosquito season, insect avoidance takes priority over risk and foraging. Optimal foraging takes precedent over risk in the late summer and fall and it is at this time that the herd expanded its range relative to numbers and forage abundance. In the winter (December to mid-March) animals sought restricted localized ranges with low snow cover to reduce predation risk. The spring migration of females may have increased risk during the interval the females were moving back to the tundra to give birth to their neonates on the low risk calving ground. In May, females sought early greens near treeline, which may have increased risk in order to provide maximum nutrition to their fetuses in the last weeks of pregnancy. The ancestors of the George River Herd during the Pleistocene, 18 000 yr. BP may have reduced predation risk by spacing-out in the Appalachian Mountains, removed from the major specie of the megafauna in the lowlands. With global warming, it is argued the major problem for caribou will be increased wolf predation rather than changing forage and nutritional regimes. It is essential that First Nation residents of the North maintain their option to manage wolf numbers if excessive predation in the future adversely affects the migratory herds of the Northwest Territories and Ungava.

Key words: caribou, climate change, Labrador, Québec, Rangifer tarandus.

Introduction

The George River Herd in Ungava increased from less than 5000 animals in the 1950s (Banfield & Tener, 1954) to approximately 650 000 animals in the 1980s and was the largest herd in the world (Williams & Heard, 1986; Bergerud, 1988a). This was the greatest eruption that we know of for an ungulate. For some 20 years 1974 to 1993 the junior author monitored the demography, physical condition, and movements of the herd. The senior author censused the herd in 1958, conducted calving studies in 1978 and 1988, and supervised optimal summer foraging studies 1988 to 1992 (see Camp & Linders, 1989).

From this data backdrop we wish to evaluate how caribou balance the trade-off between predation risk and optimal foraging in their annual use of space and its effects on demography. There is a growing concern among caribou biologists about the impact of global warming on caribou. But the concerns voiced (Russell, 1993; Gunn, 2000; Griffith et al., 2000) relate solely to optimal foraging considerations to the exclusion of how predation risk will be altered as temperature increases in the Arctic. We feel a more balanced approach is needed for certainly predation risk will be affected by climatic change and predation impacts will be the primary means by which survival rates will be altered.

Lima & Dill (1990) stated that the behavior options to a feeding animal lie on a continuum between energy maximization and minimization of risk (Fig.1). Animals are free to choose and their

choice may affect their survival and reproductive fitness. Belosky (1991) stated that insect and predator avoidance will "constrain" optimal foraging but Lima & Dill say there is nothing constraining a free choice of the two options; neither choice is more fundamental than the other. Clearly neither option is desirable and optimal behaviour will lie somewhere in between (Lima & Dill, 1990).

Bergerud (1996, fig. 9, p. 111) has noted that habitat choices for caribou have a hierarchical scale in space. For example, for the George River herd, all the Labrador tundra was a low risk habitat within which the animals could select smaller scale habitats to optimally feed. In fact, the animals on the calving grounds generally shifted locations between years in response to a degraded flora from a previous grazing.

Caribou ecology could be described and understood by balancing predation risk and optimal foraging in this hierarchical space and habitat framework.

Predation risk versus optimal foraging: a synthesis

We have divided the annual cycle into 6 phases where we argue that the importance of risk vs. foraging changed from the previous phase:

1. Calving (June): Risk more important than optimally foraging for females but males optimally forage.
2. Mosquito season (July): Insect avoidance is more central than risk or foraging
3. Late summer and fall (August through November): Optimal foraging takes precedent over risk.
4. Winter pause (December to mid March): Risk is a greater problem than foraging
5. Spring Migration (mid March and April):

Table 1. Weather statistic recorded at Schefferville 1955-56 to 1992-93 by students of the McGill Sub-Arctic Research Laboratory (Snowfall statistics based on biological year June to May, Julian dates for Y in freeze-up and break-up). Mean with standard error of the mean ($s_{\bar{x}}$) in parenthesis.

Weather parameter	Mean ($s_{\bar{x}}$)	Maximum	Minimum	Annual trend
July temperatures °C	12.4 (0.16)	14.4 (1959)	9.8 (1965)	Y=34.116-0.011X r=0.121, P=0.46
January temperature °C	-23.1 (0.61)	-15.9 (1958)	-30.4 (1991)	Y=184.814-0.104X r=0.312, P=0.05
Annual temperature °C	-5.0 (0.15)	-2.7 (1981)	-7.9 (1972)	Y=49.179-0.027X r=0.355, P=0.04
Annual snowfall (cm)	382.5 (16.50)	612.8 (1980-81)	209.0 (1992-93)	Y=-4877.641+2.666X r=0.287, P=0.085
Fall freeze-up (Knob L.)	Oct 29.1 (1.87)	Nov 16 (1978)	Oct 3 (1956)	Y=175.348+0.064X r=0.056, P=0.76
Spring break-up (Knob L.)	Jun 12.0 (1.14)	Jun 29 (1992)	Jun 1 (1956)	Y= -91.963+0.129X r=0.212, P=0.20

Females may increase risk to return to the calving ground.
6. May: Optimal foraging is the priority within the constraints of having made the return migration to the low risk tundra.

All would agree that in the absence of predators, caribou will optimally forage especially at times that will influence reproductive fitness. Again if a range is overgrazed animals may be prepared to take greater risks especially if the reproductive fitness of conceiving and or producing viable neonates is involved.

The sequences we discuss for the George River Herd 1958-1993 should act as a "control" relative to global warming. The weather in Ungava has remained relatively constant in temperatures in the past 40 years compared to the warming trends that have and are taking place in Alaska and western Canada (Table 1).

In comparing risk vs. foraging choices the density of caribou or total numbers are needed in some analyses. Three regressions of numbers (Y=1000s of animals) on years (X=last two year digits) were calculated. (1) The first regression was based on census results 1954 to 1988 (1993 censuses excluded) (Y=750/(1+1614718e$^{-0.177X}$) (r=0.972). (2) The second regression was calculated based on the ages of 2267 caribou aged by annulations 1973-74 to 1987-

88 using the Cagean program (Deriso et al., 1981) commencing with a population estimate of 176 000 in 1973-74 (expanded from Wetmore, 1973) and excluding declining estimates in 1985,1986, and 1987 ($Y=0.0078e^{0.137X}$) ($r=0.991$). (3). A third regression was based on the conifer scar data of Morneau & Payette (2000) for the years 1943 to 1988 and excluded their last tally for 1988 to 1992 that showed a decline in scarring ($Y=0.002e^{0.114X}$) ($r=0.967$).

We also calculated the expected population size in 1993 based on adult mortality and spring recruitment statistics annually commencing with the 1984 census (Crête et al., 1991). The expected population based on the M/R procedures gave an estimate in 1993 of 400 000 (Bergerud, 1996). This estimate was in agreement with the root scar data 1988-92 from Morneau & Payette (2000) and consistent with a decline since 1984 based on the Cagean program.

We argue that the censuses in 1993 (Couturier et al., 1996; Russell et al., 1996) were too high to represent internal growth of the George River Herd and that animals from the Leaf River Herd were present and counted in these estimates; we did not include these counts in our equations of population growth of the herd. In both 1988 and 1993 Leaf River animals were associated with George River calving females (Bergerud, 1996). More recently a news release at this conference showed 5 of 23 satellite George River animals associated with Leaf River satellite animals (April 17-22) and Couturier et al. (this conference) gave a paper titled "Is the metapopulation theory useful in conservation?--A test with the Quebec-Labrador caribou". When we have two large adjacent migratory herds that winter in the same areas at high numbers, one with a severely degraded low risk calving range and the other with a much larger above treeline, low risk calving habitat, (Crête & Huot, 1993; Crête et al., 1990; Bergerud, 1988b; 1996; Manseau et al., 1996), might not we expect exchange?

1. Calving (June)

Female caribou migrate to calving grounds in North America to reduce predation risk for their neonates (Bergerud, 1974a; Whitten & Cameron, 1980; Bergerud & Page, 1987; Bergerud, 1996; Heard et al., 1996). Predators are less common on the calving grounds than winter ranges as documented for the Porcupine Herd (Garner & Reynolds, 1986) and the herds in the Northwest Territories (Kelsall, 1968; Fleck & Gunn, 1982; Heard et al., 1996). Males lag behind females in spring migration while foraging on early greens (Whitten & Cameron, 1980; Russell et al., 1993; Heard et al., 1996).
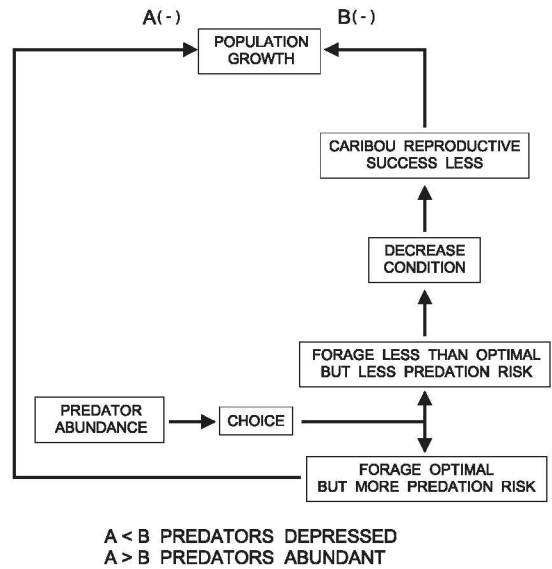
Fig. 1. Caribou optimal foraging/predation risk trade-off model.

The per cent nitrogen in the feces of females on the Caribou House calving ground of the George River Herd in 1988 was 24% less than that of males who were foraging in the Lac Champdoré area (Bergerud, 1996), a former calving ground of the George River Herd (Wetmore, 1973). Males were seeking Menyanthes trifoliata with 3.98% (standard error of the mean $s_{\bar{x}}=0.35$) nitrogen whereas females 130 km further NE were utilizing Scirpus cespitosus 2.54% ($s_{\bar{x}}=0.26$) nitrogen and Arctostaphylos alpina 2.80% nitrogen.

The Naskapi of Schefferville in 1958 (then called Knob Lake) told Bergerud that caribou calved in the taiga between Knob Lake and Indian House Lake. A calving ground, Lac Champdoré, was found in this area at the headwaters of the Wheeler and Whale Rivers in 1970 (Westmore, 1973). Thus some George River cows in the 1960s were calving south of the treeline and where the growing season commenced about June 5 or just as calving commenced. On June 4, 1972 Westmore (1973) also located a much larger concentration of cows calving on the Québec-Labrador provincial boundary southwest of Hebron Fiord; this ground we named Caribou House in respect of Naskapi mythology. The growing season at Caribou House commences about June 20, 15 days later than that at Lac Champdoré. By 1980 all the females had deserted Lac Champdoré and moved to Caribou House but males continued to graze there in May and June. It was at Lac Champdoré that we found males in 1988 and recorded their much higher fecal nitrogen than the cows at Caribou House.

We believe that a change in wolf predation pressure was responsible for the females moving to Caribou House. In the 1960s wolves were nearly extinct in Labrador. Some excerpts in 1958 from hunters that traveled inland extensively by dog team seeking the few remaining caribou were:

Hopedale hunter: abundant when a boy, none for about 20 years.

Nain hunter: 50 years ago there were plenty, have never seen any.

Davis Inlet hunter: none for 15 years, plentiful 45 years ago.

We postulate that in the absence of wolves in the 1960s [the wolverine (Gulo gulo) had also disappeared (Novak et al., 1987)], a major portion of the herd calved below treeline dispersed in the taiga at Lac Champdoré. The growing season commences earlier at Lac Champdoré than any other area in central Québec and Labrador. This hypothesis is consistent with the greater abundance of root scars from caribou hooves in this region in the 1950s than further north (Morneau & Payette, 2000). Without predators the cows were able to optimally forage prior to calving. By the 1970s the herd exceeded 100 000 and wolves were becoming more abundant. Luttich saw three on his first spring trip in 1974. As the herd increased and attracted more attention from wolves the cows deserted their prior calving ground and moved as far northwest from treeline as snow-cover permitted (to Caribou House). Possibly the presence of bears along the Labrador coast influenced the extent of their eastern shift. They traded optimal foraging for reduced risk.

By 1988 they had severely overgrazed Caribou House compared to the western tundra where the Leaf River Herd calved in the 1970s (Fig. 2; Bergerud, 1988) while forage was still abundant at Lac Champdoré (Table 2). They remained above treeline in the low risk tundra even though the habitat continued to be degraded especially from trampling (Table 2). The physical condition of the females was reduced (Couturier et al., 1988; 1990). The pregnancy rate declined from 93% ($s_{\bar{x}}$=0.55) (1976 to 1982,
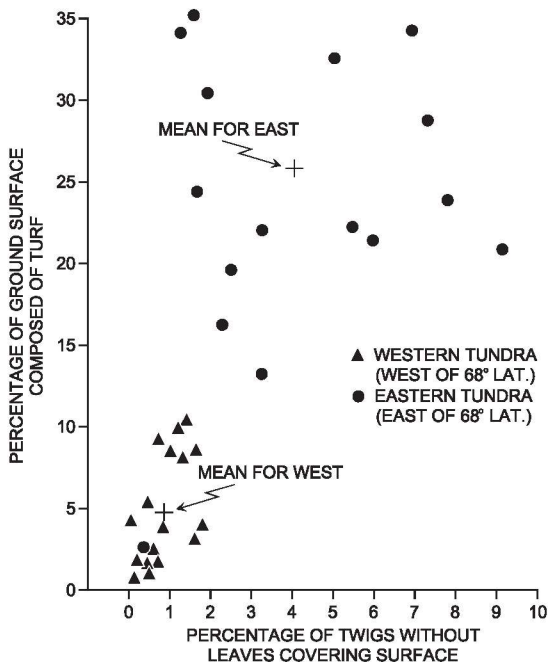

Fig. 2. Grazing and trampling on the Québec-Labrador Peninsula.

Note: The eastern tundra on the Labrador Peninsula was more heavily grazed and trampled in 1988 than the western tundra that was generally north of the Koksoak River and west of 68°W. Data based on 34 range stations. Each station centered in a 60' x 30' longitude x latitude grid. Each grid approximately 3500 km^2.

7 counts in 6 years, n=16 819 females) to 69.3% ($s_{\bar{x}}$=2.28) for the interval 1983-1993 (13 counts in 10 years, n=25 421 females). The body size of fall calves was reduced which increased their vulnerability to wolf predation (Bergerud, 1996). It was this trade-off of risk over foraging that more than any single other factor started the decline of the George River Herd in the mid 1980s.

In the later stages of degrading of the above treeline range, the animals did compromise risk by mov-

Table 2. Comparison of the range destruction in % (standard error of the mean in parenthesis) between the deserted Lac Champdoré calving ground and the Caribou House calving ground, 1988.

Weather parameter	Mean ($s_{\bar{x}}$) at Lac Champdoré	Sample size	Mean ($s_{\bar{x}}$) at Caribou House	Sample size
The ground covered with broken twigs	0.74% (0.62)	3	5.8% (1.02)	9
Turf cover created by caribou hooves	3.00% (0.62)	4	23.0% (2.87)	9
Percentage of birch dead	10.0%	1	37.7% (5.57)	9
Percentage ground lichens shattered	11.5% (0.76)	4	94.4% (2.98)	9

Table 3. Phenology dates (month/day) relative to summer energy budgets (1988-92). (Standard error of the mean in parenthesis).

Phenology parameter	1988	1989	1990	1991	1992*
First mosquito bite	6/27	6/24	7/4	7/9	nd
Peak mosquitoes	7/22-29	7/12	7/12-15	7/25-8/3	nd
Mosquitoes downwind sweep	20.9 (3.25)	5.2 (2.17)	4.6 (1.26)	4.7 (1.59)	nd
First warble fly	7/25	7/11	7/7	7/22	nd
Insect relief acts/minute	1.2 (0.18)	0.5 (0.16)	0.6 (0.14)	0.2 (0.11)	nd
Days caribou observed	18	13	12	21	nd
Date birch full leaf	6/28	6/18	6/28	6/29	7/8
Per cent birch (July diet)	34 (4.4)	58 (7.0)	66 (7.6)	41 (6.8)	58 (6.4)
Feeding days observed	17	15	14	15	6

ing nearer the treeline but remained on the tundra. On average 32% ($s_{\bar{x}}$=6) (n=16, 1974 to 1990, 1983 missing) of the calving ground each year resulted from range extensions that were not within the perimeters of earlier calving distributions. These annual percentage additions were not correlated with the annual size of the calving ground each spring, r=-0.107 (Y=annual addition, X=annual size of ground, km² in 100, Y=31.176-0.0256X) nor with year, r=-0.294 (Y=annual addition, X=year, last two digits, Y=110.453-1.005X). The regression of the perpendicular distances of the annual centers of the calving grounds to the George River (approx. treeline) on year (last two digits) was significant, Y=426.714-4.420X, r=-0.849, n=21, 1973 to 1993).

In the years when pregnancy rates were reduced (1984 to 1993) this range rotation nearer treeline was not followed by increased risk since calf mortality to autumn was not significant (Y=33.089+0.081, r=0.251, n=10 fall recruitment, Y=calves/100 females) regressed on distance from the George River (X=km). Also these shifts closer to treeline with greater forage may have stabilized physical condition since there was no detectable decline in pregnancy rates 1984 to 1993, r=-0.067, (Y=pregnancy/parous) on X (year last two digits, Y=84.720-0.172X, C.V. of annual tallies of pregnancies 12%).

The other large herd in Ungava, the Leaf River Herd, also calved near treeline when first discovered in 1975, both males and females were present and the overall density was less than 1/km² (Le Henaff, 1975). In the 1980s as this herd increased it contracted the size of the calving ground by increased aggregating and shifted north. By 1999, it was calving 425 km farther north than 1975 (Couturier, pers. comm.). As it increased it shifted from an area where the growing season commenced June 15 to

that of June 30 and like the George River the males, optimally foraging, had been left further south. This shift north may be a movement to reduce risk since if the animals were seeking a greater green phytomass they should have moved closer to tree line as the George River females did.

2. Mosquito season (July)

The mosquito season for the George River Herd commenced at the end of June or early July (Table 3). However peak harassment of caribou generally occurred in the last half of July when the major species (Aedes punctor) hatched. Lewis & Weber (1984) indicated the peak abundance of Aedes punctor should occur in the last week of July and this was the case in 1988 and 1991 (Table 3). Mosquitoes were more abundant in 1988 than 1989-91 and caribou were bothered more in 1988 than in the three other seasons (Table 3).

Toupin et al. (1996) felt that insect harassment of George River animals was not serious and contributed little to the negative energy balance of females during the first month of lactation. Their studies were in 1992 and 1993; 1992 was the coldest spring since weather records have been kept at Schefferville. We feel mosquitoes have a major impact on July energy budgets (Table 4). The energy budgets of females in 1988 did not turn positive until the mosquitoes abated in the first week of August even though caribou walk more but lie less in daylight hours with oestrid harassment than mosquitoes (Fig. 3 and Camps & Linders, 1989). During the insect seasons 1988 to 1991 the combined activity budget of caribou was 12% lying, 19% standing, 37% walking, and 41% feeding between and 0600 and 2200 hours, 1988-91, n=49 410 caribou. In the absence of insects during the growing season their budget was 18% lying, 2% standing, 20% walking, and 60% feeding (n=43 515 animals). When insects

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* nd=no data.

were absent they fed more, walked less and reduced their travel speed (Fig. 3). Travel rates were greater in July and August than in any other month except November and in some years April (Fig. 4). The Porcupine Herd also has had its greatest travel rates in during the insect season when bothered by mosquitoes (Whitten & Fancy, 1990).

The males joined the females in forming large post calving aggregations in July when the mosquitoes became abundant. This same sequence occurs in all the other large arctic herds in North America (Kelsall, 1968; Skoog, 1968; Curatolo, 1975; Roby, 1978) and is the basis of the post-calving census technique developed in Alaska. The George River bulls by leaving the treeline and moving to the tundra in July left an area with better birch (Betula glandulosa) than that present on the tundra. The percentage of the birch dead on their vacated range was 26% ($s_{\bar{x}}$=5) (5 stations) vs. 38% ($s_{\bar{x}}$=6) dead on the female tundra range (8 stations). Birch was the dominant forage in July (Table 3). This male movement to the tundra was to gain insect relief; they had been in an area of greater predation risk along the treeline and also of greater forage, yet moved to the overgrazed and trampled range of the females.

Commonly the females in the latter half of June, after calving, moved north staying on the low risk tundra but following a green-up, moving from the calving ground where the growing season commenced about June 20 to more northern locations where the season commenced 10 days later. When the mosquitoes became bothersome at these higher elevations the animals generally returned south paralleling the north-south treeline travelling over the range they had previously foraged. They appeared channeled to open wind-swept relief habitat. But as soon as the mosquitoes abated in the last days of July or early August they turned immediately, moving
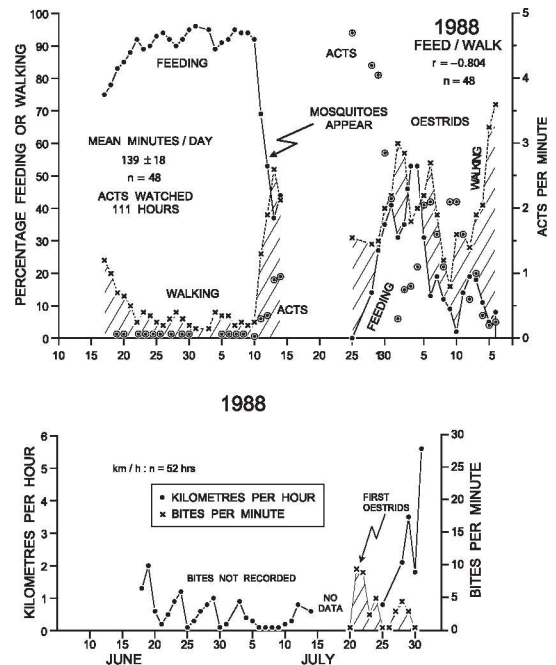

Fig. 3. Feeding and walking schedules and mobility compared with the biting of mosquitoes and the presence of oestrids in 1988.

Note: The majority of the camps were in the vicinity of the George River. Horizon scans generally at 8, 12, 16, and 20 hours as well as the bites received per minute on an exposed arm without repellant. Feeding and walking percentages based only on active caribou (not lying). Mobility rates based on observing caribou in small groups generally less than 5 animals for at least 5 minutes, noting their positions and then pacing the distance covered. Insect act per minute based on observing a single animal for one minute and counting head shakes, leg stamps, bites to the body, and tail/ear flicks. Similar data was gathered in 1989, 1990, and 1991.
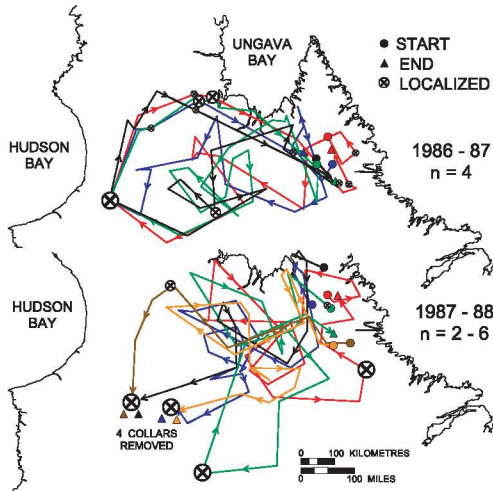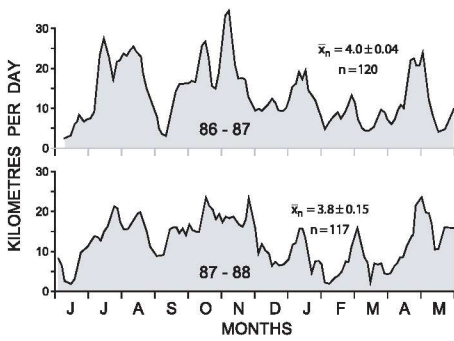
Fig. 4. a) Annual mobility cycle in 1986-87, and 1987-88 based on the biological year June 1 to May 31. (Below) b) Routes taken in 1986-87 and 1987-88 by the satellite collared females showing the localized ranges.

Table 4. Energy expenditures and intake compared between days insects were active and not active, George River 1988-90.

Dates observed (month/day/year) and insects	Energy budget (kJ in 1000s)		
	Expenditures	Intake	Difference
Mosquitoes present and active			
7/12/1988	18	3	-15
7/13/1988	16	1	-15
7/14/1988	20	5	-15
7/28/1988	23	11	-12
7/13/1990	24	11	-13
Means	20.2	6.2	-14
Mosquitoes present but not active			
7/29/1988	32	34	+2
7/30/1988	42	51	+9
7/31/1988	43	53	+10
Means	39.0	46.0	+7
Warble flies and tabanids active			
8/1/1988	12	2	-10
8/4/1898	12	2	-10
8/8/1988	25	13	-12
7/11/1989	20	5	-15
7/13/1989	29	21	-8
Means	19.6	8.6	-11.0
Warble flies & tabanids present but not active			
8/3/1988	42	50	+8
8/7/1988	41	52	+11
8/24/1988	39	56	+17
Means	40.7	52.7	+12.0

[1] Methods in Camps & Linders, 1989.

west towards the treeline where forage was more abundant and less trampled even though oestrids had taken up the chase. The mean date of crossing the George River going west was closely synchronized with end of major mosquito harassment, July 30 (Julian 211.4 ($s_{\bar{x}}$=4.04), n=7 years, 31 UHF radioed females involved). In July mosquito relief took precedence over optimal foraging even resulting in negative energy balances and applied to both sexes. The wind swept tundra provided mosquito relief and open habitat where the animals could aggregate to further mitigate mosquitoes. A bonus of remaining on the tundra was that risk was also lower, the trade-off was the insufficiency of forage. But reduced mosquito harassment was the primary incentive for choosing the wind-swept tundra, in insect season. The calving ground got a double whammy, first at calving and then a return visit to mitigate insects in July. The tundra area available to the George River Herd (47 000 km²) is smaller than that of any of the other large herds in Canada

(Bergerud, 1996): an unfortunate location for the largest caribou eruption in modern times to have occurred.

3. Late Summer and Fall (August through November)
The dispersal of the late July aggregations coincided with the end of mosquito abundance. In the words of Kelsall (1968) the animals were "released" when heavy mosquito harassment ceased. This August dispersal did not occur as proposed by Curatolo (1975) and Roby (1978) as a response to oestrid harassment (but see Dau, 1986). Our best disproof of the oestrid hypothesis occurred on July 27, 1990 when biologist Lo Camps visited an aggregation of >100 000 animals south of Indian House Lake. These animals
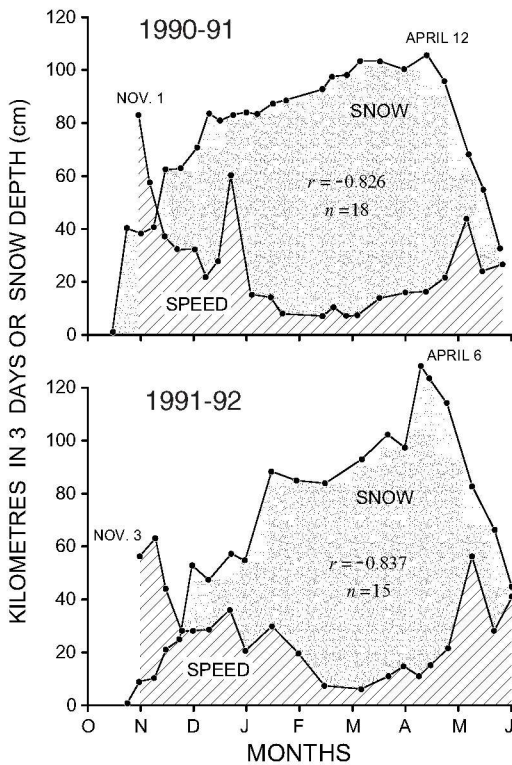
Fig. 5. Mobility rates and snow depths.

Note: Mobility rates declined as snow depths increased between the start of snow cover and the date of maximum depths 1990-91 and 1991-92. This data gathered in 6 years (see Table 7).

Table 5. Activity budgets and frequency of insect related activity during attack of different numbers of oestrids ($s_{\bar{x}}$ = standard error of the mean).

| | Number of Oestrids per Caribou | | | |
	1	2	3	≥4
PER CENT ACTIVITY				
Feeding	23.1	0.2	1.8	0
Walking	9.6	18.6	5.0	1.4
Standing	66.0	75.4	93.2	98.6
Running	1.3	5.9	0	0
FREQUENCY OF ACTIVITY	(min⁻¹)			
Head shake	3.0	3.0	2.1	10.1
Body shake	1.8	2.6	1.1	6.9
Leg stamp	1.2	1.4	1.0	4.8
Bite body	0.3	0.6	0.4	0.9
(min:sec)	81:00	63:27	55:48	8:32
Mean Group Size ($s_{\bar{x}}$)	3.05 (0.77)	1.82 (0.56)	1.0	1.0
(n)	(20)	(17)	(6)	(6)

were severely bothered by mosquitoes, blackflies, oestrids, and tabanids. The animals remained massed milling about. The following four days were stormy and cold and the herd disbanded in the absence of all insect harassment and the mosquito season never resumed but oestrids reappeared after the stormy weather. In other years in late July a common observation was to see large herds disband when mosquitoes and oestrids abated due to inclement weather but again mass when both insects resumed their harassment. In each year, 1988 to 1992, we were unable to find large aggregations after the mosquitoes abated regardless of oestrid abundance. Also, Toupin et al. (1996) observed animals still aggregated between 19-30 July 1993 when oestrids were present. The rather abrupt abandonment of the late July aggregations coincided with the cessation of mosquito abundance and not with the arrival of oestrids, although the end of the mosquito season and the commencement of the oestrid season can occur within days of each other. One cannot use the term "insect harassment" without referring to a certain insect group. Oestrids and tabanids fly only in warm and mostly in sunny weather, whereas mosquitoes do not seem to like strong sunshine (Anderson & Nilssen, 1998; Anderson et al., 2001). Clearly, regional differences in insect abundance explain why study results differ. In Norway, mosquitoes had little influence on reindeer activity patterns, contrary to oestrids. Moreover, in the absence of oestrid flies, weather parameters had no influence on reindeer activity pattern. (Hagemoen & Reimers, 2002; Colman et al., 2003).

Without mosquito harassment the scattering bands left the overgrazed June/July tundra and moved toward more abundant phytomass west in the taiga. Their return to treeline increased their predation risk; 28 of 105 VHF collared females died primarily from predation adjacent to the treeline in this study. Risk increased but was not extreme since open water was still available for escape and snow cover to impede escape flights did not accumulate until mid November (Fig. 5). Their direction in August led them back to

habitats where the larvae of oestrids had pupated that had emerged from male caribou in June. They also moved closer to the vast muskeg areas northeast of Schefferville (see Hare, 1959: Map 1) where tabanids (Chrysops spp. and Hybomitra spp..) pupate (McElligott & Lewis, 1996). These deer and horse flies are much more abundant in Ungava than on the ranges of more northern migratory herds in NWT. These tormentors caused severe landing and biting harassment when the animals were in the taiga on sunny warm days and trees blocked wind flow. The animals had not returned to the taiga to mitigate fly attacks but to forage now that mosquito attacks had ceased.

Fly attacks may hasten the August dispersal. Caribou often ran splitting from groups and acting more independently but animals in small groups were more bothered by oestrids than were the members of larger groups (Table 5). The explanation of Heard et al. (1996:42) for this August dispersal is the correct one: "When insect numbers decline [meaning mosquitoes] in August the large aggregations break-up and caribou amass large amounts of fat even though plants are senescing...we suggest caribou attempt to reduce competition for food by spacing out as widely as possible."

The most abrupt and consistent pause in the annual movement cycle occurred in the first week of September every year 1986 to 1992 on a mean date of September 5.2 ($s_{\bar{x}}$=1.78) resulting in a minimum mean speed of 5.4 km/day, s_x=1.63 (Fig. 4) (see also Bergman et al., 2000). This pause happened exactly as the oestrids ceased. The last oestrid we saw in 1988 was on August 30. This pause was to accelerate forage intake. Interestingly this major feeding break did not occur for the Porcupine Herd in 3 years that Whitten & Fancy (1990) followed satellite caribou. In those years the June/July range of the Porcupine Herd was not heavily overgrazed (Russell et al., 1993). This pause then for George River females was a compensatory feeding period, again illustrating the adaptability of this species when faced with a food shortage.

Heard et al. (1996) had it right again when they said this fall feeding period could explain the density-dependent range expansions and contractions observed in migratory caribou populations. Each year as the George River Herd increased 1973 to 1984 the distance between the calving ground and the rutting range increased (r=0.931, Y= -2241.11+32.063X, Y=km between calving and rutting ranges, X=last two digits of year, n=12). After 1984 the distances commenced to retract. The size of the calving grounds also increased 1974-87 with numbers (r^2=0.723, n=13) but continued to

increase with overgrazing after 1987 when numbers began to decline. It was the size of the fall range that expanded in a density-dependent manner 1978-79 to 1986-87, >300 000 animals to 644 000 animals, [expansion equation (Y=14 518.490/(773.612-X), Y and X in 1000s, r^2=0.719), the area of fall range was only available for 13 years]. The density-dependence was still apparent when the herd declined 1987-88 to 1991-92 (Y=6.343$e^{0.0044X}$, r^2=0.752, n=6).

The movements in this period in late October and November are classically called the fall migration. We believe this is a misnomer; the animals are not trying to reach a goal. They are trying to forage rapidly before snow level hinders forage intake and predation risk increases. The coldest temperatures in the subarctic are in the higher latitudes where leaf fall occurs earliest and snow becomes persistent first. Thus caribou in the NWT commonly cross the tree line in late summer moving south but in Ungava where the tree line runs north and south the George animals go west. Hence movements in this season are the reverse of following the advance of green forage north as temperatures moderate in the spring.

The mean monthly travel rates of the satellite females in October and November in 7 years were positively correlate with our population estimates for those years, but the travel rates were not correlated with herd numbers for August and September:

August: 18.7 km/day, $s_{\bar{x}}$=1.17, not correlated with numbers r=0.312, n=7
September: 14.7 km/day, s_x=1.17, r=0.018, n=7
October: 17.5 km/day, $s_{\bar{x}}$=1.50, correlation coefficient, r=0.614 n=7
November: 16.6 km/day, $s_{\bar{x}}$=1.15, r=0.738, n=7

The November correlation is nearly significant ($r_{[P=0.05]}$=0.754). The lack of correlation in August might relate to differences between years in oestrid numbers. In September the lack of correlation between numbers and travel rates would be nullified by the September pause and in October another delay for breeding. However the correlations in mobility and travel rates in October and November suggest foraging interactions between animals and strengthen the view of the priority of maximum foraging in this interval.

Further evidence that the fall period was directed at foraging rather than reducing risk was the many turns the animals made (Vandal et al., 1989; Bergman et al., 2000). The frequency of turning peaked when the first frosts resulted in reduced greens in September and again in late October when lake ice formed (Table 6). Such major changes in direction in September might be to reach lower elevations and remaining greens. The increased frequency of changing travel directions in October

Table 6. The frequency of major turns made by satellite females >15° on moving azimuths.

Dates by weeks	Number of turns	Remarks
September 1-7	0	
September 8-14	7	Searching for
September 15-21	6	remaining
September 22-30	24	greens
October 1-7	7	
October 8-14	2	
October 15-21	4	Lakes freeze &
October 22-31	11	more searching
November 1-7	11	for forage
November 8-14	1	
November 15-21	7	More snow,
November 22-30	12	searching for low risk
December 1-7	3	areas of reduced snow
December 8-14	3	and localizing
December 15-21	2	
December 22-31	4	

when lakes formed a highway could have provided the opportunity to move in new directions seeking out forage still not covered by snow; the animals could take advantage of traveling on the ice surfaces where predators could be better detected and the reduced snow cover favored rapid escaped flights.

4. Winter pause (December to mid-March)
This period began with the localization of caribou on restricted winter ranges as snow cover increased. We define a localized winter range as a restricted area where travel rates were less than 10 km per day and the satellite animals made many acute angle turns within a restricted region (Fig. 4). Animals generally localized and reduced travel rates in late November or early December when snow cover reached >50 cm (Fig. 4 and 5, Table 7).

The herd was more widely scattered in winters when snow cover was low. The extent of the annual winter ranges (km²) was negatively correlated with winter snow depths in 11 winters (r=-0.736). In shallow snow winters animals were further south where snow depths are usually deeper; in heavy snow winters they ranged further north often moving into the tundra beyond the treeline that generally parallels the Leaf River. The percentage of the annual winter distributions that was north of treeline varied from 75% in 1983-84, a hard winter, to less than 5% in 1992-93, a mild snow winter, and was positively correlated with snow depths in 12 winters (r=0.661).

The propensity of caribou to occupy areas of low snow profiles has been recognized since the earliest winter studies (Banfield, 1954; Skoog, 1956; Bergerud, 1963) and has recently been well documented for the Porcupine Herd (Russell et al., 1993). It has been assumed that this selection was for energetic considerations since digging craters to uncover forage has a significant cost (Thing, 1977; Russell et al., 1993).

We compared the distribution of caribou in 18 winters by tabulating their presence in 60x30 degree long. by lat. map-grids with: (1) estimates in the same grids of the general height of snow (based on the branchless part of spruce stems (see Hustich, 1951:Fig. 9) or the height of bushes and Krumholz) and (2) with the percentage of terrestrial lichen cover in the range station grids. The presence of caribou was not correlated with the abundance of lichen cover (r=-0.135, n=50) but with snow depths (r=-0.637, n=52 grid stations). Caribou selected regions of low snow rather than lichen biomass per se.

Two recent studies in Alaska have shown that wolves are more successful killing caribou in deep snows, even resulting in surplus killing (Dale et al., 1995; Mech et al., 1998). The winter mortality rate of VHF radioed females for the George River confirmed this predator advantage. The mortality rate of females in 8 winters increased with deep snows (r=0.824); these females did not have depleted fat reserves (Bergerud, 1996: Fig. 4). Additionally the annual mortality rates of females in the Delta and 40-Mile herds in Alaska were correlated with winter severity (Delta Herd r=0.634, n=17 years, 40-Mile r=0.792, n=8 seasons) (Boertje et al., 1995; 1996, Valkenburg et al., 1996; Valkenburg, 1997). These animals were also not predisposed to predation by reduced condition.

Caribou are the most cursorial of the surviving deer species (Geist, 1998). Their rapid escape rate is maximized with minimum leg and hoof lift on wind-swept frozen lake surfaces. Even a few centimeters of snow increase the cost of locomotion and reduce their high speed advantage over wolves.

Caribou should choose tundra landscapes in deep snow winters if they wish to reduce predation risk, but at a trade-off in reduced forage. Lichens are the primary winter food of the large migratory herds on the mainland of North America. These lichens are less common north of trees than in the taiga (Kelsall, 1968; Skoog, 1968; Bergerud, 1971; Russell et al., 1993, Thomas et al., 1996) and are especially limited on the high elevation tundra of Labrador (Bergerud, 1988b). Caribou may have forfeited weight and condition to occupy these wind-swept safer environments with less phytomass in both

Table 7. Role of snow cover on mobility rates and winter localizations.

Winter season	Correlation km/3 days vs. snow depth (n)	Winter localization dates	Kilometers/day before; after	Snow depth (cm) localized	Maximum snow date (cm)
1986-87	-0.730 (20)	Nov. 23 to 26	11.9; 9.3	49	March 23 (93)
1987-88	-0.521 (20)	Nov. 27 to 30	27.4; 6.17	56	March 22 (115)
1988-89	-0.432 (22)	Dec. 1 to 5	11.3; 6.18	45	April 9 (99)
1989-90	-0.752 (23)	Dec. 16 to 20	12.2; 7.8	89	April 23 (113)
1990-91	-0.826 (18)	Dec. 5 to 8	13.9; 8.5	84	April 12 (107)
1991-92	-0.837 (15)	Nov. 26 to 29	15.4; 8.8	53	April 6 (129)

Ungava and Northwest Territories (Tables 8, 9, and 10).

5. Spring migration (mid-March and April)
Guess the name of the species: "A herd of —roams over desolate snow-covered plains. With the onset of spring, most —migrate north. Males disperse to forage on herbs and grasses during a scant three-month growing season, while females trek to calving grounds. After giving birth, the females return south with their young, but nearly half the newborns perish on the way," (National Geographic inside front cover, Vol. 198, No 3). It is the chiru, Pantholops hodgsoni or Tibetan antelope that like the caribou and the Asian saiga (Saiga tatarica) (Bannikov et al., 1967) make long spring migrations of females to calving grounds with harsher environments to reduce predation risk.

Satellite females of the George River Herd left their localized winter habitat to return to the calving grounds (1987-1992) as early as February 26 and as tardy as May 6 (mean April 8, Julian date 98.4, $s_{\bar{x}}$=0.53, n=18). A number of these females were migrating prior to the accumulation of maximum snow depths. The releasing mechanism appeared to be knowledge of how far the females had to go to return to the Labrador tundra. The correlation between the initiation date and the distance to the George River was highly significant (r=-0.742, n=18, Y=1024.884-5.784X; Y=Julian date, X=straight line distance km to the George River). None of the females followed the shortest route to the Labrador tundra. The difference between the shortest route and the trail taken, averaged 55 km, $s_{\bar{x}}$=11. If the females were west of 73°W and north of 53°N, they followed the tree line northeast adjacent or between the Koksoak and Leaf Rivers, turning southwest as they passed Kuujjuaq. The snow on the ground in the central interior (Schefferville) that they avoided, averaged 85 cm at the end of March 1951-90 but was 19 cm shallower on the route they

took by Kuujjuaq, 66 cm (1951-90) (Jacobs et al., 1996). The average depth of snow along the treeline, based on our measurements of the height of the branchless gap on spruce, gave a depth of 45.7 cm, $s_{\bar{x}}$=0.61 (n=10 stations) whereas a direct path east at 57°N gave a depth of 62.5 cm, $s_{\bar{x}}$=0.62 (n=10). Their indirect route had less snow cover.

Physiography may also influence the route chosen to return east. The Laurentide ice sheet finally melted at about 5500 BP in central Ungava--the last remnant was located northeast of present day Schefferville. The topography left in this core area in the central interior was linear ridges running north and south, bold hills and north-south oriented lakes; all at right angles to the shortest return route. In contrast the travel route the females commonly followed northeast between the Leaf and Koksoak rivers is a rocky plain with northeast-southwest parallel eskers (Hare, 1959). We do not argue for topographical funneling, a hypothesis of earlier decades (Bergerud, 1974a). Still the more uniform and reduced snow cover and improved visibility of travelling along the tree line may have facilitated less risk; the ecotone of tundra and taiga would provide a mix of lichens and alpine evergreen shrubs available under reduced snow cover.

Pregnant caribou that began the return to their calving ground at the end of March could be nutritionally stressed as were the females of the Kaminuriak Herd, NWT. in the 1960s (Dauphiné, 1976). However Huot & Goudreault (1985) showed that with high numbers and an overgrazed summer range George River animals were in better condition in April than September. But these long return migrations had an energy cost. The mean distance that the 18 satellite cows migrated 1987 to 1992 to reach the George River was >512 km (extremes from 245 to 1125 km). When cows had migrated a similar distance in 1982 (475 km) their mean Kidney Fat Index based on Huot & Goudreault's (1985) formula (FATP=-3.29+3.73lnKFIR) had declined from

Fig. 7. Summer mortality and birth weight of calves.

Note: Summer mortality index (calves/100 females at birth minus calves/100 females in October) declined as calf birth weights increased for those years (after 1982) after the physical condition of females had declined (Fig. 6). Calves at birth based on mean 69.3% $s_{\bar{x}}=2.27$, per 100 females, (1984 to 1993); the regression of parous percentages 1984 to 1993, $Y=84.712-0.172X$, $r=-0.067$ (X last two year digits, 13 observations, 422 autopsies, 24 611 parous counts). Data from literature included. Newborn weights in 1991 and 1992 provided by S. Couturier, pers. comm. Data for 1991 are from Leaf River herd.
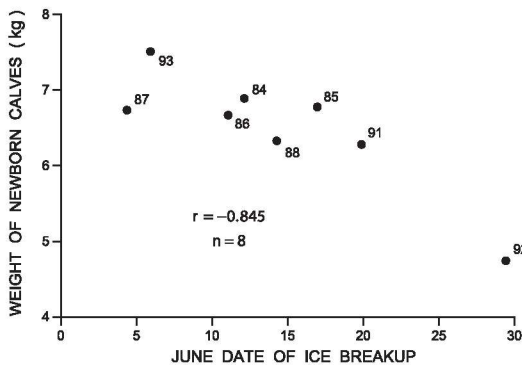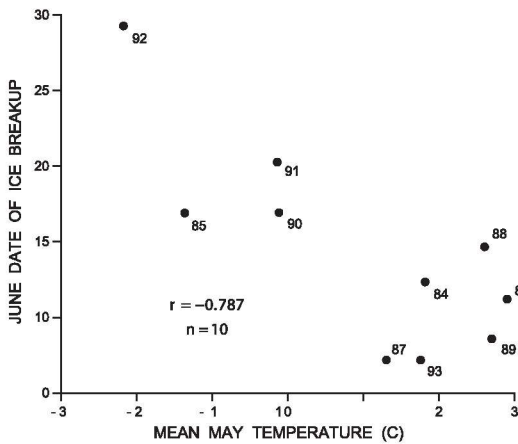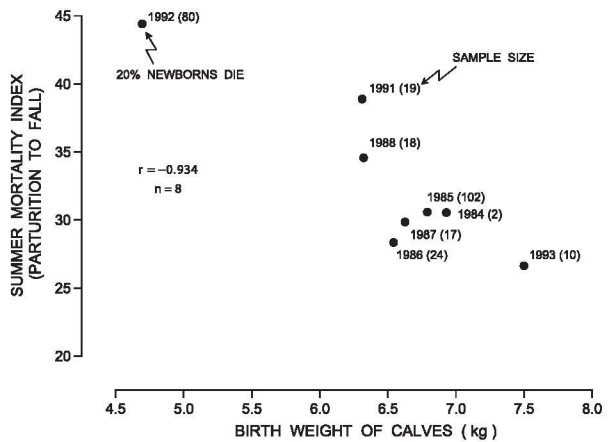

Fig. 6. a) The date of ice clearing Knob Lake, Schefferville was correlated with May temperatures. b) The weight of newborn calves was correlated with the date of ice break-up and spring phenology.

Note: The weight of calves listed only for the years after pregnancy rates declined (after 1982); weights in kg were also taken in 1978: 7.5, $s_{\bar{x}}=0.35$, (n=12), 1979: 7.4, $s_{\bar{x}}=0.61$, (n=3), 1980: 7.3, $s_{\bar{x}}=0.25$, (n=2), and 1981: 6.4, $s_{\bar{x}}=0.29$, (n=15). The correlation of the weights in these 4 latter years with ice break-up was $r=-0.462$. Newborn weights in 1991 and 1992 provided by S. Couturier, pers. comm.

65.2 g, $s_{\bar{x}}=13.27$, (n=9) in March 1-10, to 35.7 g, $s_{\bar{x}}=1.44$, (n=36) by April 15-29, when the herd was again sampled. Backfat reserves from these same females had declined from 21.4 mm, $s_{\bar{x}}=4.40$, in March to 4.3 mm, $s_{\bar{x}}=1.89$, April 15-29. The regression of maximum back fat of pregnant females on spring migration distances for George River females during this study was $Y=-5.604X^{0.268}+32$, $r^2=0.982$, n=19 collection periods (data from 15 years between 1976 and 1993, total animals 1293, some data from the literature included). Animals that had a return distance >600 km could arrive on the calving ground with less than 1 mm of backfat.

The rate of travel of the herd in April in 7 years of following the satellite females (1987-1993) was positively correlated with our population estimates generated from mortality/recruitment schedules, $r=0.794$ ($P_{0.05,\,5df}=0.754$) (Table 11). Our 1988 range survey indicated that the migration routes were heavily grazed and the density dependence likely resulted from interactions between animals searching for reduced supplies rather than from social facilitation; the migrating columns are not readily distinguished by group sizes (Duquette & Klein, 1987). These authors showed that animals migrating long distances fed more and reclined less than herds with shorter migrations. It appears that routes followed provided a reasonable compromise between risk and optimal foraging and that both were involved in the choices made.

6. May

In April in the 1980s the George River females commonly returned to the Labrador tundra passing

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Table 8. Weight (mean and standard error of the mean in parenthesis) of females in March or April compared to their location relative to tree line[1].

Year	Kilometers from tree line	Mean weight in kg	n
1976	160 km below tree line	101.0 (1.70)	21
1982	At tree line	95.9 (1.46)	36
1983	48 km below tree line	89.2 (0.73)	5
1984	132 km above tree line	84.1 (1.72)	11
1986	At tree line	87.0 (2.40)	12
1987	At tree line	96.3 (3.80)	11
1988	160 km below tree line	102.3 (3.29)	16
1993	152 km below tree line	97.6 (2.25)	20

[1] $Y = 101.240 - 0.137X$, $r = -0.837$ (X coded: 175 km below=0, tree line=70, 150 km above=130).

southeast from the Ungava Coast (Parker, 1981). A common sequence was that the animals traveled through where they would later calve and moved further south pausing near treeline. Here they fed on early greening graminoids little affected by over-grazing. This sequence increased the risk of preda-tion but allowed maximum energy intake in the last trimester of pregnancy.

Calf survival at parturition has been shown to be correlated with birth weight (Whitten et al., 1992; Adams et al., 1995) and Skogland (1984) pro-posed that forage at this stage of the fetus growth was critical. In 1992, the year of the latest phenolo-gy in Ungava since weath-er records have been kept at Schefferville (early 1950s), the calves born were extremely small (Couturier, unpubl. data; Fig. 6). We recorded a neonate mortality rate, from cows with a large udder not followed by a calf, of 20% (n=308) com-pared to the rate of 6.6%, $s_{\bar{x}}$=1.24, in 8 other springs. Calf weights at birth were correlated with spring phe-nology based on May tem-peratures and ice break-up (Fig. 6) and also correlated with summer mortality (Fig. 7). Females improved

their reproductive fitness by maximizing the weight of their calves at birth by optimally foraging in May.

A similar optimal foraging strategy may occur for the Porcupine Herd in Alaska. Calf survival in June in 10 years (1986-1995) was correlated with the abundance of green phytomass at calv-ing as measured by the Normalized Difference Vegetation Index (NDVI) (Griffith et al., 1998). Hence early sur-vival would also be correlated with the abundance of green phytomass in the latter stages of gestation. Cows in the Porcupine Herd, similar to the George River, calve in a low risk habitat on the coastal plain adjacent to the Brooks Mountains where predators are rare compared to the adjacent Brooks Mountains (Garner & Reynolds, 1986; see Bergerud, 1996: Fig. 1). But prior to parturition these Porcupine females are fur-ther south (Russell et al., 1992) foraging in an earli-er NDVI and where the bulls forage optimally after the females move north to the less risky coastal plain for calving (Russell et al., 1993).

We regressed the parturition weights of cows from 24 herds in the world against calf birth weight (Y=

Table 9. Comparison of the body condition of caribou in the Beverly Herd, Northwest Territories in March 1984, above treeline (Sifton) and below treeline (Porter) taken from Thomas & Kiliaan (1998). Mean value, standard error of the mean ($s_{\bar{x}}$) in parenthesis.

Condition measurements sex and age	Porter 70 km below	Sifton 130 km above	Difference Porter-Sufton
Kidney fat in g ($s_{\bar{x}}$)			
Females >3 years	126.5 (4.6) (n=63)	98.6 (9.5) (n=14)	+27.9
Males >3 years	116.8 (10.2) (n=10)	65.3 (4.4) (n=6)	+51.5
Percent marrow femur ($s_{\bar{x}}$)			
Females >4 years	87.3 (0.5) (n=52)	80.5 (3.5) (n=6)	+6.8
Males 2-4 years	87.0 (0.8) (n=13)	77.7 (3.1) (n=9)	+9.3
Total body fat in kg ($s_{\bar{x}}$)			
Females >4 years	12.5 (0.2) (n=60)	11.0 (0.6) (n=9)	+1.5
Males >2 years	11.0 (0.2) (n=17)	10.0 (0.3) (n=11)	+1.0
Body weight in kg ($s_{\bar{x}}$)			
Females >4 years	87.8 (0.9) (n=60)	77.8 (2.0) (n=9)	+10.2
Males >5 years	117.8 (5.0) (n=4)	92.7 (3.0) (n=3)	+25.2
Back fat in mm ($s_{\bar{x}}$)			
Females >4 years	21.0 (1.1) (n=60)	6.9 (2.9) (n=9)	+14.1
Males 3-5 years	4.6 (2.0) (n=14)	1.1 (0.4) (n=9)	+ 3.5

[1] Animals in better condition when below tree line 1981, 1982, 1985, and 1986 except 1980 than above tree line 1983 and 1987 (Thomas & Kiliaan, 1998).

Table 10. Condition of female caribou collected in April 1980 between a sample mostly above treeline (Hebron) and tree line (Nain)[1]. Mean value, standard error of the mean in parenthesis.

	Hebron April 3-4		Nain April 5-15		Probability of No Difference
10 month-of-age					
Mean backfat (mm)	0	(n=3)	0.2 (0.15)	(n=13)	0.3370
Mean kidney fat (g)	20.1 (7.80)	(n=3)	22.1 (1.69)	(n=13)	0.8390
Mean femoral fat (%)	52.3 (9.61)	(n=3)	57.8 (3.84)	(n=13)	0.5845
Mean body weight (kg)	42.1 (1.40)	(n=3)	45.? (1.04)	(n=13)	0.0944
Mean total warbles	119.7 (48.72)	(n=3)	59.0 (8.91)	(n=13)	0.3403
22 month-of-age					
Mean backfat (mm)	0	(n=4)	3.6 (1.18)	(n=14)	0.0100
Mean kidney fat (g)	22.9 (8.32)	(n=14)	40.8 (5.04)	(n=13)	0.1206
Mean femoral fat (%)	55.5 (17.89)	(n=4)	88.6 (0.86)	(n=16)	0.1612
Mean body weight (kg)	64.1 (3.54)	(n=4)	73.3 (1.88)	(n=15)	0.0711
Mean total warbles	146.0 (21.30)	(n=4)	53.7 (10.17)	(n=15)	0.0145
≥34 month-of-age					
Mean backfat (mm)	0	(n=10)	6.0 (0.72)	(n=87)	0.0001
Mean kidney fat (g)	39.6 (5.75)	(n=8)	84.8 (3.24)	(n=71)	0.0001
Mean femoral fat (%)	73.1 (6.13)	(n=10)	90.1 (0.42)	(n=88)	0.0214
Mean body weight (kg)	88.5 (2.33)	(n=10)	93.7 (0.82)	(n=91)	0.0602
Mean total warbles	50.3 (15.68)	(n=7)	39.1 (3.98)	(n=88)	0.5124
Fetus weight (kg)	2.1 (0.09)	(n=8)	2.5 (0.13)	(n=15)	0.0063

[1] Raw data sheets provided to A. T. Bergerud by G. Parker.

-0.104+13.543X, r=0.852). The weight of newborn calves for the George River herd was only 4.7 kg, s_x=0.13, (n=80) in the late 1992 year when calves died at birth and 3.2 kg greater the very next year, 7.5 kg, s_x=0.37, (n=10) in 1993 (Fig. 6). The predicted weights of their dams based on the calf/dam weight regression was 63.5 kg in 1992 and 101.5 in 1993. This weight disparity would have translated into major differences in milk supply. The neonate is the most vulnerable animal and requires the safest environment; the adult female is more able to cope with predators than her calf will be at birth and can afford the greater risk in May to produce a larger bodied calf in June.

By migrating early prior to green vegetation and then pausing to partake of the more nutritious forage relative near the lower risk birthing habitat she can contribute more resources to her fetus. One might predict the dates at which she abandons higher quality forage and moves to the calving area habitat, will be a product of the disparity in forage quality between the two locations assessed against the risk factor in both locations. In the mountains of British Columbia where predators were common and early calf mortality extreme, cows left forage of high quality in the lowlands to move to safer alpine birth sites

with low phytomass only a few days before parturition (Bergerud et al., 1984). On the George River satellite females in 5 years moved to the vicinity of their calving sites more than two weeks prior to parturition (mean date May 21, s_x=1.93, n=15 females).

Predation risk in the Pleistocene

Did the ancestors of the George River Herd alter ranges in response to predation risk 18 000 yr. BP when caribou in eastern North America persisted only south of the Laurentide Ice sheet that extended south to 40°N? The megafauna at 18 000 BP existed in abundance with its huge mastodons, mammoths, stag-moose, woodland muskox and more, as well as an assortment of large predators including the sabertooth, dire wolf, timber wolf, great short-faced bear and other cat and bear species.

We compared the locations of dated caribou fossils (C14-normalized) (from the literature) with the forest habitat types existing in those times reconstructed by paleobotanists from pollen core samples. We examined the vegetative maps of Delcourt & Delcourt (1981) of 18 000, 14 000, 10 000 and 5000 yr BP to determine the major dominant arboreal vegetation existing during the span of fossils from the Pleistocene and Holocene. We also consulted the Pleistocene-Holocene vegetational analyses of Ritchie (1987), Davis & Jacobson (1985) and the Historical Atlas of Canada, Vol. I, Univ. of Toronto Press, Plates 3 and 4.

Most biologists probably assume, as we did, that caribou living 18 000 years ago and south of the Laurentide ice were inhabiting the tundra/taiga zone immediately adjacent to the ice sheet. Banfield (1961:34) said "we may conclude that at the height of the Wisconsin glaciation reindeer were distributed in a tundra belt across the south of the ice sheet." He also noted they might frequent taiga habitats in the winter. But the fossil locations are not consistent with this arctic tundra/taiga paradigm; there are no fossil liter-

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Table 11. Mobility rates (standard error of the mean in parenthesis) of females in April to the Labrador tundra correlated with the population estimates based on mortality and recruitment calculations.

Year	Km/day[1] ($s_{\bar{x}}$)	Sample size	Herd size (in 1000s)[1,2]
1987	14.30 (2.16)	40	632
1988	11.53 (2.27)	30	644
1989	9.28 (1.63)	32	592
1990	6.33 (0.98)	18	575
1991	8.46 (1.10)	66	546
1992	5.80 (0.67)	84	492
1993	6.05 (0.88)	56	428

[1] Correlation coefficient, km/d vs. herd size, r=0.798, n=7.
[2] Herd size estimated from mortality recruitment schedules.

ature citations of Pleistocene animals dying in either the tundra or taiga zones for the interval 20 000 to 16 500 BP (Table 12). The 7 fossil caribou (5 locations) in this interval were all in the Appalachian Mountains: (1) New Trout Cave, Pendleton Co., West Virgina 29 500, 28 250, 17 600 yr. BP (Grady & Garton, 1982); (2) Beartown Cave, Sullivan Co, Tennessee, 20 000 BP. (Guilday et al., 1975); (3) Guy Wilson Cave, Sullivan Co., Tennessee, 19 700 BP. (Guilday et al., 1975); (4) Baker Bluff Cave, Sullivan Co, Tennessee 19 100 BP (Guilday et al., 1975); and (5) Yarborough Cave, Bartow Co., Georgia, 18 610 BP (Martin & Sneed, 1989).

For the period 16 500 to 12 500 BP caribou fossils were also predominately in the Appalachian Mountains (3 of 4 locations) (Table 12). Again there was a fossil bone (14 315) in Yarborough Cave , another in Saltville, Smyth Co., Virgina, 13 460 (Ray et al., 1967); a third in Darty Cave, Virgina, 14 650 (Faunmap, 1994), and the lowland exception was at Christensen Bog, Hancock Co., Indiana; the oldest fossil there 14 545 BP (Faunmap, 1994).

The Appalachian Mountains in those times was not an optimal foraging habitat. There was little altitudinal zonation in vegetation. The entire mountain chain was dominated by jack pine (Pinus banksiana) with spruce (Picea spp.) subdominant with a minor area of alpine tundra (Delcourt & Delcourt, 1981; Figs. 6 and 7). In this era more nutritious forage would have been available at lower elevations where there was a longer growing season. More mesic sites would also have been down below. Furthermore there was a large area of the forest type called the Mixed Conifer-Northern Hardwoods south of the Mountains, which would have been a richer habitat. This latter biotype was suitable habitat since caribou did move into these forests after 12

000 BP (Table 12). The floral mix in this association was analogous to the present day forest classification "The Lake State Forest." Caribou have been recently introduced to a Lake State Forest Association on Michipicoten Island, Lake Superior and are prospering in the absence of other ungulates and predators (Bergerud, A. T., unpubl. data).

Caribou began recolonizing habitats north of the Appalachian Mountains approximately 12 000 BP (Table 12). The distribution of animals 12 000 to 8500 BP did not suggest that they were selecting any major forest type (Table 12). Their range was shifting north as the ice retreated, but they could physically have made this move several millenniums earlier. This northward dispersal coincided with the disappearance of the Megafauna herbivores and predators. The last appearance dates of 45 megafauna species from fossil beds in North America based on ^{14}C dating showed a rapid extinction sequence between 12 000 and 10 000 BP (data from Kurten & Anderson, 1980: Table 19.6, pp. 364-365). Ten species had more than one last appearance date based on two or more fossil locations:

17 900 to 16 000 BP 2 disappearance dates
15 900 to 14 000 BP 1 date
13 900 to 12 000 BP 5 locations
11 900 to 10 000 BP 31 locations
9900 to 8000 BP 17 locations
7900 to 6000 BP 8 locations
5900 to 4000 BP 0 locations

We believe the caribou were in the mountains 20 000 to 13 000 BP spacing-out from most of the megafauna that were more common at lower elevations. Bergerud & Page (1987) refer to spacing-out as being dispersed from other caribou at calving and away from alternative prey species and their predators (Bergerud & Page, 1987). Dr. Dick Harington (Canadian Museum of Nature) indicated that the megafauna predators likely selected the young of the large herbivores in the Pleistocene (pers. comm.). Caribou were of the size to be selected. Montane caribou at present space-out from each other and alternative prey and their predators in the mountains of British Columbia (Bergerud et al., 1984; Bergerud & Page, 1987). The antler morphology of 8 of the 9 antlers of Pleistocene caribou described or depicted in the literature appear similar to present day montane antlers with the characteristics of some compression of the main beam (oval cross section), palmated high tops, and high bez tines (as described by Butler, 1986). These antlers conform to neither

Table 12. Locations of dated caribou fossils in the Pleistocene in Eastern North America compared between forest types existing at that time.

Time period and forest type	Size of area (km² in 1000s)[1]	Number of fossil locations		
		Observed	(No. of ages)	Expected
20 500 to 16 500 BP				
Appalachian Mts.	150	5	(7)	0.43
Tundra	340	0	(0)	0.98
Open spruce (taiga)	105	0	(0)	0.30
Spruce and jack pine	530	0	(0)	1.52
Jack Pine and spruce	560	0	(0)	1.61
Mixed conifer and hardwood	55	0	(0)	0.16
Total	1740	5	(7)	5.00
16 500 to 12 500 BP				
Appalachian Mts.	150	3	(3)	0.31
Tundra	340	0	(0)	0.70
Open spruce (taiga)	565	2	(6)	1.17
Spruce and jack pine	900	0	(0)	1.87
Jack pine and spruce	345	0	(0)	0.72
Mixed conifer and hardwood	110	0	(0)	0.23
Total	2410	5	(9)	5.00
12 500 to 8 500 BP				
Appalachian Mts.	150	4	(6)	1.86
Tundra	110	1	(1)	1.36
Open spruce (taiga)	265	4	(5)	3.28
Spruce and jack pine	415	2	(4)	5.14
Jack pine and spruce	330	5	(16)	4.09
Mixed conifer and hardwood	425	5	(10)	5.27
Total	1695	21	(42)	21.00

[1] The distributions and areas of the forest types based on Delcourt & Delcourt (1981) Figs. 5, 6, and 7 and include the region from the Atlantic Coast west to 98 degrees west longitude, north to the Laurentide Ice Sheet and Gaspé and south to the southern boundary of the Mixed Conifer and Northern Hardwood type. The Appalachian Mountains encompasses the area classified as Oak-Chestnut at 5000 and 200 BP in Delcourt & Delcourt (1981), Figs. 8 and 9. The area of the Appalachians subtracted from the other forest types located there at 18 000, 14 000 and 10 000 yr. BP.

sedentary woodland or migratory barren-ground animals. There should have been only one common gene pool south of the ice in the Pleistocene. Which is consistent with genetic studies of present day caribou living in eastern North America by Røed et al. (1991) and subspecies classifications of Banfield (1961) made on the basis of extant skull measurements.

These southern mountains provided a stable and survivable environment during the period of maximum ice and even during the global warming trend of the Holocene. The fossils at Baker Bluff Cave spanned 19 000 years (19 100 to 555 BP, Faunmap, 1994); nearby Beartown Cave had a 20 000 year old fossil. There was still a ridge of spruce on these Blue Ridge sites at 200 BP (Delcourt & Delcourt 1981, Fig. 9). The Pleistocene animals put survival and risk first and optimal foraging second; a sequence we believe continues to the present.

Discussion

Females with neonates select low risk habitats. They did so for the George River Herd even when the calving range was sufficiently degraded that pregnancy percentages declined by 25 percent (cf. Parker, 1981 vs. Crête et al., 1996). For the past two decades, biologists in Alaska have tried unsuccessfully to prove that economic development of the Arctic coastal plain calving range would displace calving females. Caribou are not going to be displaced from economic developments simply because the constructs are there. The opposite is more likely. There are numerous examples in the literature that document how other ungulate species in the absence of hunting have sought benign human activity if their predators avoided these areas. Visit the "Down Town" elk (Cervus elaphus canadensis) of Jasper or Banff, Alberta. It is myth that caribou are wilderness species that cannot coexist with development in the North (Bergerud, 1974a).

We do not agree with Klein (1988:190) who argues that caribou researchers to be "ethical" should: "undertake an active role in preventing human-induced environmental degradation". To be professional we should remain removed from debates that assume that human activity is synonymous with degradation and remain committed to documenting without prejudice the life history traits of our beast,

including their adaptability to their environment, regardless of the fall-out.

Our intent in this paper originally was to present some of the highlights of the research on the George River Herd 1974 to 1993. But on reading some of the conference proceedings on climatic change it was evident that caribou researchers were focusing on forage/energy considerations without discussing changes that warmer temperature might wrought on the interactions of wolves and caribou. We changed our emphasis to compare optimal foraging vs. predation risk observations 1974-93 and to provide control reference data on these contrary views. During our study there was no evidence of warming temperatures in Ungava. Our conclusions were that risk outweighed optimally foraging at calving and during the deep snow season (December through March). Forage considerations dominated from the end of the mosquito season (August 1) until snows generally exceeded 40 cm in early December and again foraging was foremost in May when early greens were available, prior to a last-minute shifts of cows to the low risk tundra range for parturition.

One major concern of arctic warming in the literature is that it will reduce the abundance of terrestrial lichens due to an increase in forest fires. Additionally with the predicted increase in snow depths it will require more energy for animals to dig feeding craters. Studies of lichen abundance have been legion during the past 40 years; some of us have spent endless field days looking in feeding craters and measuring lichen abundance (Bergerud, 1974c; 1971; 1988; Miller, 1976; 1980; Russell et al., 1993; Thomas et al., 1996). No demographic impacts have been documented in these investigations. Yet the attempts go on. (Arseneault et al., 1997) stated (page 66) "density-dependent limitation of winter forage... has not yet been described for large, lichen dominated, continental ranges of wild caribou." Their lichen studies for the George River encompassed Landsat imagery 1989 vs. 1992. For the George River Herd the range has historically been heavily burned repeatedly (Hare, 1959, Payette et al., 1989, Couturier & St-Martin, 1990). There was so much ablaze in July 1988 that we could not fly west of 72°W for range studies.

The George River Herd has had the highest number of caribou of any of the major herds in North America and these animals have had to crater in the deepest snows of any migratory herd. Even with an overgrazed summer range, fat reserves of pregnant females in March 1982, 1986, and 1987 averaged 11.7 kg, $s_{\bar{x}}=0.63$, of fat (1986 and 1987 from Couturier et al., 1989). These fat reserves are similar to that of females in the Beverly Herd and that pro-

jected for the Porcupine herd (Russell et al., 1993; Thomas & Kiliaan, 1998) and were greater than that for the Kaminuriak (Dauphiné, 1976). Thomas & Kiliaan (1998) showed that the condition of the Beverly herd in March of 8 years 1980 to 1987 was superior to the condition of caribou in the Kaminuriak Herd in early April in 3 years (1966-68). The superior condition of the Beverly Herd compared to the Kaminuriak occurred despite the finding that there were reduced lichen supplies on the Beverly Herd compared to the Kaminuriak in both the 1960s and 1980s as a result of forest fires, and despite the fact that densities were 3-4 times greater for the Beverly in the 1980s than the Kaminuriak in the 1960s (Parker, 1972; Miller, 1976ab; 1980; Thomas et al., 1996, Thomas & Kiliaan, 1998). We might rank these four major herds that have been investigated as to late winter body condition (Porcupine-1980s, George River-1980s, Kaminuriak-1960s, Beverly-1980s) as follows:

Snow Depths:
George>Kaminuriak>Beverly>Porcupine
Population densities:
George>Beverly>Porcupine>Kaminuriak
Lichen abundance:
George>or=Kaminuriak>Beverly>Porcupine
Body Condition:
Porcupine>or=Beverly>George>Kaminuriak.

There is no obvious relationship between snow cover, lichen abundance, animal densities or physical condition. The highest persistent density of caribou in North America (1974-1999) has been on the Slate Islands in Lake Superior (6 to 14/km²) (Bergerud, 1996). These islands have a history of logging and forest fires; there are no terrestrial lichens and there are no arboreal lichens within reach of the animals except on blowdowns. Changes in lichen abundance or winter energetics should not be a first order priority when evaluating impacts of climate change.

The other area where caribou biologists have voiced concern that climatic change could impact caribou is alterations in their summer foraging regime and energy budgets. The most persuasive arguments are those of Russell (1993) who raised concern about possible foraging problems with climatic warming in the Arctic based on a 1986 conference where the following predictions were made: (1) a 2-4 week earlier period of snow melt, (2) a 2-4 °C increase in summer temperatures. He reasoned that mosquito harassment might decrease foraging budgets and plant phenology and senescence could occur earlier in the growing season affecting the

availability of nutritious forage when lactation demands were high.

Mosquitoes are a major problem for caribou, but the biology of these insects is so complex, it is difficult to predict how they will react to warming temperatures and water level change. Each mosquito species has evolved it own life history schedule. We have even been more bothered at times in the Arctic by mosquitoes than in doing waterfowl research in the Manitoba potholes. At Indian House Lake during our energy budget studies in the summer there were major differences in mosquito harassment between years (1988-92) in numbers and annual chronologies. Peak abundance occurred in 1988 at 10 to 11 °C and in 1991 at 22 to 23 °C. On June 23 1989 the temperature reached 33 °C at Indian House Lake (44 °C in the sun) and the entomologist operating from Schefferville (McElligott, E. K., pers. comm.) felt the larvae might die from physiological stress in the warm waters. We had far fewer mosquitoes in 1989 than 1988.

We view the early growing season predicted with climate warming as a plus for caribou. Cows will be in better condition at parturition and birth weights will increase. The body size of caribou is determined by the length of the growing season. The correlation of total body length (Y) with the length of the growing season (days) for 24 herds in North America for males: $Y = -82640/(X-518.84)$, $r^2 = 0.799$ and for females $Y = -72949.13/(X-506.16)$, $r^2 = 0.784$. We may have larger caribou. Klein (1970) has argued that that the flora of the arctic is of higher quality than that foraged by woodland caribou, but it is the days available to forage on growing vegetation that drive growth. In time, with climatic warming, calving dates may also advance which might advance lactation demands to keep abreast with the earlier phenology. The dates of calving also vary with the length of the growing season. The correlation between the Julian Date of peak calving (Y) in 23 herds in North America had a high coefficient of determination with length of growing season (X) $r^2 = 0.991$, $Y = 129.680X/(-12.547+X)$. We believe caribou should benefit nutritionally with warming spring and summer temperatures.

Wolf predation is now accepted as the major limiting factor for moose and caribou in North America (see 24 references in Bergerud & Elliott, 1998). With global warming we can expect wolf numbers and their impacts to increase. We suggest four sequences of concern, and other workers would list other predation consequences. First, a warming Arctic could result in a decline in the tundra and with it the abundance of lemmings and arctic foxes (Alopex lagopus). Wolves inhabiting ranges overlapping arctic foxes are exposed to the Arctic fox rabies vector (MacInnes, 1987) and there have been serious outbreaks in Alaska (Weiler & Garner, 1987; Ballard & Krausman, 1997) and in Ungava (Bergerud, 1996). Rabies outbreaks in Labrador are documented back to the early 1800s (Elton, 1942). At that time it was called the arctic sled dog disease (MacInnes, 1987). The George River Herd exceeded the carrying capacity of its summer range about 1982 after the wolf population crashed; based on the mean pack size, the decline was 61% or on harvest statistics 81% (Bergerud, 1988). In the absence of this disease wolf populations in the Arctic would be limited by the prey biomass (Fuller, 1989) and might frequently exceed 7 wolves/1000 km² which could result in caribou declines (Bergerud & Elliott, 1986).

Second, with warmer winters we could expect greater snowfalls and depths. Caribou are more vulnerable to predation in deep snows, at times resulting in surplus killing (Mech et al., 1998). With excessive snow caribou might not reach the increased safety of their calving grounds. This happened in the case for the Nelchina Herd in 1964, 1965, and 1966 (Bergerud & Ballard, 1988) and recently for the Porcupine Herd resulting in major mortality. It is not that caribou can not cross 100% deep snow cover; in the mountains of British Columbia animals commonly move over extensive snow fields when brown substrates are available elsewhere; but in the Arctic extensive snow at lower latitudes may signal that calving grounds are still covered and lack brown substrates for concealment of newborns.

The caribou in the Northwest Territories and Ungava that winter in the relatively level physiography use frozen lake surfaces of the Canadian Shield to mitigate predation risk and enhance escape possibilities (Kelsall, 1968; Miller, 1976). They don't have the advantage of the reduced snow and open vistas in the mountains as does the Porcupine Herd or the advantage of being above an approaching predator. If climate change reduces the extent and duration of the frozen lake period this coupled with deeper snows in the forest would greatly enhance the effectiveness of wolf predation and caribou would be spending more time on the tundra in diminished physical condition.

Our fourth concern is the most serious. With increased warming and the advance of the tree line we can expect moose (Alces alces) to further extend their range north. Moose have been pushing north for decades increasing the prey base for predators and increasing the abundance of wolves. With the advance of the tree line this movement will be accelerated. This enhanced abundance of wolves, coupled with the loss of habitat that has reduced the spacing-

out advantages of woodland caribou, has resulted in an alarming rate of extinction of local populations on the southern edge of their range (Bergerud, 2000). When caribou returned to Ungava during the Holocene they were not followed by moose--the moose were still dispersing south from Beringia (Kurten & Anderson, 1980). Now moose are at the door. It takes only 0.10 moose per km^2 to allow wolves to reach 7/1000 km^2, a number too high to maintain caribou numbers (Bergerud & Elliott, 1986).

Whereas there is little we can do to reverse the adverse affects of climate change on forage/energy considerations, we can manage wolf numbers if warming temperatures result in increased predation rates. The problem is that the timber wolf is the icon predator of North America. This species is the most revered mammal in the Southern continental United States of America, more books, more paintings, more calendars than any other mammal, the symbol of wilderness, the balance-of-nature monarch.

However recently there has been some movement in the sentiments of professional biologists towards predator management. Many ground nesting birds in the United States are losing the habitat to space-out to minimize nest predation (Bergerud, 1988c; 1990) and this has recently been recognized in a special section of the Wildlife Society Bulletin "Impact of Predation on Avian Recruitment" Vol. 29, No. 1. Also several biologists researching woodland caribou have recognized that their subspecies is losing their race with wolf predation as their habitat is alienated for spacing-out and moose populations spread north expanding wolf numbers (see Rangifer Special Issues 9 and 10). Additional insights involve the recent introductions of wolves to Yellowstone Park and the wilderness area of Idaho. Now biologists in the lower 48 have had more contact with wolves and have the opportunity to test their ideas and evaluate the data published by biologists that have worked with moose-caribou-wolf systems in Alaska and Canada. But it is one thing to undertake the reduction of opossums, raccoons for game birds and another to gain public support to manage wolf numbers. Anti-hunting, animal rights groups, and some environmental groups would rather the caribou go extinct than reduce wolf numbers or interfere with the "natural balance." They don't relate to the George River Herd lesson of the 1950s; if you lose your caribou you lose your predators.

In reality with the present negative public opinion on predator management there are only two places left in North America where wolves could be reduced if it is shown that caribou numbers are threatened, the Northwest Territories and the Ungava Peninsula. It is our dearest hope that the First Nation people of the north can maintain their option to practice wolf management if climate change results in excessive wolf predation. However some environmentalists will try and take this option away. Note the recent article in the Globe and Mail newspaper, berating wolf hunting in the Northwest Territories. The wildlife programs in the North need to be developed so that wolf management is not subject to economic blackmail. Who would have thought that the Newfoundlanders could have lost their seal hunt, or that the grizzly bear hunt might end in British Columbia after animal rights people in London, England, who knew nothing about bears, promised boycotts? The declines of caribou in North America have generally resulted from overhunting and wolf predation (Bergerud, 1974b). Both can be managed. Come what may, if the abundance of the icon of the North can be supervised the George River deer will continue to assemble at "Caribou House" in the spring and pass by the ancient tent rings at Indian House Lake going west as in past millenniums.

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