The relationship between food intake and predation risk in migratory caribou and implications to caribou and wolf population dynamics

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Abstract: We examined the hypothesis that spring migration in barren-ground caribou (*Rangifer tarandus*) enhances access to high quality food, reduces predation risks or both. We related our findings to the hypothesis that one of the consequences of migration is that prey populations cannot be regulated by predation because predators are unable to respond numerically to changes in abundance of migratory prey. In the Northwest Territories, migration to calving grounds by pregnant cows reduced the risk of predation on neonates. Wolf (*Canis lupus*) densities on calving grounds averaged only 22 % of winter range densities because most wolves denned near tree line. The quality and quantity of food that was available to cows that migrated to calving grounds was lower than for bulls and other caribou that lagged far behind the pregnant cows during spring migration. Fecal nitrogen levels were higher in bulls than in cows in late May and early June but there were no differences in mid or late June. Areas occupied by bulls in late May had a greater biomass of live sedges than on the calving ground in early June. It appears that although food in July is abundant and nutritious, insect harassment prevents efficient feeding. Body fat reserves in both sexes declined to almost zero by mid-July, the lowest level of the year. Insect numbers declined in August and body fat levels increased to the highest level of the year by early September. Because the timing of caribou's return to the hunting ranges of tree line denning wolves was related to caribou density, our data were inconsistent with the suggested consequence of migration. Tree line denning by wolves and density-dependent changes in caribou migration suggests a mechanism for population regulation in caribou and wolves. We suggest that the process is as follows; when caribou numbers increase, some density-dependent factor causes range expansion in August (e.g., competition for food) causing caribou to return earlier to the hunting ranges of tree line denning wolves, more denning wolves have access to caribou, wolf pup survival increases and wolf numbers increase. The effect on caribou population growth will depend on the timing and magnitude of the wolf numerical response.

Introduction

Migration in large herbivores has probably been shaped by selection to reduce predation risk, to enhance access to high quality food or both (Fryxell & Sinclair; 1988, Fryxell *et al.*, 1988). Where migration reduces predation risk because predators are unable to follow migrants, predators may not be able to respond numerically to changes in prey abundance and migrants will more likely be regulated at relatively high densities by competition for food rather than by predation.

The causes and consequences of the migration of barren-ground caribou (*Rangifer tarandus*) to calving grounds have been debated for some time. Klein (1970, 1992) and Whitten & Cameron (1980) stated that caribou move to track seasonal changes in plant nutrient content and digestibility. Kuropat & Bryant (1980) suggested that by migrating to cal-

ving grounds Western Arctic herd cows were following an optimal foraging strategy and Eastland *et al.* (1989) argued that nutrient levels and digestibility were probably higher on the Porcupine caribou herd's calving ground during calving than in completely snow free areas further south. Conversely, Whitten & Cameron (1980), Skogland (1989, 1990) and Cameron *et al.* (1992) found that plant phenology was later and that plant biomass was lower on calving grounds during calving than in the more southerly areas occupied by bulls. Food quality (Bergerud, 1990), digestibility and biomass (Russell *et al.*, 1993) were found to be lower on calving grounds during calving than in the more southerly areas occupied by bulls. A simulation model indicated that pregnant cows would have an energetic advantage if they migrate with the bulls rather than migrating to calving grounds (Russell *et al.*, 1993).

Wolves (*Canis lupus*) and other predators are relatively rare on caribou calving grounds during calving (Whitten & Cameron, 1980; Heard & Calef, 1986; Bergerud, 1988; Fancy & Whitten, 1991; Cameron *et al.*, 1992; Heard & Williams, 1992). Messier *et al.* (1988) reasoned that because caribou migrate beyond the reach of denning wolves, whose movements are largely confined to the vicinity of their dens, then wolves could not show a numerical response to increased caribou numbers. Bergerud (1980), Heard & Calef (1986) and Heard & Williams (1992) suggested that wolves could show a numerical response to changing caribou densities because caribou show density - dependent range expansion and contraction. At high caribou densities more caribou return earlier to areas near tree line where most wolves den. If this results in higher wolf pup survival then wolves may show a numerical response to changing caribou densities. The timing and magnitude of the numerical response would determine when, or if, predation is inversely density-dependent (depensatory) or regulatory (see Messier, 1994).

In this paper we present data relating to the proposed causes and consequences of the migration of barren-ground caribou to calving grounds. Data were collected primarily on the Bathurst caribou herd, but also from 3 of the other large herds of migratory barren-ground caribou in the Northwest Territories; the Bluenose, Beverly and Qamanirjuaq (previously spelled Kaminuriak; see Williams & Heard, 1986)

Methods
In May and June 1990, 1991 and 1992 we documented the general movements of bulls and pregnant cows in the Bathurst herd during unsystematic flights in Cessna 185 and Bell 206B aircraft. In May and June 1990 we collected feces from the surface of the snow both on the calving ground and from areas occupied by bulls. In 1991 and 1992 we shot about 10 bulls and 10 cows in each of 3 seasons; May-June (28 May for cows in 1991, 29-30 May for cows in 1991, 3-6 June for bulls in 1991, 25-26 May for bulls in 1992), late July (27-29 July in both years), and early September (4-6 Sept in 1991 and 3-8 Sept in 1992). Total fat was estimated from backfat depth and weight of all fat adhering to both kidneys and total muscle was estimated from gastrocnemius weight based on the relationships in Adamczewski *et al.* (1987). Fat and muscle weights were divided by metatarsus weight to adjust for variation in body size. Diet was inferred from the analysis of plant fragments, collected from the rumen and feces of the shot animals, that were identified by microhistological analysis at the

AAFAB Composition Analysis Laboratory, Fort Collins, Colorado, USA. The concentration of nitrogen in the feces was determined using the micro kjeldahl technique and was used as an index of nitrogen in the diet.

Vegetation was sampled in both upland and lowland habitat. Biomass was determined by removing all vegetation, except mosses, from 10 2000 cm² sampling plots placed at random in each habitat type in areas occupied by bulls and cows in late May and early June, July and September 1990. Cut vegetation was immediately sorted into the following categories; lichen, live sedge and other monocots, dead sedge and other monocots, live forbs, live woody vegetation and other dead vegetation.

We estimated the magnitude and causes of neonatal mortality on the Beverly herd's calving ground between 11 and 16 June 1993. The sex, age and reproductive condition of all caribou observed were recorded from a helicopter while flying along lines systematically spaced across the calving ground. The helicopter was flown about 50 m above the ground at 100 kmhr⁻¹ although speed and altitude varied. Caribou were classified as neonates, yearlings, two year old or older males, and two year old or older females. Breeding females (pregnant or post-partum) were identified by the presence of a distended udder or hard antlers. Females without hard antlers and without a calf at heel but with a distended udder were assumed to have given birth and the calf had died. Barren cows had neither udders nor hard antlers but they carried about 10-15 cm of new antler growth. Field necropsies were carried out on all dead calves found during those flights. Calves with appropriately spaced puncture wounds and associated subcutaneous haemorrhaging were considered to have died from wolf predation.

Relative wolf densities were based on wolf sighting rates collected during calving ground surveys conducted between 1963 and 1993 and from spring composition surveys 1976 - 1994.

Results
Distribution and Movements
Spring and summer movements of both bulls and cows in the Bathurst herd were similar in 1990, 1991 and 1992. In late May and early June of 1990, 1991 and 1992, all pregnant cows were on the calving ground near Bathurst Inlet (no neonates were seen anywhere else) while the only place we found bulls was near treeline between 200 and 300 km further south (Figs. 1 and 2). Because our sampling for caribou distribution was not systematic we cannot rule out the possibility that there were no bulls elsewhere on the tundra or still within the boreal
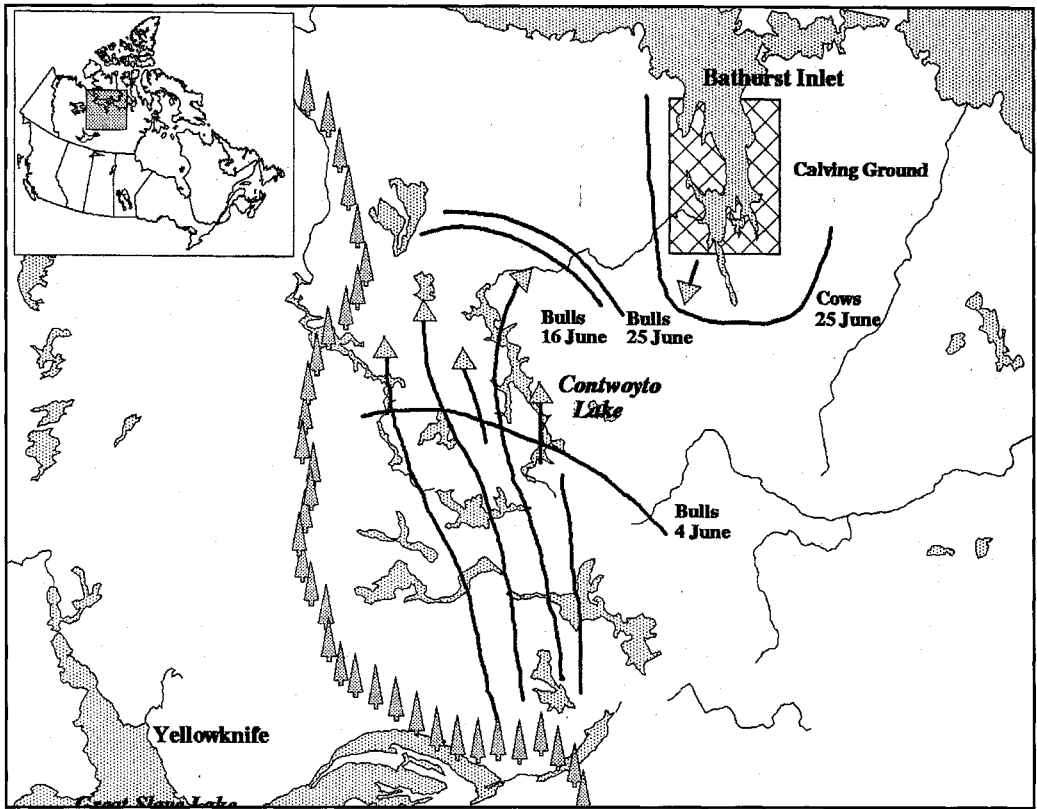
Fig. 1. Distribution of bulls and cows in the Bathurst caribou herd in June 1990. Concentric lines indicate the location of the most northerly bulls on June 4, June 16 and June 25, the location occupied by calving cows between 4 and 16 June and the location of the most southerly of the cows and neonates on 25 June.

forest but bulls typically make up only about one per cent of the animals on calving grounds e.g., 1.3% (23/1778) of the one year old or older animals classified on the calving ground of the Bathurst herd in 1986, 0.65% (17/2597) in 1990 and 0.49% (22/4533) and 0.59% (20/3408) on the Beverly herd's calving ground in 1988 and 1993 respectively. After calving, cows moved southwest and by 25 June 1990, the front of the cow distribution had almost met with the most northerly bulls which had moved north during that period. The sexes occupied the same general areas in July and September (Fig. 2).

Plant Biomass
Sedges (*Carex* and *Eriophorum* spp.) are the first plants to produce new spring growth after snowmelt and they were either the first or second most common food item in the diet of both sexes in late May and early June. The biomass of live sedges in lowland habitats was higher within the areas occupied by bulls than the biomass of live sedges in lowland habitats on the calving grounds (Table 1; Mann-Whitney U-test, U=7, n_1=n_2=10, P<0.01). Biomass of live sedges was highest in July.

Diet quality
Between 1 and 4 June 1990, nitrogen in feces collected from areas occupied primarily by bulls was greater than nitrogen in feces collected on the calving ground (Fig. 2; t=4.77, df=32, P=0.0001) There were no nitrogen concentration differences in feces collected from areas occupied by bulls and cows on 13-15 June 1990 (t=0.29, df=19, P=0.78) or 25-26 June 1990 (t=0.49, df=34, P=0.62). Similarly, in late May and early June of both 1991 and 1992, fecal nitrogen from bulls shot near treeline was significantly higher than in cows collected on the calving ground (Fig. 3; F=16.99, P=0.0002), but there were no differences between the sexes in July of either year when they occupied the same area. We shot one cow that was with the bulls in June 1991. Plant fragment analysis of fecal and rumen samples indicated that her diet was more similar to the bulls collected in the same area than it was to the diet of cows on the calving grounds. Nitrogen in the feces of that cow (2.05%) was also more similar to the fecal nitrogen of bulls collected in the same area ($\bar{x}$=2.08%) than it was to the fecal nitrogen of cows on the calving grounds ($\bar{x}$=1.76%).
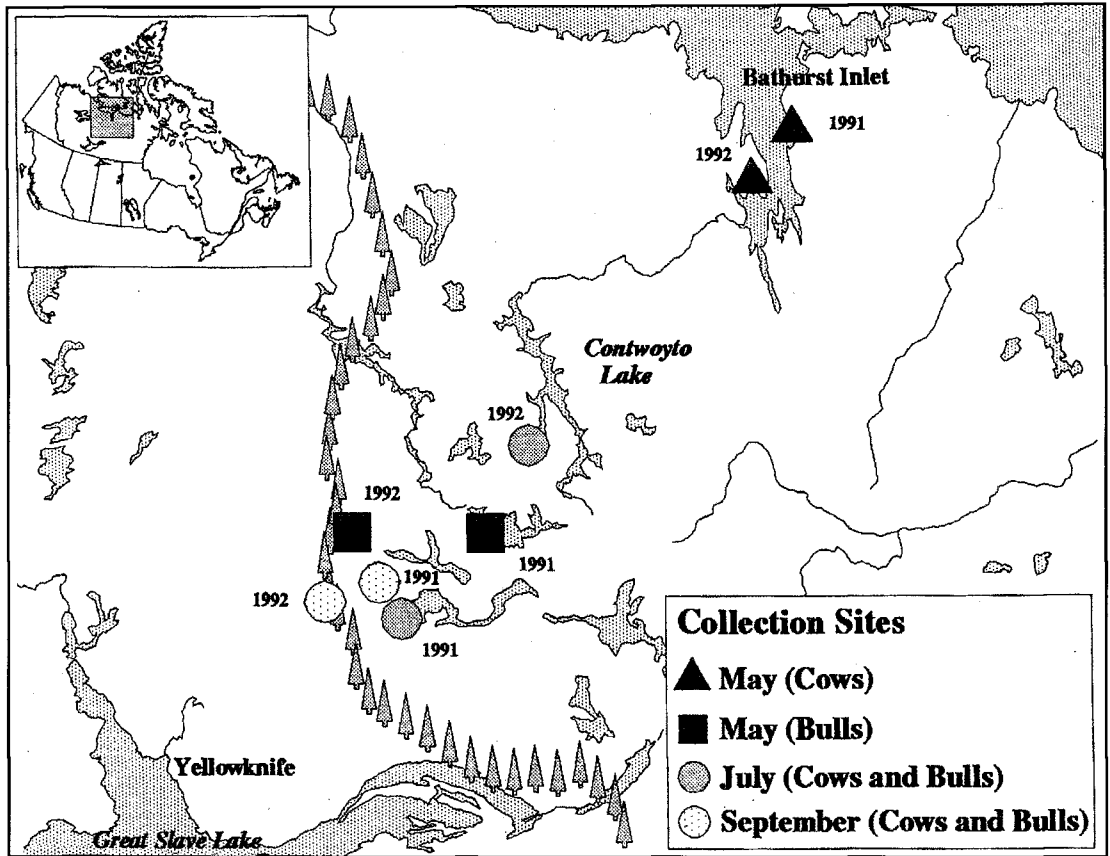
Fig. 2. Locations where we collected caribou from the Bathurst herd in 1991 and 1992. May collection sites were in different places for bulls and cows. Because the sexes occupied the same general areas in July and September both bulls and cows could be collected at the same site.

Body condition
Body fat and muscle decreased in both sexes from May to July and increased from July to September in both years (Table 2). Seasonal differences in fat weights were significant for both sexes when years were combined (cows, $F=28.13$, $P=0.0001$; bulls, $F=29.92$, $P=0.0001$). When years were combined, seasonal differences in muscle weights were significant for cows, but not for bulls where the sample

size was small (cows, $F=23.13$, $P=0.0001$; bulls, $F=2.72$, $P=0.08$). Both sexes had significantly more fat in July 1992 than in July 1991 ($F=120.31$, $P=0.0001$) but years did not differ in May or September (May, $F=0.92$, $P=0.34$; September, $F=3.5$, $P=0.07$).

Wolf density and predation on neonates
Wolf densities on calving grounds during calving, as

Table 1. Mean biomass (SE) of lichen and live sedges within 10 2000 cm^2 sampling plots on the Bathurst caribou herd's range in 1990.

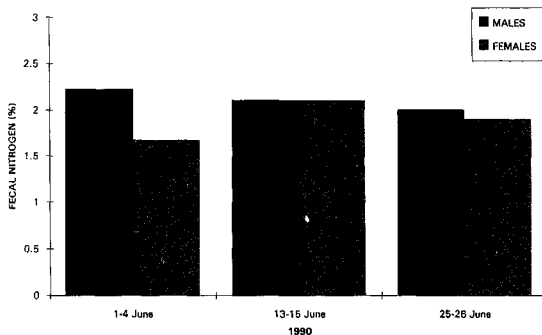| Sampling location	Lichen biomass (g/m^2)		Live sedge biomass (g/m^2)	
	Upland	Lowland	Upland	Lowland
Bull distribution, May-June	21 (7.3)	0.2 (0.11)	0.1 (0.07)	6.6 (2.78)
Cow distribution, May-June	13 (1.6)	0.3 (0.30)	0.0 (0.0)	1.5 (0.66)
Distribution of both, July	12 (3.1)	3.3 (1.35)	1.0 (0.36)	12.8 (2.62)
Distribution of both, September	390 (69)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

Fig. 3. Fecal nitrogen concentrations from areas occupied by bulls and cows in the Bathurst caribou herd in 1990.

indexed by the wolf sighting rate, averaged only 22% of densities on caribou winter and spring ranges, i.e., in March and April. This trend was the same for all 4 herds (Table 3). On the Beverly herd's calving ground in 1993 we saw 16 wolves in 64.2 h of flying (24.9 wolves/100 h) and wolf predation accounted for 70% of neonatal deaths (23 of 33 calves examined). By 1 week after the peak of calving 11.4% (4,310 of 37,654 parturient cows) of neonatal calves had died. Based on the proportion of necropsied calves that had died from wolf predation, 8% were killed by wolves (0.70 x 11.4) and 3.4% died of other causes.

Discussion

Our data suggest that by migrating to calving grounds, cows sacrificed foraging benefits which would have been available to them had they migrated as the bulls did. The differences between the sexes, in March to July movements, were similar to other migratory barren-ground caribou herds (e.g., Parker, 1972; Fancy et al., 1989) and other researchers have also noted that plant phenology is later and that plant biomass is lower on calving grounds, than in the more southerly areas occupied by bulls (Whitten & Cameron, 1980; Russell et al., 1993). However, even though food biomass on calving grounds was low, it is possible that biomass was high enough for calving cows to obtain foraging benefits, when coupled with the increased digestibility of new plant growth. Our data on fecal nitrogen

Table 2. Seasonal changes in fat and muscle weights of bulls and cows in the Bathurst caribou herd in 1991 and 1992.

Sex/ Collection period	Fat index						Muscle index					
	1991			1992			1991			1992		
	Mean	sd	n	Mean	sd	n	Mean	sd	n	Mean	sd	n
Cows												
May-June	4.6	2.2	11	6.2	3.7	10	0.19	0.02	11	0.20	0.02	10
July	-1.4	0.37	10	1.4	0.6	8	0.15	0.02	10	0.15	0.02	9
September	22.4	12.8	8	7.0	6.8	9	0.20	0.03	8	0.18	0.02	9
Bulls												
May-June	5.3	3.7	9	5.5	2.0	10	0.18	0.04	9	0.19	0.02	10
July	1.1	4.6	8	2.3	1.4	10	0.16	0.03	10	0.17	0.02	9
September	18.4	12.3	11	14.5	8.8	10	0.16	-	1	0.20	0.02	4

Table 3. The number of wolves seen per 100 hours when flying over caribou in March and April and on the calving grounds during calving in June (number of years of data; number of flying hours).

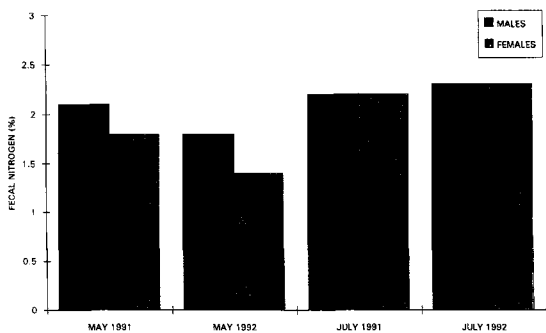|	Bluenose	Bathurst	Beverly	Kaminuriak
March and April	38 (11;507)	100 (11;483)	106 (15;655)	70 (6;589)
June calving ground	1 (4;200)	8 (11;531)	45 (8;414)	6 (8;400)
Weighted means:	March and April = 80			
	Calving ground = 17			

Fig. 4. Fecal nitrogen concentrations from bulls and cows collected from the Bathurst caribou herd in May and July of 1991 and 1992.

concentration show that this was not the case. Nitrogen intake by cows on the calving ground, as determined from fecal nitrogen, was lower than nitrogen intake by bulls. The difference in food quality between the sexes was probably important ecologically because comparatively small differences in food quality or protein intake can markedly influence weight gain and survival in ungulates (Albon & Langvatn, 1992). Moreover the greatest differences may have occurred in late April and throughout May, before our collections began, not in late May and early June. Although green vegetation was rare in early June on calving grounds, before that it was entirely absent. The general phenology of the environment suggests that bulls would have had green food available to them much earlier than cows. Differences in fecal nitrogen were unlikely the result of differential foraging between the sexes at that time of year because fecal nitrogen did not differ between sexes when they occupied the same area. Fecal nitrogen from the one cow we collected in June 1991 was similar to that of the bulls with which she was associating and fecal nitrogen did not differ between the sexes in late May in caribou on Southampton Island, where both sexes occupy the same area (Heard & Ouellet, 1994),

The advantage of migrating to calving grounds appeared to be a lower predation risk for neonates. Bergerud (1988, 1990), Fancy & Whitten (1991) and Cameron et al. (1992) also made this argument but our paper provides data on relative wolf abundance, based on wolf sighting rates, to support that conclusion. There are fewer wolves on caribou calving grounds because most wolves den near tree line often hundreds of kilometres away (Heard & Williams, 1992). Relatively more wolves den near the Beverly herd's calving ground and sighting rates are correspondingly higher. We suggest that our estimate of 8% wolf predation mortality of all neo-

nates by one week after the peak of calving, in a year when wolf abundance was close to our long term average, represents strong selection for cows to attempt to reduce predation risks. Our estimate of 70% of all neonatal mortality from wolf predation was similar to the mean wolf predation mortality for the Beverly herd in, 1981,, 1982 and, 1983 of 68.5% (Miller et al. 1988).

We suggest that changes in body fat and muscle over the summer is primarily related to the level of insect harassment which affects time spent feeding (Klein, 1992; Russell et al., 1993). Caribou aggregate into dense groups and body fat reserves decline in July when insect harassment is greatest. When insect numbers decline in August, the large aggregations break up and caribou amass large amounts of fat even though plants are senescing. Because the time period of fat assimilation is so short, we suggest that caribou attempt to reduce competition for food by spacing out as widely as possible. This could explain the density-dependent range expansion and contraction observed in migratory caribou populations (Simmons et al., 1979; Bergerud et al., 1984; Heard & Calef, 1986; Valkenburg & Davis, 1986; Messier et al, 1988; Couturier et al., 1990) even at the cost of increased predation risk.

The potential exists for wolves to show a numerical response to changing caribou densities because wolf pup survival appears to be related to caribou availability (Williams & Heard, unpubl. data). We suggest that when caribou numbers increase and caribou expand their summer range, more caribou come earlier within the hunting ranges of tree line denning wolves, pup survival increases and wolf numbers increase (Heard & Williams, 1992). There is little variation possible in the wolf functional response because their diet is almost exclusively caribou throughout the year (Williams & Heard, unpubl. data). The effect of the resulting change in predation rate on caribou numbers will depend primarily on the timing and magnitude of the numerical response.

Our understanding of caribou population dynamics would increase if we knew more about the trade-off between food intake (or some other density-dependent cause of range use changes) and predation risk in August. A test of our hypothesis requires that predation rate be measured and evaluated as being either independent of density, depensatory (inversely density-dependent) or density-dependent and of sufficient magnitude to stop herd growth (Messier, 1994). The dynamics of the George River herd (Couturier et al., 1990) represents a potential test of our hypothesis. As the size of the George River herd has increased, competition for summer food has increased, as indexed by

reduced fall fat and pregnancy rates (Couturier *et al.*, 1990), caribou are expanding their summer range, caribou are arriving earlier at tree line (John Russell pers comm.), and wolf numbers are increasing (Toby Anderson and other Nain hunters, pers comm.). Herd size may still be increasing (see Couturier these proceedings). Those observations are consistent with our hypothesis but the effect of wolf predation cannot be determined until population growth stops.

Acknowledgements

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