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ECOLOGY OF AN INTRODUCED CARIBOU POPULATION ON SOUTHAMPTON ISLAND, N.W.T., CANADA

BY

JEAN-PIERRE OUELLET ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Abstract

Caribou (*Rangifer tarandus groenlandicus*) were hunted to extinction on Southampton Island by 1955. In 1967, 48 caribou were captured on neighboring Coats Island and released on Southampton Island. I documented the population dynamics from introduction to 1991, based on aerial survey data. I explored the relationships among growth, body condition, reproduction, and food availability. I analyzed short-term impact of caribou grazing on the vegetation using a series of small exclosures (5m X 5m; n=13) located in the dominant plant communites; long-term impact was assessed using historical data. Finally, I determined the consequences of defoliation on the net production and chemical composition of the vegetation by performing clipping experiments, in large exclosures (22m X 22m; n=4), on the dominant forage types available to caribou (deciduous, evergreen and semi-evergreen shrub species, two types of graminoids, and lichens). Since introduction, the population has increased at a rapid and steady rate (lambda = 1.276) and was estimated at 13 700 one year old and older caribou in summer 1991. Associated with this population increase there has been a reduction in lichen standing biomass. *Per capita* winter food availability was high on Southampton Island, and results obtained for physical growth (i.e. size at physical maturity, sexual dimorphism), body condition (i.e. spring body condition), and reproduction (i.e. yearling pregnancy rate) relative to previous reports, including the nearby Coats Island herd, suggest that these processes may react in a density-dependent manner in northern predator-free populations. Based on the observed population growth rate, caribou on Southampton Island did not show high winter mortality in some years as reported on Coats Island. This suggests that the effect of adverse climatic conditions on population dynamics increases under resource limitation. From experimental clipping, I found that defoliation modified the net production and chemical composition of forage plants. Defoliation can reduce plant net production, but the response differed among forage types. However, defoliation can enhance forage quality. Clipped graminoids contained nitrogen, magnesium, potassium and phosphorus levels above the maximum concentration obtained from controls at any point during the growing season. With respect to management, a significant increase in the annual hunting quota is recommended.

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Chapter 1.

General Introduction

Caribou were common on Southampton Island in the early 1900s although few records describe their early distribution and abundance. However, by 1925 the population was estimated to be no more than 30 caribou, and the last animal apparently died in 1953 (Mikitok, Bruce pers. comm.). The decline has been attributed to high hunting pressure by native people inhabiting the island (Parker 1975). In 1967, 48 caribou *(Rangifer tarandus groenlandicus)* from Coats Island (≈100 km southeast of Southampton Island) were re-introduced to Southampton Island (N.W.T.), as a means of supplementing the diet of the local Inuit community, Coral Harbour (Manning 1967).

The Department of Renewable Resources, N.W.T., was concerned about the future of the Southampton herd because of the demographic behavior of certain *Rangifer* populations introduced on other islands. Leader-Williams (1988) summarized the results of introductions of reindeer and caribou to islands, or isolated portions of islands, throughout the world. Out of 31 introductions, five failed initially, whereas the remainder entered irruptive oscillations (Riney 1964; Caughley 1970). Of these 26, 11 have been considered successful, seven unsuccessful, one uncertain, and five too recent to categorize, and two probably successful, including the Southampton Island herd. Factors such as island size, latitude, and previous caribou habitation, do not seem to explain successful versus unsuccessful attempts. However, successful introductions occur only when reindeer or caribou depend on vascular species instead of lichens for their winter forage. Lichens are probably the major components of winter diet on Southampton Island (Gates *et al.* 1986b). Leader-Williams (1988) pointed out that a key factor is the degree of resilience of the vegetation to grazing. Scheffer (1951) outlined events following liberation of reindeer on St Paul Island, Alaska. The population increased for a period of 27 years and then declined dramatically. The decline was associated with the depletion of lichens that were an important food source during winter (see also Klein 1968, 1987). Unfortunately, in the Arctic very little is known about the ecology of introduced herds (Leader-Williams 1988). Nevertheless, a substantial depletion of winter food resources (lichens), followed by a dramatic population crash, can be considered a possibility for the Southampton Island herd. Therefore, it is crucial to describe the fate of the animals introduced to the island and monitor the impact of caribou on the vegetation.

Bergerud (1980) has suggested that continental caribou populations in North America are limited largely by hunting and predation. According to Messier *et al.* (1988), this view may be incorrect for large caribou herds in tundra and forest-tundra ecosystems. Messier *et al.* (1988) suggested that year-round competition for food resources and greater energy expenditure associated with range expansion, are probable regulatory factors for the George River herd (northern Labrador-Quebec). They argue that the nature of caribou-habitat interactions in continental regions generate long-term fluctuations in caribou numbers if human exploitation remains low. Assuming that lichens are the major source of food, a rapid increase in caribou population density cannot be cued closely to annual plant biomass production; a condition required for long-term stability of plant-herbivore systems (Caughley & Lawton 1981). Because lichens grow slowly (Pegau 1968), standing crop represents an accumulation of many decades of growth. More recently, Crête *et al.* (1990) proposed that the quantity of deciduous shrubs could be the main regulatory factor for the George River herd. Although these two hypotheses differ they both suggest that animal-plant interactions may play a crucial role in the population dynamics of caribou populations subjected to predation (see also Klein 1970).

For predator-free areas, intraspecific competition for winter food regulates reindeer numbers (Leaders-Williams 1980; Skogland 1985, 1990). For example, reindeer density on South Georgia (Antarctic) gradually declined when their preferred winter grass, *Poa flabellata*, was reduced in quantity (Leaders-Williams 1980). Competition for food affects tooth wear, growth, and body weight, and, ultimately, reproduction and survival (Skogland 1985, 1990). However, winter climatic conditions (snow depth and hardness) may restrict forage availability (Gates *et al.* 1986a; Miller *et al.* 1982; Reimers 1982, 1983) and consequently affect population numbers. Density-dependent processes have not been investigated for caribou populations experiencing no predation. Consequently, analyzing the relationship between growth, condition, reproduction, and density would help in understanding the dynamics of caribou populations living in predator-free areas.

Grazing can modify productivity and chemical composition of forage plants. There is a continuum of plant response to herbivory, from undercompensation to overcompensation of growth (Maschinski & Whitham 1989), and from reduction (Bryant *et al.* 1983) to enhancement (McNaugthon 1984) of quality. Assuming that caribou may be food limited, these responses in productivity and chemical composition of the vegetation could also have important consequences on the dynamics of caribou population. However, only a limited number of studies have considered the impact of herbivory on forage species available to caribou on the tundra (see Archer & Tieszen 1986).

The importance of caribou and reindeer to man has resulted in the initiation of a wide range of studies in the Arctic. However, the direct influence of man (e.g. overhunting) upon most herds has sometimes made it difficult to investigate the ecology of the species in the wild (Leader-Williams 1988). The Southampton Island caribou herd provides this opportunity, as human activities have had a limited impact on the herd since re-introduction. In addition, because Southampton Island is predator-free, an ecological study in such a "simple" system may provide some insights into the ecology of continental herds. Clearly, the present system represents an interesting population management problem and a good opportunity to address some fundamental questions relevant to population dynamics. It also provides a unique chance to document the ecology of an introduced caribou herd.

The study is summarized in four papers that were intended to meet the following specific objectives:

Chapter 2: Document the dynamics of the Southampton Island caribou population from introduction (1967) to 1991;
Chapter 3: Explore the relationships between growth, body condition, reproduction, and food availability in caribou;
Chapter 4: Investigate the consequences of caribou grazing on the vegetation cover;
Chapter 5: Analyze the response, net production and chemical composition, of caribou forage to defoliation.

In each chapter an attempt was made to discuss findings in regard to the dynamics of caribou populations. Finally, a general discussion (Chapter 6) integrates findings and explores management options for the introduced Southampton Island caribou population.

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Chapter 2.

Population dynamics of caribou

Introduction

Caribou *(Rangifer tarandus groenlandicus)* and wolves (*Canis lupus*) were common on Southampton Island until the early 1900's (Parker 1975). But caribou were rare by 1935, and the last individual died in 1953 (Mikitok, Bruce pers. comm.). In 1967, 48 caribou (19 cows, 7 yearling females, 2 female calves, 6 bulls, 6 yearling males and 8 male calves) were captured from neighboring Coats Island and released at Native Point, Southampton Island (Figure 2-1) (Manning 1967). The typical response by a population after such introductions is an irruption, which follows a well-defined sequence of four stages (Riney 1964; Caughley 1970). However, the outcome has differed among introduced *Rangifer* populations. Leader-Williams (1988) summarized results of introductions of caribou and reindeer to islands, or isolated portions of islands, throughout the world. Out of 31 introductions, 5 failed initially, whereas the remainder entered irruptive oscillations. Of these 26, 11 have been considered successful, seven unsuccessful, five too recent to categorize, one uncertain, and two probably successful, including the Southampton Island population. None of these populations experienced heavy hunting pressure. Factors such as island size, latitude, and previous caribou habitation, did not seem to determine success. However, successful introductions of caribou and reindeer appear to occur only when vascular species rather than lichens are the dominant winter forage (Leader-Williams 1988). Unfortunately, in the Arctic very little is known about the ecology of introduced herds (Leader-Williams, 1988). Nevertheless for the caribou on Southampton Island which rely heavily on lichens in winter (see Chapter 3 and Chapter 4) a substantial depletion of winter food resources, followed by a dramatic population crash, can be considered a possibility. Consequently, it is important to monitor the fate of the caribou introduced on Southampton Island.

On Southampton Island there are no predators. This factor is assumed to be responsible for sexual segregation of caribou (Jakimchuk *et al.* 1987; Tom Bergerud & Doug Heard, unpub. data). Consequently, I might get some insight into this attribute by looking at distribution and group composition in caribou introduced on Southampton Island.

The objective of this chapter was to document the population dynamics, distribution and social organization of a caribou population from introduction (1967) to 1991.

Study area and methods

Southampton is a 43 000 km^2 island lying at the north end of Hudson Bay (Figure 2-1). It is almost always surrounded by open water, even in winter. The west half and most of the southwest (Bell Peninsula) of the island consist of low flat limestone plains dominated by *Dryas* barrens and sedge meadows (Parker 1975). The remainder of the island is steep to rolling Precambrian shield dominated by *Alectoria* and *Cetraria* lichens and heaths. An abrupt escarpment divides these two geological formations. The cold waters of Hudson Bay contribute to a cool, windy climate similar to that found on arctic islands of higher latitude. The average wind speed is 20 km/h, mean annual temperature is -11°C with mean daily temperatures above freezing only in July and August. Snow cover persists from mid September until mid June. Precipitation averages 13 cm of rain and 133 cm of snow per year, twice the amount at Baker Lake, located on the mainland at the same latitude (Parker 1975).

In November 1978, a stratified systematic aerial strip transect survey was performed to estimate caribou numbers. The survey was flown in a DeHavilland Beaver, 120 m above ground level, with an observer on each side counting caribou of all ages within a 440 m wide strip (Table 2-1). In 1983 (between 25 June and 12 July), as part of a general wildlife inventory of the island, arbitrary flights in a Cessna 337 fixed-wing aircraft and a Bell 206 helicopter covered all parts of the island and provided data on both distribution and composition.

Between April 1980 and April 1984, eight trips were made by snowmobile to determine caribou group composition. Observers drove through the areas of known caribou distribution and recorded the age and sex of all animals seen. Spotting scopes and binoculars were used to avoid disturbing the caribou.

In June 1987, caribou numbers were estimated using a stratified random block design (Table 2-2). A Bell 206B helicopter was flown at various speeds and altitudes, depending on viewing conditions. Observers in the rear seat reported all caribou they saw to a navigator. Each animal seen, including those detected by the navigator and the pilot, was approached more closely so that its age and sex could be determined. The census zone was divided into five strata, each receiving differential coverage, based on population density information obtained from a reconnaissance flight and previous census data (Table 2-2).

In March 1990, a stratified systematic aerial strip transect survey was performed to estimate caribou numbers and distribution. The survey was flown in a Cessna 337 fixed-wing aircraft at 120 m above ground level with an observer on each side counting caribou of all ages within a 400 m wide strip (Table 2-3).

In 1991, the census followed the same methodology as in 1987 (see above). However, to allocate the effort better and to cover the entire island, the two strata defined as low density (strata 4 and 5) were surveyed using an aerial strip transect survey flown with a Cessna 337 fixed-wing aircraft (Table 2-4).

Caribou counted in June and July 1983, June 1991, and during snowmobile trips in April 1980 and 1981 were classified only as calves (< 1 year old) or older animals. No composition data were recorded in November 1978, in March 1990, and for part of the June 1991 census (i.e. strata 4 and 5). During snowmobile trips in November 1981, May 1982, December 1982, April 1983, November 1983, and during the April 1984 census conducted by helicopter, older animals (> 1 year old) were also classified as males or females.

In 1987 and 1991 (strata 1 to 3), caribou were classified as either calves (< 1 month olds), yearlings (1 year old), cows (2 year old and older), bulls (two year old and older) and unknowns. Calves were distinguished by their small size and reddish colour. Yearlings had short faces and small bodies. Many bulls could be recognized by their large antlers but sex determination of small antlered animals were based on external genitalia. Unknowns were one year old and older caribou that were not classified to age or sex. Unclassified animals (n=45 in 1987, n=21 in 1991) were allocated proportionally among classified bulls, cows and yearlings.

The Jackknife technique (Cochran 1977) was used to determine the mean and variance of the age and sex ratios. Calculation of population estimates and their standard errors followed Jolly (1969). Aggregation size was defined using Jarman's measure of typical group size; the size of a group experienced by the average individual (Jarman 1974).

Results

Distribution

Only the March 1990 and the June 1991 surveys were designed to document the distribution of caribou (Figure 2-2). For both surveys, caribou were seen along the ridge north of Mount Soarre, the coast of Bell Peninsula and Cape Low, and the upland areas north of Coral Harbour. Caribou were rarely seen far from the coast of Bell Peninsula and Cape Low, or west of the ridge of Mount Soarre and in the high country along the northeast coast. There did not seem to be a difference in winter and summer distribution, but deep snow (see Chapter 4) may have forced the animals to avoid the northeast coast in winter. The November 1978 survey was restricted to a small part of the island but the June 1983 and 1987 surveys were much more extensive (Figure 2-2). Although the surveys did not give systematic coverage to the entire island, caribou distribution within the areas surveyed in 1983 and 1987 was similar to 1990 and 1991. Consequently, these surveys did not document any obvious density-dependent changes in caribou distribution between 1983 and 1991.

Bulls and cows were rarely found in the same area. Most bulls were found around Cape Low and Coral Harbour, but both bulls and cows were seen on Bell Peninsula and on the east coast south of Cape Donavan. Based on late June distribution surveys, cows did not appear to concentrate on a particular calving ground. Yearlings were found in all areas used by adults of both sexes.

Group size and composition

In all samples, typical group size (one year old and older caribou) of groups with calves was larger than groups that did not contain calves (Table 2-5). The only seasonal pattern to group size variation was that groups with calves tended to be large after the rut in November. Excluding November groups, there was a significant linear relationship between typical group size of "all" groups and population size (r^2=0.713, n=8, *P*=0.008).

Mixed groups of cows and bulls were most common in November, closest to the rutting period, and least numerous in June after calving (Table 2-6). It appeared that calves began to leave cow groups when they were 10 months old. All calves were in cow or mixed sex groups in the springs of 1982 and 1983, but the results may be somewhat biased because there were few bull groups in those samples (Table 2-6). In April 1984, there was more sexual segregation among adults and 28% of the calves were found in bull groups. This trend continued through June when, with greater sexual segregation among adults, more calves (now yearlings) had segregated from their mothers (Table 2-7). By late June 1987, 78% of the yearlings were in all-yearling or bull groups, and by late June in 1991 the corresponding value was 49%.

Population Composition

The large variation among surveys in both the estimated calf:female ratio and sex ratio (Table 2-8; Figure 2-3) could have occurred only if there were some years with low productivity and high mortality alternating between the sexes in subsequent years. These circumstances are unlikely considering that consistently high survival was required to achieve the observed growth rate of the population (see below). The variation in calf:female and sex ratios probably arose because calves associated with males after April (see above), and males and females were not always sampled representatively. Therefore, the calf:female ratio depended in part on the sex ratio of the sample (Figure 2-3), and could not be used to determine calf production and survival (i.e. recruitment). Therefore, in this case statistics based on calf:females should be interpreted with care.

The 1987 survey was probably the best estimate of population composition. This survey was done from a helicopter and resulted in broader coverage than earlier ones that were done from the ground. The 1991 survey was also done from a helicopter but groups were larger and newborn calves could not be counted. Further the 1991 survey sampled a much lower fraction of the population, which may explain the low sex ratio. In 1987, the calf to cow ratio for the entire island was estimated at 93 ± 1.3:100. The yearling to cow ratio was estimated at 69 ± 3.9:100. The yearling to cow ratio is a less precise measure than the calf:cow ratio because of the segregation of cows and yearlings. The bull to cow ratio was estimated at 107 ± 27.5:100. Assuming an equal sex ratio among yearlings, the sex ratio among one year old and older caribou was 104 ± 19.3 males:100 females.

Mortality

Since 1977, about 400 females and 1700 males have been killed by hunters. Hunting quotas were increased from 25 males per year begining in 1977-78 to 300 males and 100 females in 1990-91. In addition, 198 caribou (51 males and 147 females) were collected between 1988 and 1991 for research purposes (see Chapter 3).

Males had a higher mortality rate than females among natural deaths recorded. Of the 17 deaths investigated between 1973 and 1991, 14 were males, 2 were females and one was of unknown sex. The cause of death could be determined in 6 cases; a two year old bull fell off a cliff, a 10 month old male died from a sparring injury to the head, a middle aged bull died from cancer (Wobeser, Gary pers. comm.), one mature bull appear to have starved to death in late winter 1991, and two bulls died after locking antlers during the rut.

One female tagged as a yearling when she was introduced to the island exceeded the maximum age ever recorded for caribou (17 years old, Parker 1981). She was shot when she was 3 months from being 19 years of age. Two other tagged caribou were almost 17 years of age when they were shot.

The population dynamics of the Southampton Island caribou herd was simulated with a population balance model (*sensu* Walters 1986). The model used the known number of individuals of both sexes (calves, yearlings, and older caribou) fertility rate (see Chapter 3), and hunting losses. Mortality rates for the three categories of individuals (calves, one year old and older males and females) were constant over time. There were no built-in density-dependent effects. Mortality rate was varied to estimate the possible range of survival. Assuming 100 % survival of individuals older than calves, the model indicates that to achieve the observed rate of growth survival rate of calves must have been at least 72 %. However, this survival rate is an underestimate as natural mortalities of individuals other than calves were reported. Conversely, if calf survival was 100% the adult survival must have been at least 92 %.

Population estimates

The 1978 census revealed that 1 200 ± 340 (S.E.) caribou (including calves) were on the island (Table 2-1). In 1987, there were 5 400± 1 130 caribou including calves, and 4 000 ± 660 of these animals were one year old and older (Table 2-2). The number of caribou increased to 9 000 ± 3 200 (including calves) by March 1990 (Table 2-3) and to 13 700 ± 1 600 one year old and older animals by June 1991 (Table 2-4).

The number of one year old and older caribou on Southampton Island grew from 38 to 13 700 in 24 years (Figure 2-4a). The population growth rate averaged 27.6 % (r = 0.244; r^2=0.998) per year over this period, based on a regression analysis where the curve was constrained to pass through the known number of one year old and older caribou introduced in 1967 (Figure 2-4b). When a correction factor is used to account for the skewed sex ratio (Heard 1990; number of introduced females times two) of one year old and older animals introduced to the island, the intrinsic growth rate was 26.2 % (r = 0.233; r^2=0.998).

There was no indication of any decline in the rate of growth with increasing population density. If the herd was increasing logistically to an asymptote of 40 000 (lambda = 1.276), the predicted carrying capacity of the island (Parker 1975), then the 1991 population size would have been 10 000. This estimate is lower than the 1991 estimate (95 % confidence interval: 10 600 - 16 800). Therefore, exponential growth appears to be most likely especially considering pregnancy rates and body fat values (see Chapter 3). Alternatively, logistic growth to a carrying capacity of 40 000 would be possible if a time lag component is considered (e.g. 20 years as suggested by Messier *et al*. 1988).

Discussion

Distribution and Social organization

Herd size increased by a factor of almost 100 between 1967 and 1983 but because caribou expanded their range over the island, densities within the areas used remained relatively low. Their range did not appear to expand after 1983 even though herd size continued to grow. Therefore, effective population density increased between 1983 and 1991. These observations are contrary to the model proposed by Riney (1964) and Caughley (1970), which describes the behavior of an introduced ungulate population. It specifies that a zone of high density (i.e., at or near carrying capacity) migrates radially from the point of liberation. Because on Southampton Island range did not continue to expand after 1983, it is likely that the remaining unoccupied areas are marginal or unsuitable for caribou. Parker (1975) predicted that caribou should use the mountainous areas north of Coral Harbour (lichen-heath felsenmeer range type) in winter, and move to other range types in summer. However, there has been no seasonal change in distribution. Therefore, Parker's estimation of carrying capacity (40 000) may not be accurate.

Predation has been used to explain sexual segregation in caribou (Jakimchuk *et al.* 1987; Tom Bergerud & Doug Heard, unpub. data; but see Main & Coblentz 1990) but, excluding the rutting period, males and females were segregated in this study. Most bulls and cows used different areas, but when their distribution overlapped the sexes were found in separate groups. This suggests that segregation might not be related to only predation.

Group associations observed in late June on Southampton Island were similar to large migratory caribou herds with most yearlings associated with bulls or other yearlings (Kelsall 1968). However, among the non-migratory caribou at Wager Bay (N.W.T.), most yearlings (81%) were associated with cows (Calef & Heard 1980, Donaldson 1981). Calef & Heard (1980) and Donaldson (1981) thought that persistent yearling-cow associations might be related to a non-migratory life history strategy, because the bond between cows and 10-12 month old calves is usually broken during spring migration. Data for caribou on Southampton Island are inconsistent with this suggestion.

There was no evidence that groups differed in size between summer (June) and winter on Southampton Island. The tendency for groups to be largest in November was also observed on Coats island (Gates *et al.* 1986), possibly because this period corresponded with the rutting season. Snow can reduce food availability and increase patchiness and many foraging hypotheses suggest that group size should change in response to food availability and distribution (Clark & Mangel 1984). On Coats Island (Gates *et al.* 1986; Doug Heard, unpub. data) and on the western Queen Elizabeth Islands (Miller *et al.* 1977), groups of caribou were smaller in winter than in summer suggesting that the availability of winter food may have limited group size. Even though snow conditions were probably similar on both Coats and Southampton Islands, snow did not appear to influence group size on Southampton because food was more abundant (Chapter 3, Chapter 4).

Population dynamics

From the time of introduction (1967) to 1991, the caribou herd on Southampton Island was in the initial phase of eruption (*sensu* Caughley 1970). There has been no indication of decline in the rate of population growth with increasing density (i.e. no density-dependent growth). Consequently, the observed rate of growth is a good estimate of the intrinsic rate of growth (Caughley 1977). The estimated intrinsic rate of increase (r_m) was 0.233 (lambda=1.257). The intrinsic rate of population increase of an animal population is specific to the environment in which it is measured (Caughley 1977). The intrinsic rate of increase obtained from Southampton Island is the first estimate for a caribou population in an arctic environment. The intrinsic rate of increase exhibited by caribou on Southampton Island is similar to previous estimates of maximum growth rates (mean $r_m = 0.26$) for reindeer and caribou populations introduced to islands in cool oceanic climates (Heard 1990).

High winter mortality has been recorded on neighboring Coats Island in the winters of 1974-75 and 1979-80 (Gates *et al.* 1986). Gates *et al.* (1986) attributed this mortality to weather, primarily snow condition. The high rate of increase and the corresponding population model suggest that such losses were unlikely on Southampton Island. Thus, the simple relationship between snow condition and over-winter mortalities is not supported here (see Chapter 3) because these two populations probably experience comparable climate due to their close proximity.

Table 2-1. Areas, sample sizes, sampling intensities and estimated numbers of caribou in each stratum for the aerial census conducted in November 1978.

Stratum number	Area (km^2) of each stratum	Number of transects flown	Sampling intensity (%)[1]	Estimated number (±SE)
1	2471	8	13	231±163
2	1594	7	13	564±219
3	2908	9	13	387±210
total	6973	24		1181±344 [2]

Note: 1, total area of transects flown within the stratum divided by the stratum area; 2, SE of the total population estimate equals the square root of the sum of the variances of the population estimate for each stratum.

Table 2-2. Areas, sample sizes, sampling intensities and estimated numbers of calves and caribou one year old or more in each stratum for the census conducted in June 1987.

Stratum number	Area (km^2) of each stratum	Number of blocks flown	Sampling intensity (%)[1]	Estimated number of calves (±SE)	Estimated number of ≥1 year old (±SE)
1	1150	7	51	39± 23	313± 65
2	1933	10	50	326± 76	1244±103
3	4425	10	25	330±165	1304±194
4	6389	6	12	662±512	1162±618
5	2144	2	11	9± 8	9± 8
total	16041	35		1366±544	4033±659[2]

Note: 1, total area of blocks flown within the stratum divided by the stratum area; 2, SE of the total population estimate equals the square root of the sum of the variances of the population estimate for each stratum.

Table 2-3. Areas, sample sizes, sampling intensities and estimated numbers of caribou for the census conducted in March 1990.

Stratum number	Area (km^2) of each stratum	Number of transects flown	Sampling intensity (%)[1]	Estimated number (±SE)
1	28462	18	4	9319±3235

Note: 1, total area of transects flown within the stratum divided by the stratum area.

Table 2-4. Areas, sample sizes, sampling intensities and estimated numbers of one year old and older caribou in each stratum for the census conducted in June 1991 from both the random block and systematic surveys.

Stratum number	Area (km^2) of each stratum	Number of transects or blocks flown	Sampling intensity (%)[1]	Estimated number (±SE)
1	1536	8	51	3242± 699
2	3802	10	50	3854± 951
3	3808	10	25	4048± 909
4	11187	13	12	1230± 300
5	22799	7	11	1304± 448
total	43132	48		13676±1584[2]

Note: 1, total area of transects or blocks flown within the stratum divided by the stratum area; 2, SE of the total population estimate equals the square root of the sum of the variances of the population estimate for each stratum.

Table 2-5. Typical group size of caribou.

Date	Typical size of groups:			SE	Number of caribou > 1 year old	Number of groups	Size of largest group
	with calves	without calves	All				
11/81	30.5			1.02	353	25	58
		2.7		0.61	7	4	4
			30.0	1.02	360	29	58
5/82	9.1			0.46	134	24	18
		4.3		0.21	132	43	10
			6.7	0.29	266	67	18
12/82	6.8			0.25	141	28	11
		4.0		0.19	37	10	6
			6.2	0.22	178	38	11
4/83	8.6			0.54	109	21	18
		6.1		0.31	98	24	12
			7.4	0.33	207	45	18
6-7/83	8.2			0.38	227	227	22
		5.0		0.26	305	305	17
			6.4	0.23	532	532	22
11/83	14.5			0.67	274	35	38
		5.3		0.39	40	10	8
			13.3	0.61	314	45	38
4/84	13.0			0.69	218	38	29
		3.4		0.16	106	42	6
			9.9	0.53	324	80	29
6/87	9.9			0.36	450	92	28
		5.3		0.13	787	261	14
			7.0	0.17	1237	353	28
3/90			12.3	0.39	1215	280	50
6/91	15.8			0.39	1509	246	60
		4.3		0.10	851	320	13
			11.6	0.28	2360	566	60

Note: In all instances, size of groups with calves differed from those without calves (Mann-Whitney U-test, $P < 0.001$).

Table 2-6. Percentage of caribou groups in different seasons that were made up of all cows, all bulls or both cows and bulls.

Date (month-year)	Group composition (%)			Number of groups
	Cows	Mixed (cows and bulls)	Bulls	
November-81	7	86	7	28
May-82	43	42	15	67
December-82	42	34	24	38
April-83	49	38	13	45
November-83	27	62	11	45
April-84	37	21	41	78
June-87	33	2	54	297
June-91	49	6	45	239

Table 2-7. Association of yearlings within groups on Southampton Island in June 1987 and 1991

Number of:	Group type					
	Cows	Mixed	Bulls	Yearlings	Unknowns	Totals
A) 1987						
groups	99	6	192	51	5	353
yearlings						
observed	42 (14)[1]	26 (8)	166 (54)	74 (24)	-	308
per group	0.42	4.33	0.86	1.45		
B) 1991						
groups	264	32	239	31	5	572
yearlings						
observed	128 (44)	36 (12)	97 (33)	47 (16)	-	290
per group	0.48	1.13	0.41	1.52		

Note: In cow groups all two year old and older caribou were cows; bull groups contained only two year old and older bulls; yearling groups contained only yearlings; unknown groups contained only unclassified individuals; within other group types unknowns were ignored. 1, represents percentage of all group types.

Table 2-8. Age and sex composition of caribou.

Date	Calves : 100 females	Males : 100 females
11/81	85 ± 1.1[2]	59 ± 2.6
05/82	23 ± 0.6	49 ± 1.4
12/82	48 ± 1.1	86 ± 3.4
04/83	24 ± 0.7	59 ± 2.5
11/83	61 ± 0.8	89 ± 1.1
04/84	77 ± 2.0	186 ± 5.4
06/87[1]	69 ± 3.9	104 ± 19.3
06/91[1]	22 ± 4.3	43 ± 19.3

Note: 1, calves were 12 month old (yearlings); 2, S.E.

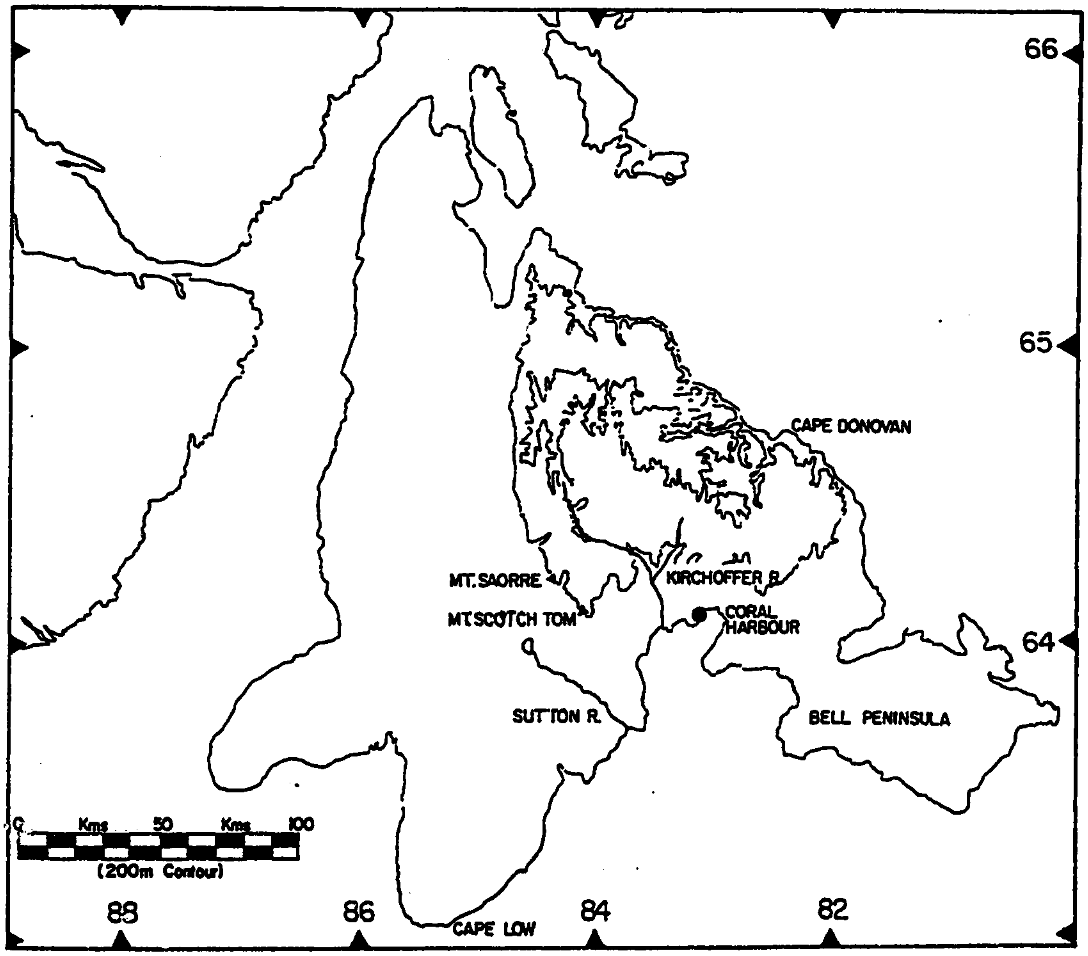


Figure 2-1. The study area and major geographic features on Southampton Island.

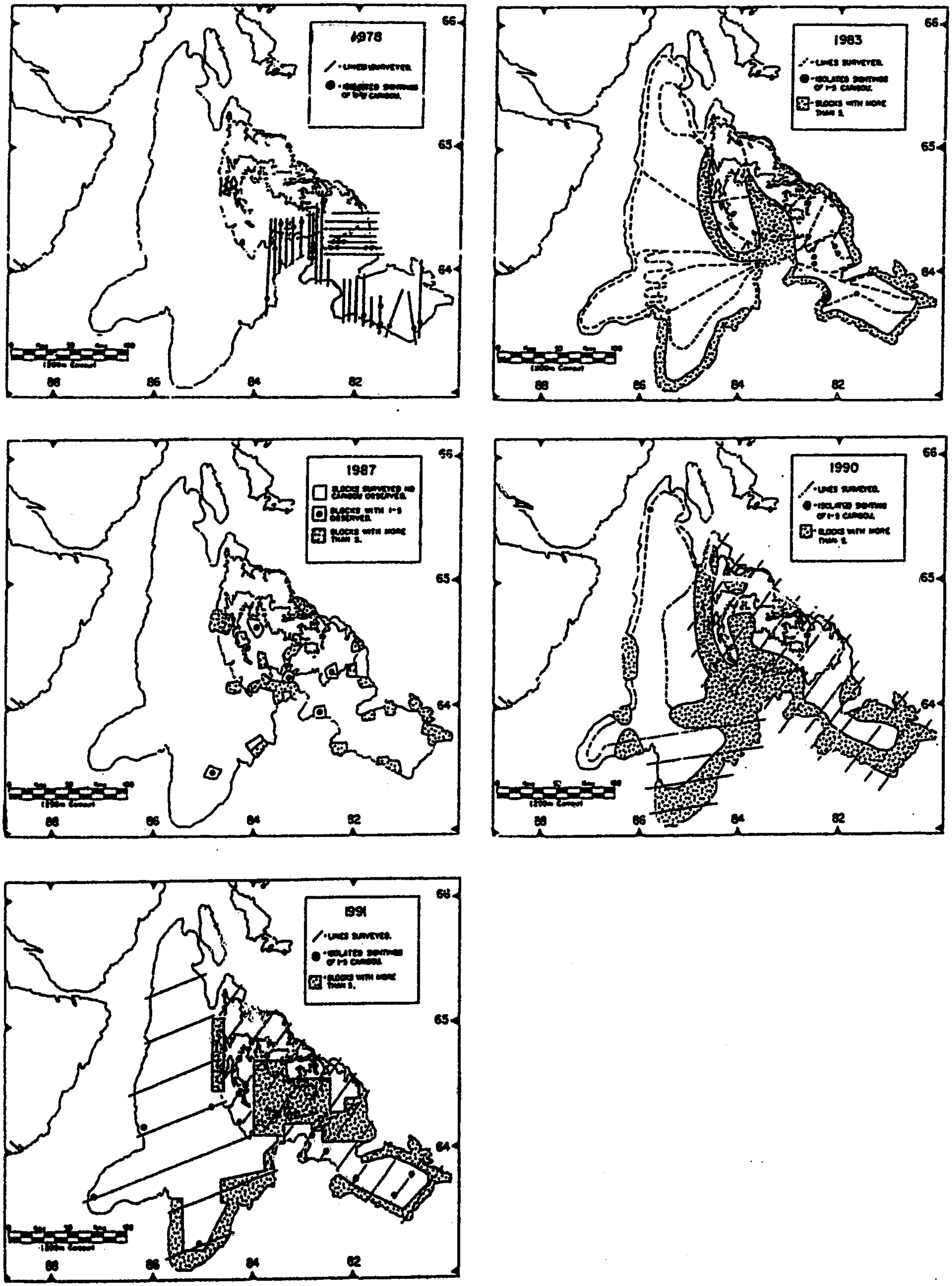


Figure 2-2. Distribution of caribou observed in 1978, 1983, 1987, 1990, and 1991.

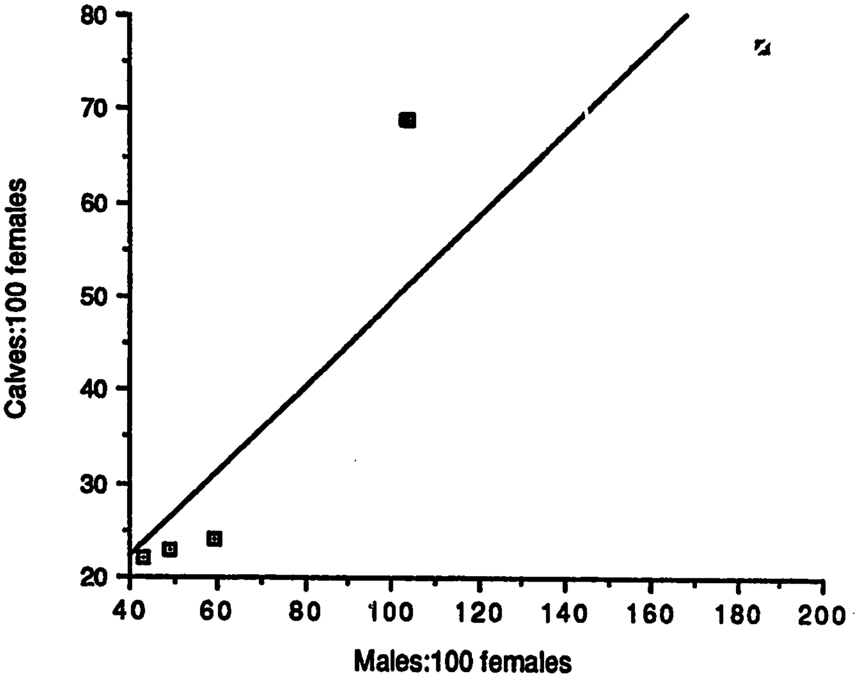
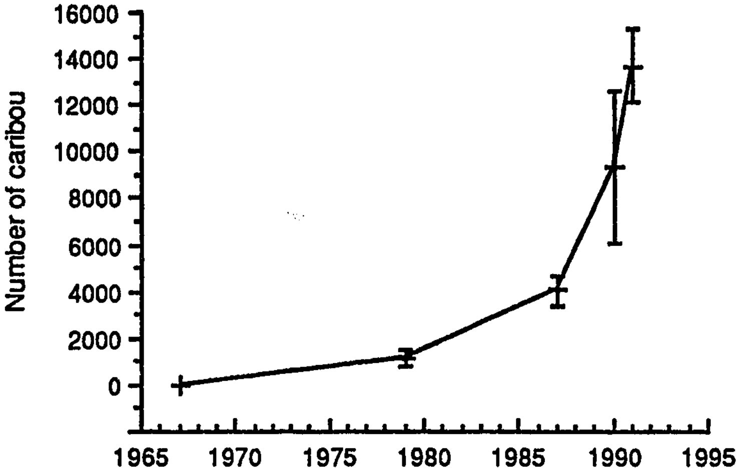


Figure 2-3. The relationship between the ratio of 10-12 month old calves:100 females and the sex ratio (males:100 females) of the sample ($y = 5.71 + 0.423\ x$; $r^2 = 0.84$, $P < 0.05$).

A) Number of caribou



B) Ln number of caribou

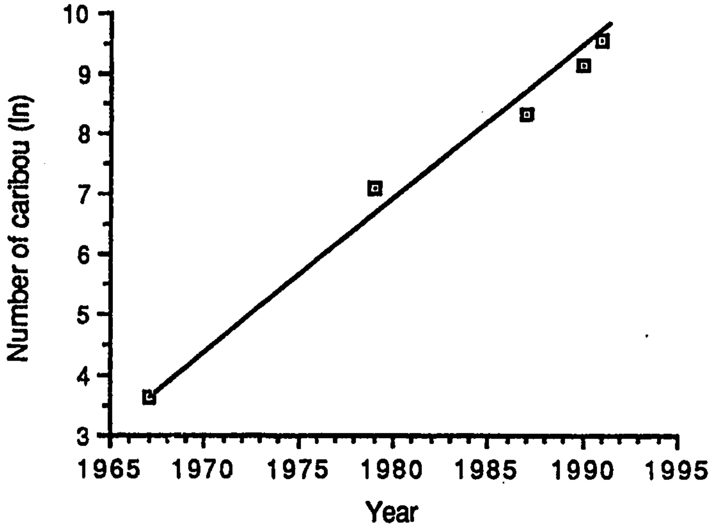


Figure 2-4: The increase in (a) the number of one year and older caribou (S.E.), (b) ln the number of one year old and older caribou ($y = 3.638 + 0.244\ x$; $r^2 = 0.986$, $P < 0.001$), since the introduction of 38 in 1967 (where x is years since introduction).

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Chapter 3.

Relationships between growth, body condition, reproduction, and food availability in caribou

Introduction

It is widely accepted that large mammals are regulated by either food supply, predation, or both. For predator-free areas, intraspecific competition for winter food regulates reindeer numbers (Leader-Williams 1988; Skogland 1985, 1990). In reindeer, competition can affect tooth wear, growth, body weight and, ultimately, reproduction and survival (Skogland 1985, 1990). Density-dependent processes have not been investigated for caribou populations experiencing no predation. Consequently, analyzing the relationships between growth, condition, reproduction, and density is a step towards understanding the population dynamics of northern caribou populations in predator-free environments. Density may be critical when viewed in the context of resource availability, therefore, a means of analyzing the above relationships is to compare growth, condition, and reproduction between populations experiencing different levels of *per capita* food availability.

The objective of this chapter was to explore the relationships among growth, body condition, reproduction, and food availability in caribou. More specifically, the effect of food availability on 1) physical growth, 2) sexual dimorphism, 3) pregnancy, 4) fetal sex ratio, and 5) seasonal variation in body reserves were addressed. These aspects were investigated in the caribou population inhabiting Southampton Island. The population has been increasing at a rapid and steady rate (26 %) since its introduction in 1967 (Chapter 2). Summer and winter food is abundant, readily available and, is of adequate quality (Parker 1975, Chapter 4, Chapter 5), and only a small fraction of the range is showing signs of overgrazing (Chapter 4). Results were compared with previous findings on other populations, particularly with Coats Island caribou (Adamczewski *et al.* 1987b). Summer food availability is high on Coats Island but, compared with the larger neighboring Southampton Island winter range food abundance is low. For example, on Southampton Island, the mean lichen biomass ranges from 69 to 263 g (dry wt) m^{-2} in the three main winter ranges (Chapter 4), whereas comparable values on Coats Island vary from 27 to 56 [g (dry wt) m^{-2}] (Adamczewski *et al.* 1988). This difference in lichen standing crop is reflected by a larger proportion of lichens in the fall and the winter diet of caribou on Southampton Island, relative to those on Coats Island (fall: 67 % vs 36 %, winter: 46-49 % vs 2-12%; Gates *et al.* 1986a). High lichen consumption in Southampton Island caribou was also confirmed indirectly by cesium level analysis of the rumen content (unpub. data). The population density was also lower on Southampton Island. When the study was conducted on Coats Island (1982-1984; Adamczewski *et al.* 1987b), the density was approximatively 0.4 adults per km^2 (Gates *et al.* 1986b) whereas the density varied from 0.1 to 0.3 yearling and older animals per km^2 on Southampton Island during this study (1988 to 1991; Chapter 2). The comparison between Southampton Island and Coats Island caribou is a powerful natural experiment to address the objective of this study, because 1) *per capita* winter food availability differed substantially between the two islands and 2) individuals introduced to the former island were capture on the latter. Therefore, differences between these populations can be attributed to food availability in winter (i.e. mainly a difference in lichen standing crop) rather than genetic differences.

Methods

Between 1988 and 1991, 49 male and 124 female caribou were collected on Southampton Island (see description of the study area in Chapter 2). Animals were harvested within 40 km of Coral Harbour, the only settlement on the island. Four collections were made during late spring (May 1988, 1989, 1990, and 1991), and one in the fall (November 1990). The methodology used and information obtained are presented in Table 3-1. After their death, animals were taken to field autopsy facilities where fresh weights were obtained. Indicator bones and muscles were frozen and their weights were taken shortly after field work completion. The representation of sex and age-classes of caribou sampled according to season and year is shown in Table 3-2. In addition, 30 one year old and older females collected in the spring and fall of 1986 and in the spring of 1987 were used for jaw length and age estimate. All caribou meat remaining was given to the local community.

Carcass composition

Carcass dissectible muscle and fat weights were estimated from equations calibrated for Coats Island caribou (Adamczewski *et al.* 1987a; ln (muscle weight [kg]) = -2.791 + 1.071 ln (gastrocnemius weight, g); dissectible fat weight [kg] = -0.246 + 1.151 depth of back fat [cm] + 26.401 Riney-trimmed kidney fat weight [kg]). Estimated dissectible fat includes fat of carcass and the internal omental and perirenal depots. The above relationships appeared to be unaffected by age, sex and condition (Adamczewski *et al.* 1987a).

Growth

Growth was described using the equations of Von Bertalanffy (Beverton & Holt 1957). For linear measurements growth is summarized by

$$L_t = L_a (1 - \exp(-k (t - t_0))),$$

where L_t = length at age t, L_a = asymptotic length, k = coefficient of matabolism), t = age, and t_0 = theoretical age at which an animal would have zero length. For weight, the equation is

$$M_t = M_a (1 - \exp(-k (t - t_0)))^3.$$

A modification of this equation that incorporates seasonal variation through a sine wave relationship was also fitted to weight data (Leader-Williams 1988). The modified equation is

$$M_t = M_a (1 - \exp(-k(t - t_0)))^3 * (1 + C \sin(2\pi t / 12 - ø)),$$

where C = proportional fluctuation about the growth curve, and ø = phase adjustment. The last parameter was established at 1 to synchronize the curve at maximum weight in November, and minimum weight in May. All other parameters, M_a or L_a, k, t_0, and C, and their 95 % confidence intervals were estimated by the Nonlin procedure of Systat 5.1 (Wilkinson 1989). Age at which growth ceased for a particular physical trait (i.e. age at physical maturity) was determined. It was defined as the youngest age (nearest age corresponding to fall or spring collections) characterized by a mean value that does not differ from the mean of older animals (Dauphiné 1976). This method was necessary to allow comparison with previous findings but, because it is suspected to be influenced strongly by sample size, a second method was also used. The second one considered the age (nearest month) at which 95 % of the asymptotic value was attained based on theoretical growth equations (see above).

Relative winter severity index

A relative winter severity index was calculated according to Gunn *et al.* (1989) based on snow accumulations recorded at Coral Harbour (Southampton Island). The index is based on percent deviations from the long-term mean (1975-1991) of accumulated snow depth on the last day of the month, for the periods of early winter (September - November), mid winter (December - February), and late winter (March - May).

Statistics

For comparisons between two groups, a one-factor ANOVA was used. For multiple group comparisons, the Tukey's HSD was used to examine which means were significantly different. Before applying these procedures, the data were tested for heterogeneity of variances with Bartlett's test. Sex ratio was examined using the G-test. Differences were considered to be statistically significant when $P<0.05$. Statistical analyses were performed with SYSTAT 5.1 (Wilkinson 1989).

Results

Linear measurements

Growth and sexual dimorphism

Body length, jaw length, and metatarsus length as a function of age in males and females, and the corresponding growth curves, are shown in Figure 3-1. Estimates of each parameter included in the model that best summarized the data are presented in Table 3-3. Although the two approaches calculated different ages at maturity, females always matured before males. Rates of growth were comparable between sexes (Table 3-3). Sexual dimorphism was not apparent in the first year of life, but after the first year males were larger than females. At any given age prior to physical maturity, females achieved a greater percentage of their adult size because of their smaller asymptotic values. For example, females at 11 months attained 85.2 % of their asymptotic value, compared to 75.8 % in males of the same age.

Theoretical models that summarize changes in skeletal measurements as a function of age, imply uninterrupted growth in young animals throughout the year (see Figure 3-1). The size attained by caribou of both sexes by their first fall (5 months old; Figure 3-1), relative to fetal size (see below), indicates rapid growth over the first summer. Skeletal growth of caribou of both sexes was also significant over the second summer of life (Figure 3-1). In females, significant changes occurred over their third summer for body length (163.7 cm [n=22] vs 179.0 cm [n=3], *P*=0.022), but not for jaw length (244.4 mm [n=21] vs 249.2 mm [n=5], *P*=0.118) and metatarsus length (253.3 mm [n=23] vs 252.0 [n=3], *P*=0.693) because physical maturity had been attained for these two characters (see Table 3-3). Males could not be tested during this period. Growth was also substantial over winter in young caribou. Significant differences in body length (144.0 cm, n=7 vs 152.5 cm, n=6; *P*=0.075), jaw length (196.7 mm, n=7 vs 218.2 mm, n=6; *P*<0.001), and metatarsus length (221.6 mm, n=7 vs 232.9 mm, n=7; *P*=0.007) were recorded between 5 month old and 11 month old female calves. The same was suggested in males (5 months old [n=5] to 11 months old [n=2]) (body length: 144.0 cm vs 153.3 cm; jaw length: 203.6 mm vs 217.5 mm; metatarsus length: 225.0 mm vs 231.5 mm). For males, measurable skeletal growth also occurred during their second winter. During that period (17 months [n=6] to 23 months [n=8]), body length of males increased from 172.5 cm to

181.3 cm (*P*=0.1), while jaw length and metatarsus length increased from 246.5 mm to 260.7 mm (*P*=0.006) and from 255.0 mm to 267.9 mm (*P*=0.003), respectively. For females in these age classes, such growth was not detected (jaw length: 250.5 cm, n=4 vs 244.4, n=21; *P*=0.08). Finally, there were no significant changes in either body length (179.0 cm, n=3 vs 170.9 cm, n=24; *P*=0.165), jaw length (249.2 mm, n=5 vs 251.3 mm, n=26, *P*=0.539), or matatarsus length (252.0 mm, n=3 vs 251.4 mm, n=24; *P*=0.818) between 29 and 35 months for females; males could not be tested due to constraints in sample sizes. Over winter, skeletal growth for females at later ages was not detected statistically (*P*>0.05); males could not be tested.

Inter-annual and seasonal variations

Due to constraints in sample sizes only yearlings (23 months old) and older females collected in the spring (1988-1991) were compared between years. Yearlings and older females were considered separately, because physical maturity was not attained in the former age-class (see above). In either group, there were no significant differences in body length, jaw length, and metatarsus length among the four years (Table 3-4). Consequently, data were pooled across year to assess seasonal variation in skeletal size. No significant differences was found in skeletal measurements between females (35 months old and older) that were collected in the spring, relative to those sampled in the fall (Table 3-5).

Weights (body reserves)

Growth, sexual dimorphism, and seasonal variation

Body weight, carcass muscle weight, and carcass fat weight for males and females were fitted to theoretical growth curves (Figure 3-2 and 3-3, Table 3-6). The models explained a large proportion of the variance in both sexes, particularly for body weight and muscle weight (Table 3-6). A marked sexual dimorphism was exhibited by these parameters but, as for skeletal growth (see above), the differences were not important within the first year of life.

There were no significant changes in body weight (38.7 kg, n=7 vs 39.3 kg, n=6; *P*=0.774), muscle weight (19.5 kg, n=7 vs 21.1 kg, n=7; *P*=0.341), nor fat weight (2.2 kg, n=7 vs 1.1 kg, n=7; *P*=0.015) of female calves over their first winter; fat weight even decreased. The same pattern was suggested in males (body weight: 42.8 kg, n=3 vs 40.1 kg, n=2; muscle weight: 21.3 kg, n=2 vs 21.1 kg, n=2; fat weight: 2.2 kg, n=3 vs 0.4 kg, n=2). Similarly, over the second winter no significant changes in body weight (70.1 kg, n=5 vs 73.1 kg, n=7; *P*=0.5), muscle weight (35.0 kg, n=6 vs 35.2 kg, n=8; *P*=0.91), nor fat weight (2.6 kg, n=6 vs 2.7 kg, n=8; *P*=0.921) were recorded in yearling males; yearling females were not tested. For older females (35 months and older), there was a significant increase in body weight and muscle weight from spring to fall (Table 7). However, the same pattern was not apparent for fat weight. There was no significant changes in fat reserves from fall to spring in adults (Table 3-7). As a means of incorporating seasonal variation in growth models describing body weight and muscle weight, a modified theoretical growth curve was used (Figure 3-2, Table 3-6). Only females were considered as few males were sampled in the fall. Parameters included in the model suggest a seasonal fluctuation of 4.5 % about the curve for body weight and 3.1 % for muscle weight. Finally, for weights as for the skeletal measurements (see above), females reached physical maturity earlier than males.

Inter-annual variation

To analyze the variation in spring body condition of females among years (1988-1991), body weight, carcass muscle weight and fat weight were compared. For yearlings, these weights did not differ significantly among years (Table 3-8). For older females, however, carcass muscle weight did not differ among samples but some differences were detected for body weight and fat weight. For example, animals sampled in 1989 were heavier by about 9.6 kg and fatter by 2.1 kg than those sampled in 1988. Muscle weight was 2.9 kg higher in 1989 relative to 1988, but this difference was not significant.

A relative severity index suggested that the winters of 1989 -1990 (index of 79) and 1990 -1991 (index of 163) were more likely to have limited the access to forage than the previous two winters (index of -22 and -5). However, variations in body reserves did not follow the expected pattern based on snow condition (i.e. they were not lower in the springs of 1988 and 1989 relative to 1990 and 1991; see above).

Ingesta weight and ruminal nitrogen

For females, ingesta weight (rumen content) did not vary between the fall and the spring (6.4 ± 0.23 kg [n=10] vs 6.0 ± 0.32 kg [n=61]; *P*=0.566). Further, no yearly variation in ingesta weight took place for females sampled in the spring. However, diet quality as suggested by the nitrogen level of the rumen content was higher in the fall (5.10 ± 0.15 % [n=13] vs 4.61 ± 0.05 % [n=71); *P*=0.001). Nitrogen level of the rumen content in the spring varied between some samples (1988: 4.66 % [n=21]; 1989: 4.94 % [n=22]; 1990: 4.44 % [n=26]; 1991: 4.38 % [n=23]), being significantly higher in 1989 than in 1990 and 1991.

Pregnancy rate: maternal age and condition

In the spring, all but three female caribou, excluding calves, were parturient. The overall pregnancy rate was 97% (90/93). The non-parturient females were five, eight and 11 years old. Consequently, the pregnancy rate was 100 % (21/21) in yearlings and 96 % (69/72) in older females. Similarly, the pregnancy rate was 100 % (59/59) for 2-4 year old females and 91 % (30/33) in older ones. The skeletal size of non-pregnant females (body length: 170.0 cm; jaw length: 266.0 cm; metatarsus length: 260.6 cm) did not appear to differ from the other females sampled (see Table 3-4 for comparison). Body weight (67.3 kg) and carcass muscle weight (32.0 kg) were also well within the range of parturient females. However, one of these three non-pregnant females had no measurable backfat and only 78 g of kidney fat, resulting in a low weight of dissectible fat (1.8 kg). The other two females had substantial fat reserves (6.0 kg and 8.2 kg) in the spring. In addition, two out of the three females had no antlers, whereas all pregnant females had antlers.

Fetal sex ratio: maternal age and condition

Overall fetal sex ratio was not significantly different (*P*>0.05) from 100 males:100 females; 44 males and 46 females were recorded. Fetal sex ratio of females 2-4, 5-7, and >8 years old was 96 (n=53), 87 (n=28), and 125 (n=9) males:100 females, respectively, and none differed significantly from an even sex ratio. Although the sample size was small (n=23), fetal sex ratio was male biased (187 males:100 females; *P*<0.05) for females that conceived for the first time (i.e. 23 months old at calving).

None of the variables describing body size and condition differed between females carrying a male or a female fetus (Table 3-9). Similarly, variables describing fetal size and condition did not differ significantly between male and female fetuses (Table 3-10); the validity of fetal kidney fat and fetal kidney fat index as indicators of fetal condition are unknown.

Discussion

Results obtained on Southampton Island (SI) are discussed in light of previous findings, particularly with data collected from the Coats Island (CI) caribou herd (Adamczewski *et al.* 1987b; Gates *et al.* 1986b). Individuals introduced to SI were captured on CI in 1967, and since then they have experienced a higher *per capita* winter food availability (for more details see the introduction). As part of a report that was an overview of body condition studies on caribou of CI (Adamczewski *et al.* 1991), an attempt was made to compare the skeletal size and body condition of CI caribou with those of SI. Differences exist in the results relevant to SI females recorded in this study relative to Adamczewski *et al.* 1991). However, no attempt was made to discuss these differences because of sampling problems. CI data were apparently based on two collections, six animals in April (1984), a month earlier than in this study (May 1988-1991), and four in November (1983) (Adamczewski *et al.* 1991, p. 92).

Growth and dimorphism

In reindeer, herds with adequate summer ranges skeletal size is strongly influenced by environmental conditions in winter (i.e. lichen biomass *per capita*) (Skogland 1983; but see Reimers 1983a). Environmental conditions in winter may also be important in caribou, as suggested by the fact that adult females from SI had a larger skeletal size than females from CI. For example, asymptotic total body length was approximatively 165 cm in mature CI female caribou (Adamczewski *et al.* 1987b), as compared to 179 cm in SI females. This observation supports previous findings for caribou that have shown density-dependent changes in skeletal size based on jaw length (Couturier *et al.* 1989; Valkenburg *et al.* 1991).

Growth advantages in SI caribou, relative to CI, were apparent in young animals during summer as well as over winter. In the fall, calves (i.e. 5 months old) were approximatively 10 cm longer on SI than on CI. Differential fetal growth, postnatal growth, or both, can be invoked to explain these differences. In reindeer and in caribou, fetal size may be related to maternal condition (Adamczewski *et al.* 1987b; Skogland 1984). However, for SI caribou this relationship was not found, possibly because females were in excellent physical condition. Nevertheless, it is unlikely that the above difference can be attributed solely to growth prior to birth because fetal weights were comparable (about 4.6 kg; Adamczewski *et al.* 1987b) between these two populations in mid-May. Therefore, differential postnatal growth during summer likely contributed to calf skeletal size differences in the fall.

Environmental conditions during the previous winter may influence calf growth by a maternal effect through lactation. Poor nutrition can reduce milk protein content (Allaye-Chan 1991). Clearly, females on SI were in far better physical condition during late gestation and early lactation than CI females (see below). Further, females on CI had to invest more into body reserves in preparation for winter than SI females (i.e. repletion, see below). Although, compensatory feeding may occur (Watkins *et al.* 1991), a greater demand on the females may have influenced calf growth through inadequate lactation. Herein lies a potential conflict, because lactating females are not inclined to sacrifice body protein (Allaye-Chan 1991).

A direct impact of winter food on growth is also possible because a significant over winter (5 months to 11 months old) skeletal growth of animals of both sexes also contributed to the growth advantage in SI caribou. In other caribou populations studied, skeletal growth stopped over winter (Dauphiné 1976; Couturier *et al.* 1989; Adamczewski *et al.* 1987b). Direct impact of nutrition on over winter calf growth has been shown experimentally in Red deer (e.g. Suttie & Hamilton 1983). Males grew significantly over their second winter, but females did not. For females, however, skeletal growth was almost completed by then and investment into reproduction during their second winter may have limited their growth. In summary, winter food availability may influence the skeletal growth of young caribou, either directly or indirectly through a maternal effect.

SI caribou were the most sexual dimorphic of all caribou populations based on jaw length. The male to female ratio for metatarsus length was intermediate relative to other caribou populations (1.06 vs 1.02 - 1.15), but it was higher than other populations (1.15 vs 1.10 - 1.12) for jaw length (for comparison see Couturier *et al.* 1989). It appears that the high degree of dimorphism resulted primarily from a growth advantage in males. For example, mean jaw lengths were comparable in SI (26.2 cm) and Kaminuriak (26.4 cm) females whereas corresponding values were greater in SI (30.2 cm) than Kaminuriak males (29.0 cm) (Dauphiné 1976). For cervids, the reproductive success of males is enhanced by large body size, to a greater extent than females.

Therefore, they should be adapted to take maximum advantage of changes in food availability (Clutton-Brock *et al.* 1984). Results of this study, along with those of McEwan (1968) for caribou and of Leader-Williams & Ricketts (1982) for reindeer, support this conclusion. For SI caribou, it appears that sexual dimorphism did not occur through differential growth rates, but rather by males continuing to grow after growth has stopped in females (see also Georgiadis 1985).

Body reserves

The seasonal variation in body weights and estimated body reserves in caribou sampled on SI was in sharp contrast to CI caribou (Adamczewski *et al.* 1987b) (Table 3-11). The fall body weight and composition did not differ between SI and CI caribou calves (5 months old). However, CI calves lost considerable weight over their first winter (11 months old), whereas SI animals were less affected. The fall body weights of yearlings (17 months old) were higher on SI relative to CI, but CI yearlings were fatter. CI mature females were fatter and heavier in the fall than SI females. Mature females on CI lost virtually all of their fat reserves and considerable muscle weight (about 30 %) over winter. For females on SI, muscle weight decreased slightly whereas fat weight remained stable over winter.

Differences exist among caribou (Dauphiné 1976; Huot 1989; Allaye-Chan 1991) and reindeer (Leader-Williams & Ricketts 1982; Reimers *et al.* 1982; Tyler 1987a) populations for body weight, body composition, and their seasonal variation patterns. However, among individuals originating from the same stock, a contrasting seasonal change in body reserves such as the one presented above (SI vs CI) has never been documented in caribou.

Several interesting points emerge from the above comparison. Adult females on SI lost 8 % of their muscle weight over winter, although the weight of fat reserves remained unchanged. This suggests that changes in protein reserves are not entirely dependent on changes in fat reserves as opposed to the model proposed by Berg & Butterfield (1976). It also illustrates that there is some flexibility in the pattern of depletion of body reserves. It is unlikely that SI caribou were energy limited because fat reserves were not depleted during winter. The diet of SI caribou was rich in lichens (Gates *et al.* 1986a; Unpub. data), provided a good source of energy but a poor supply of protein (Thomas & Kroger 1980). Muscle catabolism can provide energy (Torbit *et al.* 1985).

Therefore, muscle may have been used by SI caribou as a supply of nitrogen (Allaye-Chan 1991; Huot 1989).

CI females showed a compensatory growth of body weight, and associated body reserves, during the summer relative to SI females. Compensatory growth is illustrated by the inverse relationship existing between weight gain from spring to fall and body weight at the end of winter, and has been shown experimentally to occur in ungulates (Renecker & Samuel 1991; Suttie & Hamilton 1983; Watkins *et al.* 1991). Compensatory growth is related primarily to higher forage intake relative to maintenance requirements (Watkins *et al.* 1991). However, CI females were heavier and fatter than SI females in the fall. Based on the weight of the rumen fill (see Adamcjewski *et al.* 1987b), it can be assumed that adult females body weight and composition from both populations were at "set point". The difference between the fall body composition of CI and SI caribou may reflect different tactics influenced by different winter conditions.

Adjustment of body reserves to ecological constraints would be adaptive, and would permit the best allocation of resources (e.g. body reserves vs. growth, see above) based on seasonal demands. However, it remains unclear as to what regulates this adjustment. Experimental conditions apparently failed to show such pattern (e.g. Suttie & Hamilton 1983; Watkins *et al.* 1991). It is possible that such adjustment take place, at the individual level, through physiological processes that integrate environmental cues over a relatively long period of time (e.g. 2 years). Experimental studies usually manipulate food supply over a short period of time (e.g. one season). Alternatively, such "adjustment" may occur at the population level through a lower selective pressure allowing greater phenotypic variation. Nevertheless, if the lower fall body weight and weight of fat reserves in SI females, relative to those on CI are a consequence of the higher *per capita* food availability in winter, then this could have several implications. First, the relative amount of fat stored, or "set point" in the fall, is not fixed. Second, food availability in winter somehow influences subsequent fall body weights and composition of caribou. Not, as has generally been assumed for reindeer and caribou (e.g. Klein 1970), that body weight differences in the fall among herds are solely related to environmental factors in the summer (Reimers 1983a). Third, caribou may increase fall body weight and fat reserves under resource limitation. Finally, inspection of fat reserve in the fall, may not be a reliable indicator of summer food availability (Verme & Ozoga 1980).

Pregnancy rate

The pregnancy rate of yearling and older females sampled on SI was higher (97 %) than that reported for other free-ranging caribou populations; all yearlings (i.e. females giving birth at 2 years old) sampled over a 4 year period having been pregnant. High adult fecundity is the general rule for caribou (Skogland 1985), but pregnancy rate of yearlings ranges from 2 to 46 % (Leader-Williams 1988). Exceptionally high pregnancy rate in yearlings on SI suggests that age at first reproduction might be influenced by forage availability. Further, results clearly indicate that being pregnant as a yearling did not prevent reproduction in the following year, as suggested by Dauphiné (1976) for caribou and Reimers (1983b) for reindeer, because pregnancy rate was 100 % in these females. The exceptional physical condition of females on SI may have prevented any carry-over effect of reproduction. Moreover, data on Southampton Island do not support the proposition that yearling females are least likely, despite sexual maturity, to conceive due to inexperience (Allaye-Chan 1991).

Pregnancy rate in reindeer can be predicted from the body weight of females (Reimers 1983b, P= 1 - exp (-0.167 [dressed body weight at rut - 21])). Obviously, this equation cannot be applied directly to caribou because they are much larger than reindeer. According to Davis *et al.* (1991), the same predictive equation could be used for caribou by using a correction factor to compensate for differences in adult body size. However, the corrected equation underestimates pregnancy rates recorded on SI (yearlings: 79 % vs 100 %; older females: 88 % vs 96 %). Further, using a correction factor to control for adult body size implies a fixed pregnancy rate for adults [88 %, the value obtained by Reimers (1983b)]! Although additional correcting factors may be required (Davis *et al.* 1991), the above discrepancies suggest that the relationship between pregnancy rate and body weight is not constant (Skogland 1985; Skogland 1990; Tyler 1987b). Pregnancy rate has also been related to the amount of body fat (Dauphiné 1976; Thomas 1982). Based on the results of Thomas (1982), the level of fat reserves in the spring predicted pregnancy rates accurately for yearlings and older females. However, most calves on Southampton Island should have been pregnant, but none of them were. Reindeer females can breed at 6 months of age, under exceptional circumstances (Leader-Williams 1988); however, at that age they are much larger, relative to adult size, than are caribou. Similar to body weight, the relationship between pregnancy rate and body fat reserves appears not to be constant. Therefore, fertility may be related to a combination of factors (e.g. body weight, body fat reserves) as suggested by Albon *et al.* (1986) for Red deer (*Cervus elaphus*). For example, Skogland (1990) suggested that the weight-specific pregnancy rate of reindeer is density-dependent because natural selection favors smaller reindeer body size at maturity under resource limitation. Clearly, further investigations are necessary to understand better the factors that could be used to predict pregnancy rate in caribou.

Fetal sex ratio: Maternal age and condition

Thomas *et al.* (1989) found a maternal age effect on fetal sex ratio, young mothers produced more females, whereas the opposite was true for old females. Kojola and Eloranta (1989) and Skogland (1986) suggested a maternal condition effect. Small bodied females produced more females, whereas large bodied ones bore more males (Kojola & Eloranta 1989). Skogland (1986) suggested that such a relationship exist across herds (but not within; see below), after comparing the sex ratio at birth among three herds that differed markedly in female body weight. He proposed that sex ratios differed among the three herds although he also indicated that none of the sex ratios tested individually differed from 100 males:100 females! On SI the sex ratio did not differ from 100 males:100 females. Consequently, it can be concluded that, at the population level for reindeer and caribou, an even fetal sex ratio is the rule because it did not differ from 100 males:100 females in any of the seven populations investigated. However, results of this study do not conform to either of the above observations linking maternal age or condition to sex of progeny. On SI there was no indication that females which produced male fetuses were in better or worse physical condition than others, and the fetal sex ratio of females reproducing for the first time was male biased. However, Thomas *et al.* (1989) assumed that producing female offspring would permit faster maturation of young mothers because the energetic costs of producing females are lower than males. Moreover, in ungulates where male success depends on fighting ability and body size, the breeding success of sons may be more strongly affected by early growth and parental expediture than the success of daughters (Clutton-Brock 1991). For example, food shortage or competition often has stronger effects on the growth (see above) and mortality of males in dimorphic species such as caribou (Clutton-Brock 1991). Considering that 1) females on SI attained physical maturity at early age despite the fact that they reproduce as yearlings, 2) there was no evidence of reproductive pause in females, 3) young of both sexes grew rapidly, 4) fetal weights did not differ between males and females, and 5) fetal weights were not related to maternal weights nor conditions; there is no evidence to believe that the argument supporting a female biased fetal sex ratio in young mothers should apply to SI caribou. Conversely, the exceptional physical condition of young mothers on SI may have "prompted" them to produce more males.

Implications for the dynamics of insular caribou populations

High winter mortality has been recorded on neighboring Coats Island in the winters of 1974-75 and 1979-80 (Gates *et al.* 1986b). Gates *et al.* (1986b) attributed this mortality to weather, primarily snow condition. However, such losses were unlikely on Southampton Island (see Chapter 2). But the impact of adverse snow conditions (density-independent factors) may increase under resource limitation (Skogland 1985). On Coats Island, the rate of growth of the population during recovery years was lower (r=0.21, theoretically this rate could have been much higher because the population was composed of a high proportion [83 %] of cows; Gates *et al.* 1986b) than the rate of increase recorded on Southampton Island (r=0.24; Chapter 2). Further, despite the fact that the population was possibly increasing, Coats Island calves (11 months old) were in particularly poor body condition in the spring relative to Southampton Island calves (Adamczewski *et al.* 1987b; see above). I suggest that the rate of growth of northern predator-free caribou populations may be strongly influenced by winter food availability which is influenced by climatic conditions and grazing. This is consistent with the observation that dramatic declines observed in two reindeer populations, on two islands off the coast of Alaska, were attributed to adverse climatic conditions (ground ice in winter) following overgrazing of the lichens (Klein 1968; Scheffer 1951).

Table 3-1. Parameters considered and corresponding methodology.

Variable (method)
Linear measurements:
total body length (distance between the tip of the muzzle and the last caudal vertebra; ± 1 cm)
jaw, femur, and metatarsus (including only the fused 3rd and 4th metatarsals) lengths (Langvatin 1977) (± 1 mm)
depth of backfat (maximum fat depth along an incision made from the base of the tail toward the animal's head along a line 45° from the spinal cord, ± 1 cm)
Weights:
body (live weight minus the weight of gastrointestinal content, gravid uterus, and some blood lost from the bullet wound) (± 0.5 lb)
antlers (sawed off at the base of the head) (± 2 g)
gastrocnemius (extraneous fat, tendons, and the flexor digitorum superficialis were removed) (± 0.1 g)
femur (tendons, ligiments, and articular cartilage were removed) (± 0.1 g)
full and empty gastrointestinal tract (± 50 g)
uterus (± 50 g)
fetus (± 50 g) and fetal femur (± 0.1 g)
Riney-trimmed kidney fat (± 0.1 g) (Riney 1955)
Others:
sex
rumen nitrogen (standard CHN autoanalyzer)
age estimate (tooth erruption pattern (Miller 1974) and counts annuli in stained cementum of the first incisor and molar, Reimers and Nordby 1968; Mattson's Laboratory, U.S.A.
femur marrow fat (dry-weight method corrected for mineral contents, ± 0.001 g; =1.0444 * (final wt/initial wt) -0.065); Neiland 1970)

Table 3-2. The representation of sex and age-classes of caribou according to season and year in which samples were taken.

Season	Year	Calves F	Calves M	Yearlings F	Yearlings M	Older F	Older M	Total
Spring	1988	3	1	4	0	17	10	35
Spring	1989	0	1	4	0	18	0	23
Spring	1990	2	0	6	4	21	7	40
Spring	1991	2	0	9	4	14	11	40
Total Spring		7	2	23	8	70	28	138
Fall	1990	7	5	1	6	16	0	35
TOTAL:		14	7	24	14	86	28	173

Note: F, females; M, males.

Table 3-3. Estimates of parameters used in growth models summarizing changes in body length, jaw length, and metatarsus length as a function of age in males and females, derived sexual dimorphism and age at physical maturity.

Parameter	k	t_0 (months)	Asymptotic value	r^2	Dimorphism (ratio M/F)	Age at physical maturity (months)	
						model	statistical
Body length (cm):							
Males	0.058	-15.9	202.1	0.79	1.13	36	47
(n=48)	(±0.002)	(±0.5)	(±0.4)				
Females	0.050	-27.7	179.0	0.61		33	29
(n=120)	(±0.002)	(±1.0)	(±0.3)				
Jaw length (mm):							
Males	0.047	-13.8	301.8	0.91	1.15	45	47
(n=48)	(±0.001)	(±0.4)	(±0.5)				
Females	0.067	-16.2	262.2	0.84		29	29
(n=139)	(±0.002)	(±0.4)	(±0.2)				
Metatarsus length (mm):							
Males	0.097	-12.7	271.7	0.72	1.06	19	23
(n=47)	(±0.025)	(4.9)	(±2.9)				
Females	0.10	-14.7	256.3	0.66		15	17
(n=123)	(±0.03)	(±6.5)	(±1.8)				

Note: 95 % confidence intervals are presented in brackets.

Table 3-4: Yearly variation in body length, jaw length, and metatarsus length in yearlings (23 months old) and older females sampled in the spring.

Variable	Collection			
	1988	1989	1990	1991
Body length (cm):				
Yearlings	162.0 ± 10.5 (n=3)	168.8 ± 3.3 (n=4)	157.8 ± 1.7 (n=6)	166.9 ± 2.5 (n=9)
3+ years old	171.7 ± 2.3 (n=16)	177.7 ± 1.3 (n=18)	175.5 ± 1.6 (n=21)	173.4 ± 1.6 (n=14)
Jaw length (mm):				
Yearlings	244.7 ± 3.7 (n=3)	246.7 ± 5.0 (n=3)	242.6 ± 1.5 (n=5)	241.2 ± 1.8 (n=6)
3+ years old	255.8 ± 1.9 (n=16)	259.9 ± 1.9 (n=17)	256.9 ± 2.2 (n=20)	257.0 ± 2.4 (n=13)
Metatarsus length (mm):				
Yearlings	252.2 ± 0.6 (n=4)	255.5 ± 3.2 (n=4)	252.3 ± 2.0 (n=6)	253.6 ± 2.1 (n=9)
3+ years old	252.9 ± 1.7 (n=17)	255.1 ± 1.5 (n=18)	256.9 ± 1.9 (n=21)	253.6 ±2.0 (n=14)

Note: Mean values and standard errors. Values in the same row are not significantly different.

Table 3-5. Seasonal changes in body length, jaw length, and metatarsus length in females aged 35 months and older.

Variable	Collection		
	Spring		Fall
Body length (cm)	174.6 ± 0.9 (n=[illegible])	*n.s.*	177.3 ± 2.4 (n=16)
Jaw length (mm)	258.0 ± 0.9 (n=83)	*n.s.*	255.9 ± 2.0 (n=17)
Metatarsus length (mm)	254.7 ± 0.9 (n=71)	*n.s.*	255.6 ±1.1 (n=16)

Note: Mean values and standard errors. *n.s.*, Values in the same row are not significantly different.

Table 3-6. Estimates of parameters used in growth models summarizing changes in body weight, carcass muscle weight, and fat weight as a function of age in males and females, derived sexual dimorphism and age at physical maturity.

Parameter	k	t_0 (months)	Asymptotic value	r^2	Dimorphism (ratio M/F)	Age at physical maturity (months)	
						model	statistical
Body weight (kg):							
Males (n=46)	0.041 (±0.001)	-24.3 (±0.7)	119.2 (±0.7)	0.81	1.69	75	59
Females[1] (n=104)	0.056 (±0.002)	-24.1 (±1.0)	70.6 (±0.3)	0.74		49 (40)[2]	41
Muscle weight (kg):							
Males (n=46)	0.056 (±0.002)	-20.0 (±1.6)	48.0 (±0.4)	0.68	1.49	53	59
Females[1] (n=104)	0.068 (±0.005)	-21.4 (±1.9)	32.4 (±0.2)	0.58		39 (38)[2]	35
Fat weight (kg):							
Males (n=48)	0.038 (±0.01)	-13.4 (±7.2)	7.8 (±0.6)	0.47	1.24	94	59
Females (n=122)	0.090 (±0.02)	-5.6 (±3.6)	5.8 (±0.2)	0.39		40	23

Note: 95 % confidence intervals are presented in brackets. 1, Corresponding values for the modified equation including the seasonal variation in weight are the following: Body weight, k = 0.060 (±0.002), t_o = -21.1 (±0.8), A = 72.6 (±0.3), and C = 0.045 (±0.002), r^2=0.77; Muscle weight, k = 0.072 (±0.004), T = -19.0 (±1.8), A = 33.0 (±0.2), and C = 0.031 (±0.006), r^2=0.60.
2, Corresponding values when the modified growth model is used.

Table 3-7. Seasonal changes in body weight, carcass muscle weight, and fat weight in females aged 35 months and older.

Variable	Collection		
	Spring		Fall
Body weight (kg)	66.1 ± 0.9 (n=60)	*	72.1 ± 1.5 (n=9)
Carcass muscle weight (kg)	31.1 ± 0.4 (n=69)	*	33.4 ± 1.3 (n=12)
Carcass fat weight[1] (kg)	5.7 ± 0.3 (n=69)	*n.s.*	5.4 ± 0.2 (n=13)

Note: Mean values and standard errors. *n.s.*, Values in the same row are not significantly different; *, Values in the same row are significantly different.

Table 3-8. Yearly variations in body weight, carcass muscle weight, and fat weight in yearlings (23 months old) and older females sampled in the spring.

Variable	Collection			
	1988	1989	1990	1991
Body weight (kg):				
Yearlings	57.3a ± 2.5 (n=3)	58.6a ± 2.2 (n=4)	58.2a ± 1.8 (n=4)	54.8a ± 2.2 (n=7)
3+ years old	60.7a ± 1.2 (n=15)	70.3b ± 1.5 (n=16)	67.4b ± 2.0 (n=15)	65.5b ± 1.6 (n=14)
Carcass muscle weight (kg):				
Yearlings	27.9a ± 1.3 (n=4)	28.9a ± 1.4 (n=4)	26.6a ± 0.6 (n=6)	28.6a ± 0.9 (n=9)
3+ years old	29.7a ± 0.8 (n=17)	32.5a ± 0.9 (n=17)	30.7a ± 0.8 (n=21)	31.5a ± 0.8 (n=14)
Carcass dissectible fat (kg):				
Yearlings	3.2a ± 0.8 (n=4)	5.3a ± 0.5 (n=4)	4.8a ± 0.9 (n=6)	5.3a ± 0.4 (n=9)
3+ years old	4.8a ± 0.3 (n=16)	6.9b ± 0.5 (n=18)	5.0a ± 0.3 (n=21)	6.0ab ± 0.8 (n=14)

Note: Mean values and standard errors. Values in the same row followed by the same letters are not significantly different.

Table 3-9. Body size and condition of mothers in the spring, categorized by the sex of the fetus.

Variable	Fetal sex		
	Male		Female
Body length (cm)	170.5 ± 1.5 (n=43)	*n.s.*	173.8 ± 1.3 (n=45)
Jaw length (mm)	252.4 ± 1.5 (n=40)	*n.s.*	255.9 ± 1.5 (n=41)
Metatarsus length (mm)	254.4 ± 0.9 (n=44)	*n.s.*	254.1 ± 1.1 (n=46)
Body weight (kg)	63.8 ± 1.3 (n=38)	*n.s.*	63.8 ± 1.1 (n=37)
Carcass muscle weight (kg)	30.1 ± 0.5 (n=43)	*n.s.*	30.4 ± 0.6 (n=46)
Carcass fat weight (kg)	5.4 ± 0.3 (n=44)	*n.s.*	5.5 ± 0.3 (n=45)
Antler weight (g)	237 ± 21 (n=39)	*n.s.*	250 ± 20 (n=43)

Note: *n.s.* Values in the same row are not statistically significant. When yearling females are analyzed separately, the above statistical decisions remained.

Table 3-10. Body size and condition of fetuses, categorized by sex.

Variable	Fetal sex		
	Male		Female
Body length (cm)	67.3 ± 1.8 (n=29)	*n.s.*	69.0 ± 1.0 (n=34)
Total body weight (kg)	4.7 ± 0.2 (n=44)	*n.s.*	4.6 ± 0.2 (n=46)
Femur weight (g)	33.8 ± 1.8 (n=25)	*n.s.*	30.7 ± 2.2 (n=20)
Kidney fat (g)	10.4 ± 1.7 (n=17)	*n.s.*	9.5 ± 1.0 (n=13)
Kidney fat index (%)	62 ± 11 (n=15)	*n.s.*	64 ± 10 (n=14)

Note: *n.s.,* Values in the same row are not statistically different. When a covariable taking into account differences in sampling dates was used in the ANOVA model the above statistical decisions remained.

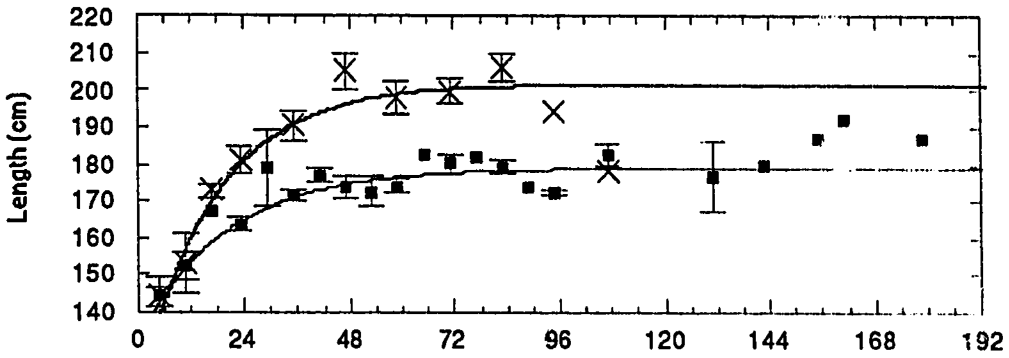
Table 3-11. Comparison of body weight and body reserves in young caribou (both sexes included) and in adult females (47 months and older) between populations on Southampton Island (SI; this study) and Coats Island (CI; data from Adamczewski *et al.* 1987b).

Variable	Age-class (season)									
	5 months old (Fall)		11 months old (Spring)		17 months old (Fall)		Adult females (Fall)		Adult females (Spring)	
	SI	CI	SI	CI	SI	CI	SI	CI	SI	CI
Body weight (kg):	40	40	39	28	70	55	72	78	66	57
Carcass muscle weight (kg):	20	19	21	10	34	27	33	33	31	24
Carcass fat weight (kg):	2.2 (5)[1]	1.5 (4)	1.0 (3)	0 (0)	8.6 (12)	8 (15)	5.4 (8)	11 (14)	5.7 (9)	1.5 (2)
Sample size	11-12	7	8-9	1	6-7	2	9-13	7	60-69	12

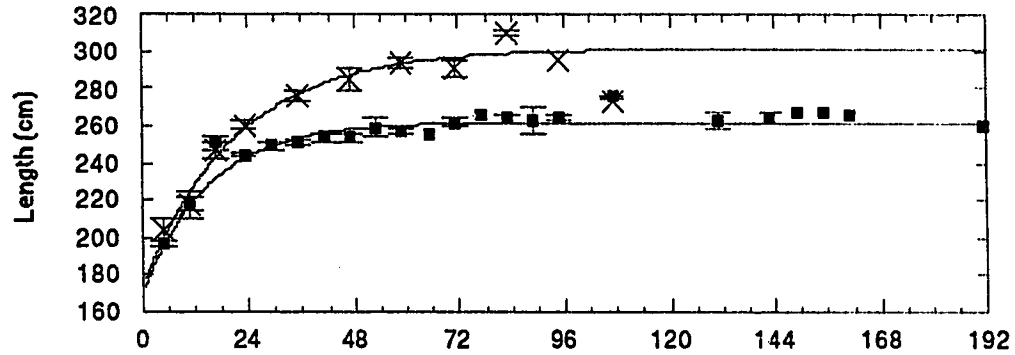
Note: To estimate ingesta + gravid uterus-free body weight I used uterus weight data from Southampton Island (fetal weights did differ between the two populations).

1, (Carcass fat weight divided by ingesta+uterus-free body weight) x 100.

A) Body length



B) Jaw length



C) Metatarsus length

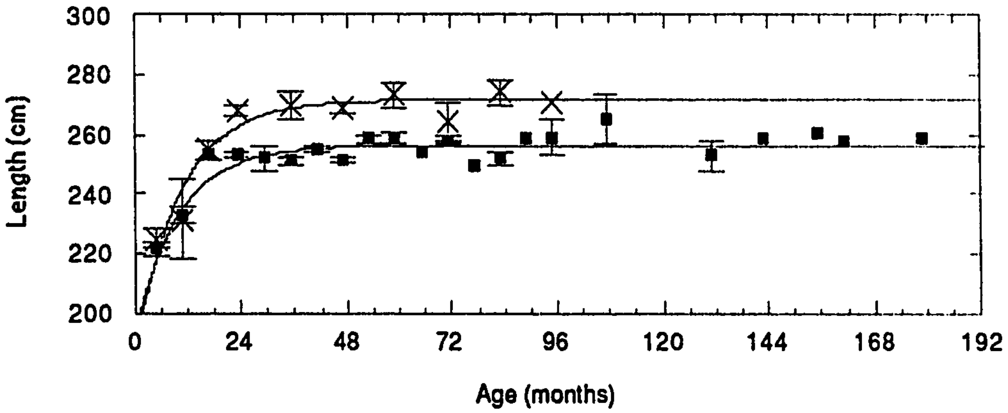
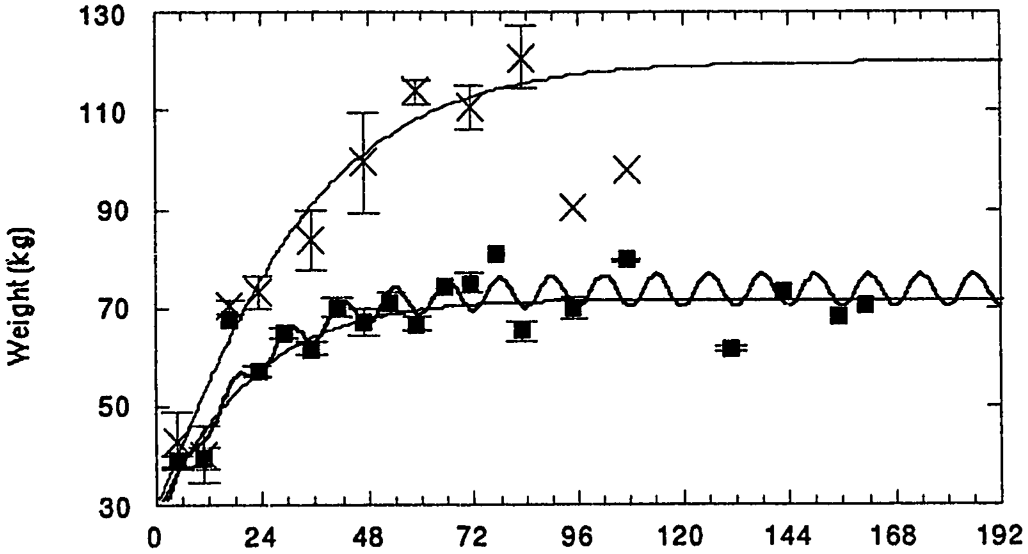


Figure 3-1. Growth (mean ± 1 SE) of (a) body length, (b) jaw length, and (c) metatarsus length in males (X) and females (.) as a function of age, and corresponding theoretical growth curves (see text).

A) Body weight



B) Muscle weight

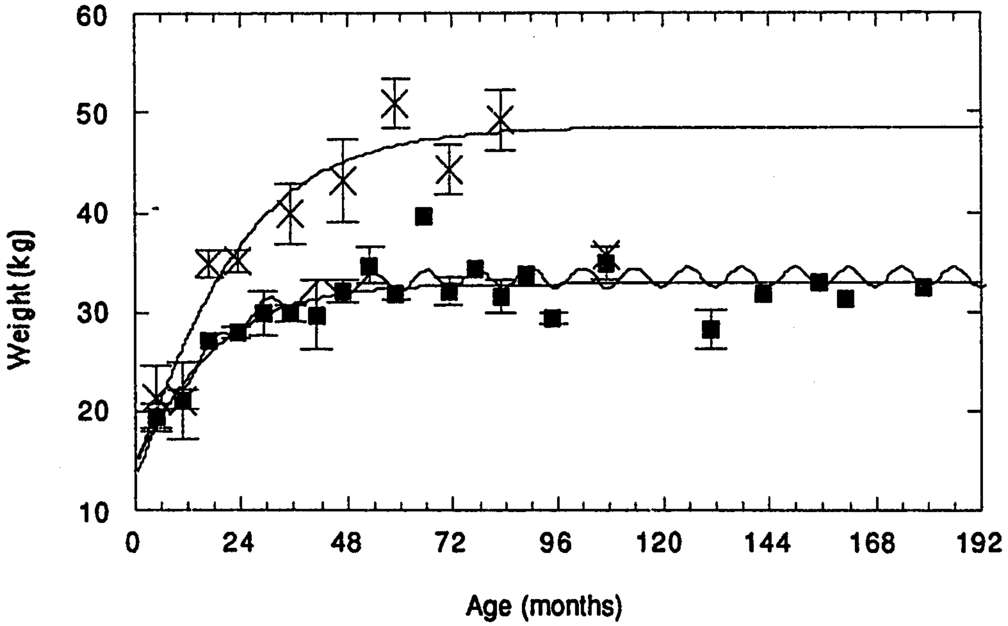
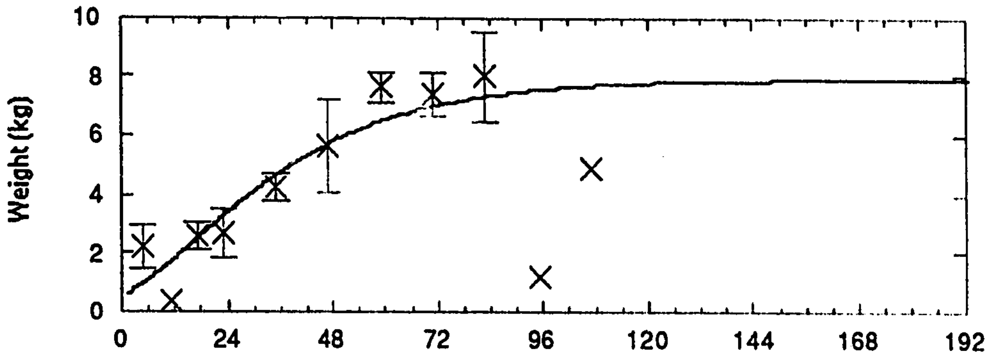
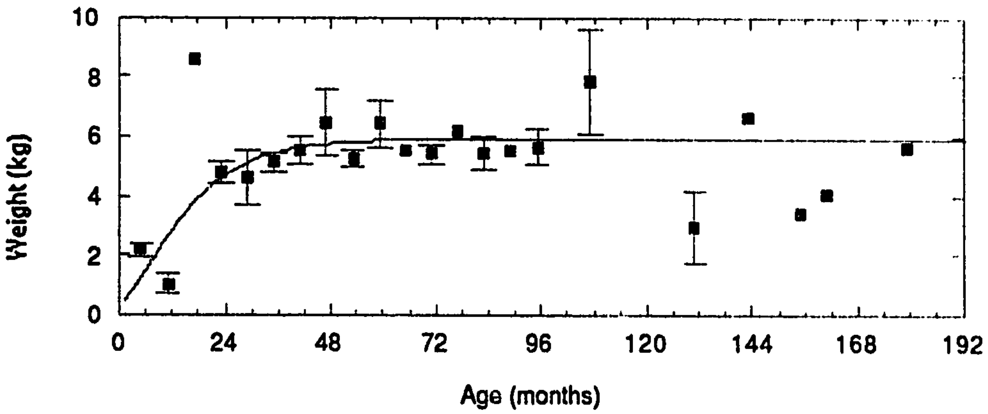


Figure 3-2. Growth (mean ± 1 SE) of (a) body weight and (b) carcass muscle weight in males (X) and females (.) as a function of age, and corresponding theoretical growth curves (see text).



A) Males



B) Females

Figure 3-3. Growth (mean ± 1 SE) of carcass fat weight in (a) males (X) and (b) females (.) as a function of age, and corresponding theoretical growth curves (see text).

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Chapter 4.

Short-term consequences of caribou grazing on the vegetation

Introduction

Introduced ungulate populations usually show a pattern of irruption followed by a decline (Riney 1964; Caughley 1970). However, not all introduced *Rangifer* populations behave in the same manner (see Chapter 2; Leader-Williams 1988). Scheffer (1951) outlined the events following liberation of reindeer on St Paul Island, Alaska. The population increased for a period of 27 years and then declined dramatically. Although vegetation changes were not monitored closely, the decline was associated with the depletion of lichens that were an important food source during winter (see also Klein 1968). Leader-Williams (1988) suggested that a key factor explaining successful vs unsuccessful introduction attempts appears to be the degree of resilience of the vegetation to grazing. However, only two introduced *Rangifer* populations have been studied with regard to the effects of grazing on the vegetation; St-Matthew, Alaska (Klein 1968, 1987) and South Georgia, Antarctica (e.g. Leader-Williams 1988).

Southampton Island represents a unique system for analyzing changes in vegetation following the introduction of a caribou population in the arctic. Caribou were common on Southampton Island in the early 1900s although few records describe their early distribution and abundance. However, by 1925 the population was estimated to be no more than 30 individuals, and the last animal is believed to have died in 1953 (Mikitok, Bruce pers. comm.). In 1967, 48 caribou *(R. t. groenlandicus)* were re-introduced to the island (Manning 1967).

Short-term data on the effects of caribou on vegetation will provide a better assessment of the status of the population in relation to its range. Long-term data will also improve our understanding of caribou-plant interactions, and how changes in vegetation affect the dynamics of introduced and insular caribou populations in northern regions. To document the effects of caribou grazing, a series of exclosures were set up on Southampton Island in 1989 to monitor short- and long-term changes in the vegetation.

Soil temperature, amount of water, and the length of the growing season are some factors influencing plant production in the Arctic (Chapin *et al.* 1979, 1985). Exclosures can possibly influence these factors. For example, the impact of exclosures on physical conditions could be a problem if they trap drifting snow. The presence or absence of extensive snow drifts in the spring may influence the length of the growing season. Surprisingly, previous studies using exclosures as an experimental tool to analyze the impact of *Rangifer* grazing (e.g. Palmer & Rouse 1945; Pegau 1970; Inglis 1975; Leader-Williams 1988) have not discussed this problem.

The main objective of this chapter was to describe short-term changes in the vegetation for various range types subjected to grazing by an introduced caribou population approaching estimated carrying capacity (see Chapter 2). Changes in the vegetation were related to range use and to prevalent snow conditions, because snow may restrict forage accessibility. Secondarily, this study tested the effect of the exclosures on factors that are known to influence the production of arctic plant communities; namely, snow condition and its disappearance in the spring, and soil temperature during the growing season.

Methods

To quantify the impact of grazing on vegetation, 13 exclosures that prevented caribou grazing were established in the summer of 1989 on Southampton Island, N.W.T. (see description of the study area in Chapter 2). Exclosures were set up in the lichen-heath felsenmeer (6 exclosures), raised lichen-*Dryas* sedge (n=4), sedge-willow meadow (n=2), and alluvial shingle (n=1) range types (see Chapter 5 for the description of the different range types; see also Parker 1975). Alluvial shingle range type covers less than 1 % of the island but is characterized by a high cover of lichens relative to other range types (Parker 1975). The four range types covered approximatively 60 % of the island surface area (Parker 1975) and were the main source of food for caribou inhabiting the island (Parker 1975; pers. obs.). Sedge-willow bogs, dominated by graminoid plants, were not considered in this study due to the high degree of resilience to grazing shown by graminoids (Chapter 5). At each site, two areas (5.5 m X 5.5 m) were selected on the basis of their similarity in terms of vegetation composition and cover. On one of these (selected randomly) an exclosure was established while the other served as a control. The distance between the two areas was at least 15 m. Exclosures (5.5 m X 5.5 m) were made of heavy farm fencing, 0.9 m high with horizontal strands about 15 cm apart, vertical stays every 41 cm (9.5 gauge galvanized wire), and 45 imp gal barrels (n=4) filled with rocks served as anchoring points. The exclosures were set up within a radius of 100 km of Coral Harbour, the only settlement on the island (see Chapter 2: Figure 2-1).

Plant cover was estimated at the of July in 1990 and 1991 within 10 quadrats (50 cm X 50 cm); five quadrats inside the exclosure and five on the control plot. Quadrats were not placed within 1 m of the fence or drums to avoid the potential effects of those structures on vegetation. Quadrat locations were randomly selected within the remaining area and permanently marked to ensure that vegetation readings were taken at the exact same location during the two years of the study. The point-intercept method (Wein & Rencz 1976) with 50 readings per quadrat was used to estimate plant cover. At each reading, a pin was lowered and every plant encountered was recorded. Successive interception of the same species within a reading was recorded as one interception. Plant species were grouped into 5 categories (non crustose lichens, shrubs, graminoids and forbs, mosses, and others [crustose lichens, bare ground, and dead matter]). This method proved to be a good predictor of lichen biomass (biomass [g (dry wt)/0.25m^2]= 0.56 lichen cover (%) - 2.16; n=15, $P< 0.001$, $r^2= 0.89$). To determine the above relationship between lichen cover and biomass, lichens from 15 sites were removed, dried at 60 °C, and weighed.

Range use at each exclosure site was determined by counting caribou pellet groups within two transects (2 m X 25 m; Neff 1968). Transects were positioned between the exclosure and its corresponding control site. Pellets were counted and removed at the onset of the study (1989) and after each subsequent year, 1990 and 1991.

Snow characteristics (depth and hardness) at each exclosure were measured twice in winter (March and May of 1990 and 1991) using a Rammsonde penetrometer (Anon. 1970; e.g. Skogland 1978). At each exclosure snow characteristics were measured along two perpendicular transects intercepting inside the exclosures. Inside the exclosure, eight readings were taken along the two transects, starting 0.5 m inside the fence. Outside the exclosure, snow characteristics were measured at 4 m and 5 m away from the fence on each side of the exclosure, for a total of 8 readings. To analyze the chronology of snow melt, three exclosures were visited four times in the spring of 1990 (21, 23, 26, and 30 of June) to estimate percent snow cover on the ground within and outside the exclosures. The melting pattern around drums was also monitored. During trips to collect snow condition data, snow characteristics were also obtained at every cratering site encountered. Snow characteristics were measured 30 cm from the edge of the crater (mean of four measurements).

Soil temperature was monitored twice during the growing season of 1991, early in summer and in mid-summer. Readings were taken at two different depths (2.5 and 5.0 cm), and at various distances from drums (0, 15, 30, 60, 90, 120, and 250 cm [control site]). All statistics were performed using Systat 5.1 (Wilkinson 1989) and differences were significant at $P<0.05$.

Results

Effect of the exclosures

Snow conditions were affected slightly by the presence of the exclosures. At the end of winter, snow was significantly deeper inside the exclosures, by 7 and 6 % for 1990 and 1991, respectively (Table 4-1). However, within 20 to 30 cm of each drum, snow depth was shallower by 66 % (based on data collected at 4 exclosures in 1991). Snow hardness did not differ between measurements taken inside and outside the exclosures. Similarly, Ram resistance, an integrated measure of snow depth and hardness correlated to water content (Anon. 1970), did not differ significantly (Table 4-1).

Snow melting chronology in the spring, based on data collected at three exclosure sites, was not affected by the presence of the exclosures. Snow disappeared on the ground within the exclosures at the same rate as the surrounding areas, except in the immediate vicinity (30 cm) of each drum, where the snow melted faster. Table 4-2 summarizes observations made at one exclosure. The other two sites showed similar patterns.

Finally, soil temperature was significantly higher in most instances within 30 cm of drums early in season, but not later (Table 4-3). However, soil temperature did not differ significantly at distances greater than 30 cm from the drums.

Range use

Pellet group counts suggested that the alluvial shingle range type, characterized by high lichen coverage (Parker 1975; Table 4-7), was used most heavily by caribou (index of 59, n=1; pers. obs.). Raised-lichen *Dryas* sedge (10 ± 3.8, n=4) and lichen-heath felsenmeer (11 ± 7.2, n=6) range types were also used, but to a lesser extent. However, the relatively high use of the lichen-heath felsenmeer range type resulted mainly from observations at one site (Last Lake A) which had an index of 46. The other sites were used to a lesser degree (mean index of 4). The sites located in the sedge-willow meadow range types were not visited by caribou in winter.

Site-use by caribou during the winter was not related to mid-winter or to late-winter snow conditions (integrated Ram resistance) or to total vegetation cover, but was significantly correlated to lichen biomass in 1991 (Table 4-4). However, cratering sites at the end of winter were characterized by shallow and soft snow (Table 4-5). Further, cratering sites generally had low lichen biomass and were located along ridges and lake margins (pers. obs.).

Snow condition (integrated Ram resistance) was highly variable, both within and between sites and years. Snow condition in late-winter was poorly correlated to snow condition earlier in winter (mid-winter) in 1990, but this relationship was significant in 1991 (Table 4-4). For example, snow condition worsened considerably from mid- to late-winter 1990 at the site referred to as Last Lake A (940 to 2630 kg . cm); whereas, snow condition remained relatively stable at Native Point A (2430 to 2380 kg . cm). Similarly, changes in snow condition between years was poorly correlated among sites (Table 4-4). For example, snow condition in mid-winter for Last Lake A was 940 kg . cm in 1990 and 650 in 1991; whereas, the corresponding values for Shoulder A were 2280 and 5980 kg . cm. Although, overall snow conditions were highly variable, snow depth was significantly correlated within and between sites.

Impact of caribou grazing

Vegetation cover estimated for each exclosure and corresponding control area is presented in Tables 4-6, 4-7 and 4-8. At the onset of the study five out of 13 sites showed evidence of caribou grazing. Sites referred as Native Point A and B were overgrazed; lichen biomass was low and the ratio of dead to live matter was high relative to the other sites (Table 4-7). Remaining lichen fragments were intermingled in the vegetation mat. Bear Cove C and D showed signs of intermediate grazing pressure, and Kirchoffer River had signs of light grazing pressure. The other eight sites did not show any apparent sign of previous grazing.

To assess the influence of grazing by caribou on the observed changes in vegetation cover from 1990 to 1991, changes in vegetation cover between the two years for each area (inside and outside exclosures) were plotted against the index of site use by caribou based on pellet group counts (Figure 4-1). There was no significant relationship between the index of site use and changes in the vegetative cover of shrubs (Figure 4-1b), graminoids-forbs (Figure 4-1c), and mosses (Figure 4-1d). However, there was a significant relationship between these two parameters for lichens (Figure 4-1a) and for the vegetation types categorized as others (crustose lichens, bare ground, and dead matter) (Figure 4-1e). It is apparent that these relationships were influenced substantially by the results obtained from two sites (Last Lake A and

Kirchoffer River, Figure 4-1). Therefore, I suggest that grazing by caribou had a significant impact on the vegetation cover at those two sites. The lichen mat at both these sites showed signs of grazing in 1991; patches of lichens were removed entirely. Lichen cover decreased by 16.4 %, for the Last Lake A site and by 24.8 % for the Kirchoffer River site. Considering that changes in lichen cover can be translated directly to changes in lichen biomass, these results imply a decrease of 18 % (16.4/90.8; reduction over-winter [1990-1991] divided by the value of 1990) and 17 % (24.8/146.2) in lichen biomass over-winter (Tables 4-7, 4-8, and 4-9). By summing the observed changes in lichen cover from 1990 to 1991 for the 13 sites investigated, it is estimated that a reduction of 4 % took place.

For sites located in the sedge-willow meadow range type there were no apparent changes in the vegetation cover (Table 4-8). Consequently, there is no reason to suspect that grazing by caribou had an effect on the vegetation of those sites that were used primarily during summer (see above).

Discussion

Effect of the exclosures

Exclosures had little effect on various physical conditions that could potentially affect vegetation growth. Excluding the immediate periphery of each drum, snow melting was not influenced by the exclosures. In addition, the amount of water resulting from snow melting in the spring was not influenced by the presence of the exclosures. Finally, soil temperature was influenced only within the immediate vicinity (within 30 cm) of each drum. Therefore, under the conditions prevailing during this study, the potential problems associated with exclosures were minimal with regard to their negative impact on snow conditions, water regime, and soil temperature. Further, excluding the two sites that were heavily used by caribou, vegetation changes over time inside the exclosures did not appear to be different than those that took place outside the exclosures. I conclude that the use of exclosures to monitor range conditions should not be considered problematic; rather it should be considered a valuable tool. However, to minimize potential problems associated with the impact of the drums, vegetation should not be sampled within 1 m of a drum. Alternaltively, smaller posts with less thermal inertia could be used.

Impact of grazing by caribou

Based on the general condition of the vegetation, I suggest that the range on Southampton Island is in good condition overall. However, lichen biomass on Southampton Island is poor relative to other ranges (see Parker 1975). Nevertheless, the overall lichen standing crop per unit area is higher than Coats Island (Adamczewski *et al.* 1988). Based on the physical appearence of the lichen mat, some areas are showing signs of overgrazing by caribou. For example, estimated lichen biomass at Native Point decreased from 255 g/m^2 (SE=1.7; Cormack, Gates Unpub. data) in 1983 to 55 g/m^2 (SE=7.1, n=4) in 1991. Lichen biomass estimates at Native Point in 1991 are comparable to those recorded on overgrazed Coats Island (Adamczewski *et al.* 1988). Sites investigated at Bear Cove, also in the raised lichen-*Dryas* sedge range type, showed signs of intermediate grazing pressure (the residual lichen biomass was higher than the above sites qualified as overgrazed). Although lichens were depleted at all of these sites (Native Point A, B; and Bear Cove C, D), no noticeable increase in lichen biomass was measured inside the exclosures from 1990 to 1991. This is in agreement with previous findings which indicated the low ability of lichens to grow back following grazing (Chapter 5; Henry & Gunn 1991; Klein 1968,1987; Pegau 1968; Palmer & Rouse 1945). For example, 22 years after the population crash (i.e. die-off) on St Matthew Island, lichens had recovered to only 10 % of the standing crop of living lichen biomass found on the adjacent island where there was no history of grazing (Klein 1987). Further, over a single winter (1990-1991) caribou grazing had a significant effect on lichen biomass at two sites in this study, Kirchoffer River and Last Lake A. Extrapolation from the results obtained at the Kirchoffer River site (i.e. reduction in lichen biomass of 17 %) suggests that the Alluvial Shingle range type, characterized by high lichen coverage, maybe deteriorating rapidly Personal observations of the impact of caribou on this range type also support this finding.

Localized overgrazing was observed on Southampton Island, despite the fact that the caribou population in 1991 (13 700 one year old and older animals) was well under the carrying capacity estimated for the island (40 000, Parker 1975). I suggest that the carrying capacity proposed by Parker (1975) might be an overestimate. Parker (1975) predicted that caribou should use the lichen-heath felsenmeer as winter range, and his carrying capacity estimate was based only on the lichen biomass found in this range type. Contrary to this prediction, pellet group counts and distribution data (Chapter 2), and signs of grazing, suggest that the lichen-heath felsenmeer range type was not heavily used by caribou in winter, but the raised lichen-*Dryas* sedge range was favored. Results of this study suggest that the lichen-heath felsenmeer range type found in the mountainous part of the island was not used heavily by caribou because available lichens are found in valley bottoms that are characterized by very deep snow (Pruitt 1959). Parker (1975) never visited the island in winter to document snow depth.

Under the prevailing snow conditions on the island, caribou winter range appears to be restricted mainly to windswept areas which are nearly free of snow. Selecting shallow and soft snow can reduce the energetic cost of cratering (Fancy 1985). However, these areas are usually characterized by low vegetation coverage (Klein 1968; pers. obs.). Fancy (1986) suggested that a 10% increase in the daily costs of cratering activity would result in 0.3 % decrease in the daily energy balance, whereas a 10 % increase in dry matter intake would result in a 61 % increase in daily energy balance. Consequently, there is a trade-off between the cost of cratering and the benefit in terms of dry matter intake. Caribou on Southampton Island, along with other caribou populations (Coats Island caribou, Adamczewski *et al.* 1988; Peary caribou, Miller *et al.* 1982), experience snow that is orders of magnitude harder than snow in forested areas (Lapierre & Lent 1977). Therefore, caribou living in the tundra are forced to dig craters in shallower snow depths relative to southern populations that have been observed to dig through more than a meter of snow (Vandal & Barette 1985). As a result, a "large" proportion of the range is not available to caribou on Southampton Island in winter.

The observed short- and long-term changes in lichen standing crop suggest that caribou on Southampton Island rely heavily on lichens in winter (see also Chapter 3). Moreover, sites available to caribou in winter (i.e. sites that are not subjected to heavy snowfalls) are poorly vegetated and locally overgrazed. Because the lichens are not resilient to grazing (Chapter 5), and under the present hunting regime, it is likely that the Southampton Island caribou herd is on its way to a population peak followed by a subsequent crash. The potential for a severe crash is accentuated by the fact that the population is growing at a rapid rate (see Chapter 2; Messier *et al.* 1988).

Table 4-1. Mean (±SE) snow characteristics measured inside and ouside each exclosure (n =13) at the end of winter 1990 and 1991.

Parameter	Year 1990 Inside	Year 1990 Outside	Year 1991 Inside	Year 1991 Outside	Exclosure effect P^1
Snow depth (cm)	65 (5.5)	61 (5.2)	71 (7.0)	67 (7.2)	0.040
Snow (Ram) hardness (kg)	33 (3.4)	38 (3.2)	28 (3.1)	29 (2.7)	0.439
Integrated Ram resistance (kg · cm)	2100 (210)	2000 (160)	2100 (300)	2000 (300)	0.995

Note: 1, exclosure effect was tested with a randomized block design ANOVA with two factors (block: site, n = 13; factors: year, 1990/1991; exclosure, inside/outside).

Table 4-2. Visual observations of snow melting chronology for one exclosure

Parameter	Date			
	21/06/90	23/06/90	26/06/90	30/06/90
Snow cover (%)				
Inside	100	80-90	40-50	0
Outside	100	80-90	40-50	0
Melting pattern around drums	snow depth was shallower (60%) within 20 cm of each drum	snow depth was shallower within 30-50 cm of each drum	free of snow within 30-50 cm + water	free of water same moisture

Table 4-3. The effect of drums that served as fence posts on soil temperature (°C).

Distance from a drum (cm)	Early in summer				Late in summer			
	Depth (cm)				Depth (cm)			
	2.5		5.0		2.5		5.0	
0	+1.0 *	(0.79)[1]	+1.0 *	(0.85)	+0.4	(0.82)	+0.6	(0.57)
10	+1.2 *	(0.49)	+1.2 *	(0.67)	+0.6	(0.91)	+0.9 *	(0.70)
30	+0.9 *	(0.48)	+0.8 *	(0.54)	+0.1	(0.50)	+0.4	(0.44)
60	+0.2	(0.55)	0.0	(0.62)	-0.2	(0.48)	-0.1	(0.37)
90	-0.4	(0.65)	+0.3	(0.40)	0.0	(0.44)	-0.2	(0.35)
120	+0.2	(0.46)	+0.1	(0.46)	-0.3	(0.52)	+0.1	(0.49)
n	19		19		12		12	

Note: Mean value of differences obtained for each drum (control [250 cm away from drum] minus drum measure [0 to 120 cm]); * , significantly different (the range of the 95 % confidence interval on either side of the mean does not overlap zero); 1, 95 % confidence interval.

Table 4-4. Pearson correlation coefficient between index of site use (pellet counts), snow condition (integrated Ram resistance) in mid and late winter, lichen cover, and total vegetation cover of 13 sites examined in 1990 and 1991.

		Parameters							
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Index of site utilization '90	(1)	-							
Index of site utilization '91	(2)	-0.163	-						
Snow in mid-winter '90	(3)	-0.027	-0.516	-					
Snow in late-winter '90	(4)	-0.106	-0.070	0.149	-				
Snow in mid-winter '91	(5)	0.051	-0.423	0.401	0.073	-			
Snow in late-winter '91	(6)	-0.070	-0.500	0.268	0.084	0.825	-		
Lichen biomass	(7)	-0.177	0.828	-0.490	-0.105	-0.264	-0.357	-	
Total vegetation cover	(8)	-0.467	0.283	-0.238	-0.330	-0.382	-0.317	0.016	-

Note: Underlined correlation coefficients are significant (P values corrected using the Bonferroni criteria).

Table 4-5. Mean (SE) snow characteristics measured at cratering and control sites at the end of winter in 1990 and 1991.

Parameter	Year				
	1990		1991		
	Craters	Controls	Craters	Controls	P^1
Snow depth (cm)	24 (1.4)	61 (5.2)	35 (2.1)	67 (7.1)	<0.001
Snow (Ram) hardness (kg)	34 (2.8)	38 (3.1)	22 (2.2)	29 (2.7)	0.049
Integrated Ram resistance (kg · cm)	790 (83)	2200 (160)	704 (100)	2000 (300)	0.001
Sample size	19	13	8	13	

Note: 1, Differences between cratering and controls sites were tested with a two factor Anova (factors: year, 1990/1991; selection, crater/control [*P* values presented above]).

Table 4-6. Estimated vegetation cover (%) in 1990 and 1991 inside and outside exclosures located within the lichen-heath felsenmeer range type.

Site		Plant categories				
		Lichens	Shrubs	Graminoids & Forbs	Mosses	Others
Last Lake A						
Inside	1990	82.4	42.8	2.8	15.6	40.0
	1991	81.2	36.8	3.2	13.6	38.0
	Difference	-1.2	-6.0	0.4	-2.0	-2.0
Outside	1990	90.8	43.6	2.0	8.8	35.6
	1991	74.4	44.8	2.4	4.4	44.4
	Difference	-16.4	1.2	0.4	-4.4	8.8
Last Lake B						
Inside	1990	42.8	36.4	6.4	6.8	56.4
	1991	40.8	36.8	4.0	1.6	56.0
	Difference	-2.0	0.4	-2.4	-5.2	-0.4
Outside	1990	51.2	54.0	2.8	10.8	41.2
	1991	52.4	48.4	4.8	8.0	37.6
	Difference	1.2	-5.6	2.0	-2.8	-3.6
Shoulder A						
Inside	1990	86.4	32.8	4.0	26.4	30.0
	1991	84.8	33.6	4.4	24.4	33.2
	Difference	-1.6	0.8	0.4	-2.0	3.2
Outside	1990	82.4	29.6	2.4	22.4	27.6
	1991	84.0	30.0	2.8	18.4	28.8
	Difference	1.6	0.4	0.4	-4.0	1.2
Shoulder B						
Inside	1990	16.8	39.6	4.4	8.4	68.4
	1991	14.8	36.0	7.2	4.8	68.4
	Difference	-2.0	-3.6	2.8	-3.6	0.0
Outside	1990	16.0	32.4	6.8	2.4	69.6
	1991	13.2	30.8	8.0	1.2	70.0
	Difference	-2.8	-1.6	1.2	-1.2	0.4
Post lake A						
Inside	1990	40.8	43.2	6.4	45.6	26.0
	1991	39.2	43.2	6.4	47.2	24.4
	Difference	-1.6	0.0	0.0	1.6	-1.6
Outside	1990	54.4	40.4	5.2	56.4	16.8
	1991	53.6	40.4	3.2	57.2	17.2
	Difference	-0.8	0.0	-2.0	0.8	0.4
Post Lake B						
Inside	1990	38.0	35.6	4.4	30.8	35.2
	1991	36.0	35.6	6.0	35.2	37.2
	Difference	-2.0	0.0	1.6	4.4	2.0
Outside	1990	51.2	46.4	4.8	41.6	17.6
	1991	49.2	45.6	2.4	44.0	22.4
	Difference	-2.0	-0.8	-2.4	2.4	4.8

Table 4-7. Estimated vegetation cover (%) in 1990 and 1991 inside and outside exclosures located within the raised lichen-*Dryas* sedge and alluvial shingle range types.

Site		Plant categories				
		Lichens	Shrubs	Graminoids & Forbs	Mosses	Others
Raised lichen-*Dryas* sedge:						
Bear Cove C						
Inside	1990	56.0	40.4	1.6	15.2	42.0
	1991	58.8	43.6	0.4	10.0	38.8
	Difference	2.8	3.2	-1.2	-5.2	-3.2
Outside	1990	46.0	41.6	0.4	14.4	40.4
	1991	47.2	34.0	0.0	13.2	40.8
	Difference	1.2	-7.6	-0.4	-1.2	0.4
Bear Cove D						
Inside	1990	54.4	40.8	4.4	3.6	48.4
	1991	54.0	38.4	2.0	3.6	51.6
	Difference	-0.4	-2.4	-2.4	0.0	3.2
Outside	1990	42.0	57.6	6.0	12.0	27.6
	1991	40.0	54.0	6.0	10.4	29.2
	Difference	-2.0	-3.6	0.0	-1.6	1.6
Native Point A						
Inside	1990	27.6	32.8	2.8	6.4	63.2
	1991	24.4	31.6	2.4	5.6	58.0
	Difference	-3.2	-1.2	-0.4	-0.8	-5.2
Outside	1990	24.0	35.6	0.4	7.2	54.8
	1991	26.0	37.6	1.2	5.2	60.4
	Difference	2.0	2.0	0.8	-2.0	5.6
Native Point B						
Inside	1990	38.8	36.0	2.8	11.6	51.2
	1991	37.6	38.0	1.6	12.8	48.8
	Difference	-1.2	2.0	-1.2	1.2	-2.4
Outside	1990	26.0	35.6	2.0	11.2	61.2
	1991	24.8	34.4	0.8	6.0	58.4
	Difference	-1.2	-1.2	-1.2	-5.2	-2.8
Alluvial Shingle:						
Kirchoffer River						
Inside	1990	131.8	29.6	8.8	1.2	26.0
	1991	126.8	32.8	9.2	0.8	27.2
	Difference	-5.0	3.2	0.4	-0.4	1.2
Outside	1990	146.2	40.4	0.4	0.0	20.8
	1991	121.4	42.4	0.0	1.6	30.4
	Difference	-24.8	2.0	-0.4	1.6	9.6

Table 4-8. Estimated vegetation cover (%) in 1990 and 1991 inside and outside exclosures located within the within the sedge-willow range type.

Site		Lichens	Shrubs	Graminoids & Forbs	Mosses	Others
Bear Cove A						
Inside	1990	1.8	29.9	12.6	25.2	31.4
	1991	2.4	28.4	11.6	22.8	34.8
Difference		0.6	-1.5	-1.0	-2.4	3.4
Outside	1990	4.6	44.6	12.9	6.6	33.2
	1991	3.6	42.0	14.8	5.6	34.0
Difference		-1.0	-2.6	2.1	-1.0	0.8
Bear Cove B						
Inside	1990	0.0	22.4	21.2	23.4	36.2
	1991	0.0	20.8	18.0	21.2	40.0
Difference		0.0	-1.6	-3.2	-2.2	4.2
Outside	1990	3.2	35.2	6.2	31.8	29.2
	1991	1.6	32.8	5.6	28.4	31.6
Difference		1.6	-2.4	-0.6	-3.4	2.4

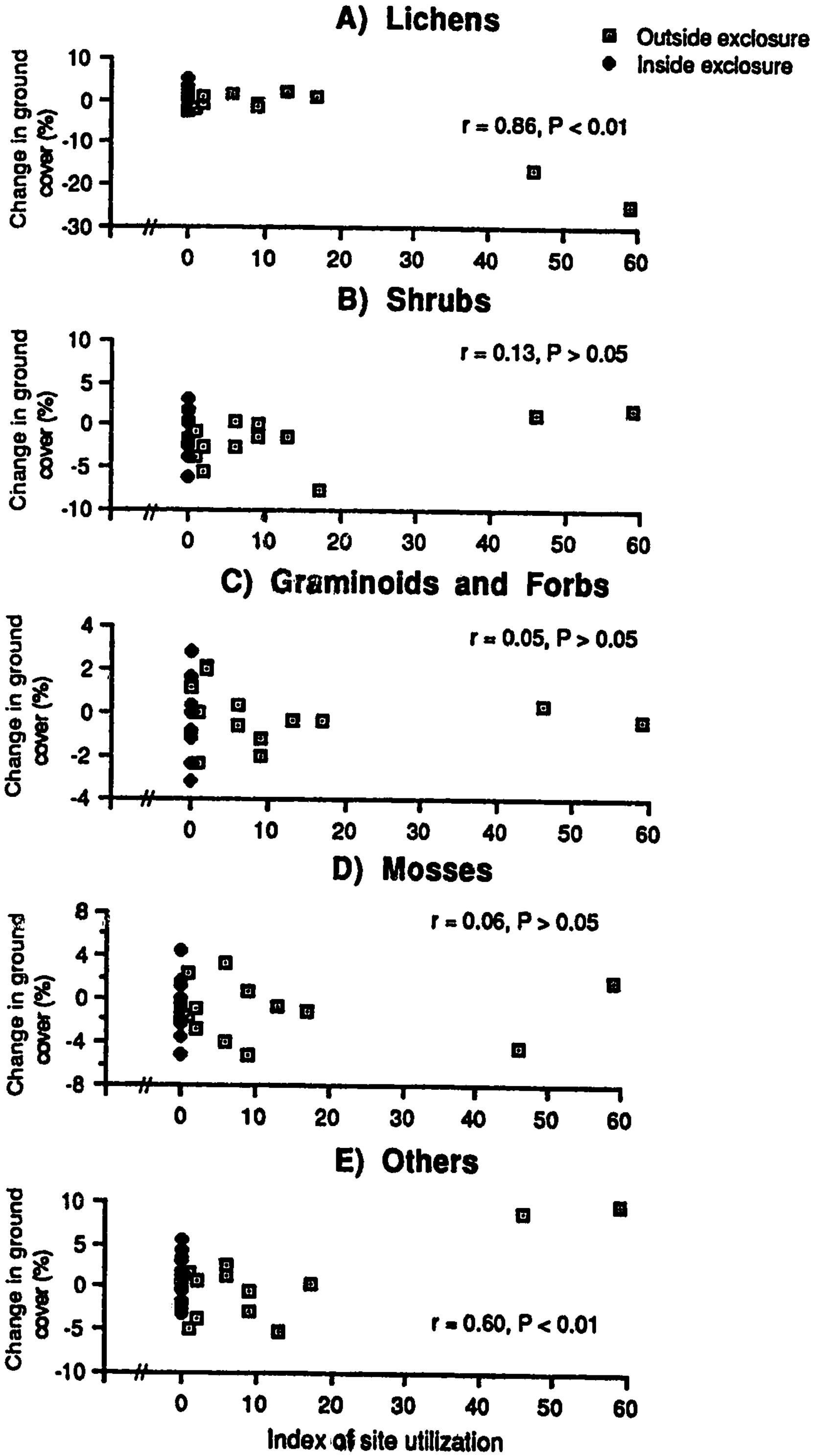

Figure 4-1. Changes in ground cover from 1990 to 1991 (% cover in 1991 minus % cover in 1990) for (a) lichens, (b) shrubs, (c) graminoids and forbs, (d) mosses, and (e) others as a function of habitat utilization by caribou (based on pellet count; see text). The two data points on the right side of the graphs are Last Lake A and Kirchoffer River, respectively.

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Chapter 5.

The response to defoliation of caribou forages

Introduction

Grazing can modify the productivity and chemical composition of forage plants. There is a continuum of plant response to herbivory, from undercompensation to overcompensation of growth (Maschinski & Whitham 1989), and from reduction (Bryant *et al.* 1983) to enhancement (McNaugthon 1984) of quality. These responses in productivity and chemical composition of the vegetation, may in turn influence the dynamics of caribou populations.

For predator-free areas, intraspecific food competition regulate reindeer numbers (Leader-Williams 1980; Skogland 1985, 1986). Until recently, hunting and predation were the suggested key factors as limiting continental caribou numbers (see Bergerud 1980, 1988). However, according to Messier *et al.* (1988), this view may incorrectly depict the demography of large caribou herds in tundra and forest ecosystems. They argue that the nature of caribou-lichen interactions may generate long-term fluctuations in caribou numbers if human exploitation remains low. More recently, Crête *et al.* (1990) proposed that the quantity of deciduous shrubs could be the main regulatory factor for the George River herd in northern Quebec. Although, animal-plant interactions may play a crucial role in the population dynamics of caribou (Chapter 3), only a limited number of studies have considered the impact of herbivory on forages available to caribou on the tundra (see Archer & Tieszen 1986).

The objective of this chapter was to assess the consequences of grazing on the dominant plant types available to caribou in the eastern Canadian Arctic. The response to grazing was determined by quantifying the effect of different experimental clipping regimes on the net primary production and chemical composition of plant tissue. Consequences of grazing were analyzed both within the growing season during which the various treatments were applied, and after one full year of recovery.

Methods

Clipping experiments were performed on the dominant plant types found on Southampton Island (see description of the study area in Chapter 2) in the summers of 1989-1991. Parker (1975) investigated the vegetation on the island and provided a classification scheme based on moisture regimes. I selected four range types (sedge-willow meadow, sedge-willow bog, raised lichen-*Dryas* sedge, and lichen-heath felsenmeer) which represent the main source of food for caribou inhabiting the island (Parker 1975). One exclosure, designed to exclude the major herbivores inhabiting the island (caribou, *R. t. groenlandicus*; snow goose, *Chen caerulescens*), was set up in each of the four range types. Because lemming densities were very low during the study (Van Wynsberghe, Nicole pers. comm.) they were not considered to be an important factor in plant consumption. The exclosures (22 m X 22 m X 90 cm high) were made of heavy farm fencing anchored on oil barrels filled with rock, placed at 5.4 m intervals. Clipping experiments were conducted within these four exclosures. Plants (single individuals or plots, see below) subjected to clipping were selected and numbered with a tag prior to the onset of the experiment. Each was subsequently assigned randomly to a treatment or control group. No plants were used within 1 m of the fence or drums to reduce the possibility of effects of the exclosures on physical conditions (Chapter 4).

The "sedge-willow meadow" range type was characterized by the presence of standing water early in the spring and in summer, but by late summer the soil surface became relatively dry. Upright willows were prominent, reaching 65 cm in height; *Salix lanata* was the dominant species in the exclosure. Mosses comprised about 50% of the ground cover. The "sedge-willow bog" range type was similar to sedge-willow meadow but willows were considerably less dominant and standing water covered a larger proportion of the ground. Common species found in the exclosure located in the sedge-willow bog were *Carex membranacea*, *Carex aquatilis*, *Carex bigelowii*, and *Eriophorum angustifolium* Raised lichen-*Dryas* sedge was dominated by *Dryas integrifolia*, lichens, and sedges. *Cassiope tetragona* was also abundant inside the exclosure, but mosses were of minor importance. Lichens principally of the genera of *Cetraria* and *Alectoria*, were the dominant plant form in the lichen-heath felsenmeer range type. *C. tetragona* and *D. integrifolia* were dominant among shrubs, but sedges were not very abundant (based on Parker 1975).

Plants were artificially clipped to simulate grazing, based on direct observations of caribou feeding and indirectly by inspecting grazed vegetation. The advantage of this approach over natural grazing is that the amount of plant tissue removed, and the frequency and timing of defoliation can be controlled (Archer & Tieszen 1980). Of course, some differences may exist between clipping and actual grazing (see Archer and Tieszen, 1980).

The effect of timing and intensity of defoliation on shrubs was studied. I removed photosynthetic tissue by hand (see Table 5-1 for a detailed description of the clipping regimes). One deciduous (*S. lanata*), one evergreen (*C. tetragona*), and one semi-evergreen (*D. integrifolia*) shrub species were investigated. *S. lanata* was studied in the sedge-willow range type, and, the other two species were analyzed in the raised lichen-*Dryas* sedge range type. Treatments were applied to individual *S. lanata*; an individual was defined as a stem that emerged above the moss surface. For the other two shrub species, treatments were applied within 400 cm^2 plots. Prior to the onset of the experiment, plot locations were carefully choosen to minimize the initial variance in standing crop among them. For *D. integrifolia* , individual leaves were removed by hand. For *C. tetragona*, I cut the terminal portion of current twigs with scissors. A 0.5 m buffer zone was allowed between all individuals or plots. Ten replicates (plots) per treatment were established for *C. tetragona* and *D. integrifolia*, whereas nine replicates (individuals) per treatment were used for *S. lanata*. Plant were clipped either after snowmelt (June 30th), early in summer (July 15th), or in late summer (July 30th), and either 50 or 100% of the photosynthetic tissue present was removed. All treatments were applied during the summer of 1990. The consequences of the treatments were assessed at the end of the growing season (August 15th) for both 1990 and 1991. Consequently, two control groups were necessary one for each growing season.

The effect of timing and frequency of defoliation was assessed on graminoids. Two types of graminoids were studied: *Carex scirpoidea*, characteristic of mesic habitat of the raised lichen-*Dryas* sedge range type and wet meadow graminoids found in sedge-willow bog range type. Treatments on *C. scirpoidea* were applied to single shoots (50 replicates; 0.5 m buffer zone between individuals). All shoots of *C. scirpoidea* surrounding the target shoot within 20 cm^2 were also clipped. For wet meadow graminoids, treatments were applied regardless of the graminoid species found within 50 cm X 50 cm treatment plots (17 replicates; 1 m buffer zone between plots) (Table 5-1b). Graminoids were clipped either after snow melt (June 30th), early in summer (July 15th), in late summer (July 30th), or all of these three times. All above ground tissue of graminoids above the moss level within the plot was clipped with scissors.

Finally, different defoliation regimes were applied to lichens found within 50 cm X 50 cm plots (5 replicates, 1 m buffer zone between each plot) (Table 5-1c). Thinning and clipping of lichens simulated light and heavy grazing, respectively (Gaare 1986). The dominant lichen species present in the exclosure, in the lichen-heath felsenmeer range type, were *Cetraria nivalis* and *Alectoria ochroleuca*. To quantify the effect of lichen removal, plant cover was estimated at the end of each growing season (after the treatments were performed in 1989, and in 1990 and 1991). Plant cover at the species level was estimated using the point-intercept method (Wein and Rencz, 1976) with 50 readings per plot. A pin was lowered to ground level, and every plant encountered was determined. Successive interception of the same species within the same reading was recorded as one interception. The method used to estimate lichen cover proved to be a good predictor of lichen biomass (biomass [g dry wt/0.25 m^2]= 0.56 lichen cover (%) - 2.16; n=15, P< 0.001, r^2= 0.89).

After harvesting, plant material was separated into live (biomass) and dead matter, oven-dried (60°C), weighed, and analyzed for nutrients, fiber, and total nonstructural carbohydrates. Nutrients of the green tissue were determined using standard CHN autoanalyzer (N) and inductively coupled plasma spectroscopic method (Ca, Mg, K, P) (A.O.A.C.1985). For calibration, *Citrus* leaves from the U.S. National Bureau of Standards were used. Total nonstructural carbohydrates (TNC), which includes sugars, starches, and fructosans were determined according to Smith (1979). Fiber fractions considered were cellulose (ADF - lignin and ash) and crude lignin fraction (lignin and ash residues; hereafter referred as lignin); methodology followed Goering & Van Soest (1970). Because the biomass collected for *C. scirpoidea* was small, the nutritional analysis was restricted to nitrogen determination. No nutritional analysis was conducted for the lichens as a non-destructive method was used to analyze the consequences of simulated grazing on lichens. Net above ground primary production (hereafter referred to as net production) was calculated as the sum of positive photosynthetic tissue biomass increments during one growing season.

Data were tested for heterogeneity of variances with Bartlett's test. A one-factor analysis of variance (ANOVA) was used to test for treatment effects. ANOVA was followed by post-hoc comparisons using the Dunnett procedure (Zar 1984) between mean values of the various treatment groups and the corresponding control group. Calculations were performed using SYSTAT software (Wilkinson 1989).

Results

Seasonal change

Biomass

Seasonal growth patterns differed among shrub species. Growth started earlier in *C. tetragona* and *D. integrifolia* than in *S. lanata*; 18 % and 47 % of phosynthetic tissue were present at the onset of the experiment (June 30th; values relative to the net production attained by control groups over the growing season) in the former two species, respectively, while in the latter species the buds were just breaking. Almost all above ground tissue production was completed by July 30th for *D. integrifolia* and *C. tetragona*, whereas growth continued during the last period (end of July to mid-August) for *S. lanata*.

The seasonal progression of above-ground biomass also differed between the two types of graminoids. At the time the first series of treatments were applied, 62 % of the final standing crop was present in *C. scirpoidea*, relative to 26 % for the wet meadow species. For *C. scirpoidea*, almost 100% of the above ground biomass was attained by mid-July, whereas growth continued at a steady rate until the end of July for wet meadow species.

Chemical composition

Concentrations of cellulose and lignin in photosynthetic tissues were relatively stable over time for most of the different forage types (Figure 5-1). However, concentration in *S. lanata* decreased from high values in the leaf bud stage before stabilizing at lower levels than other forage types. Concentrations of lignin recorded for wet meadow graminoids, were the lowest of all forage types.

Excluding the transition from buds to leaves for *S. lanata* the seasonal changes in total nonstructural carbohydrates (TNC) followed a similar pattern in all forage types (Figure 5-2a). Concentrations decreased slightly in the spring, increased during summer and finally declined in the fall. *D. integrifolia* and *C. tetragona* had a higher level of total nonstructural carbohydrates relative to *S. lanata* and the graminoids.

Nitrogen content for *C. tetragona* was essentially constant over the study period (Figure 5-2b). However, for the other forage types the nitrogen content tended to decline slowly over time. This pattern was slightly different for *S.*

lanata; nitrogen content increased during leaf expansion to a peak early in summer, and then declined. For wet meadow graminoids the percentage of nitrogen increased slightly after the initial growth. Nitrogen content differed between species. For *S. lanata* and the wet meadow graminoids, nitrogen content was high relative to the other forage types.

Calcium content of forage types increased during the growing season (Figure 5-3a), whereas potassium and phosphorus contents generally showed the opposite trend (Figure 5-3c and 5-3d). Magnesium content remained relatively constant, except for *S. lanata* which showed a general increase over time (Figure 5-3b). Excluding calcium, *S. lanata* and the graminoids had higher concentrations of minerals than the other forage types.

Consequences of defoliation

Net Production

The growth response of the three shrub species after defoliation treatments are shown in Tables 5-2, 5-3, and 5-4. Net production of *S. lanata* was negatively affected by clipping, with the exception of plants clipped late in summer at an intensity of 50 % which did not exhibit significantly lower net production relative to the control group during the treatment year (1990) (Table 5-2). Overall, relative net production (mean net production of all treatment groups divided by the production achieved by the control group expressed as a percentage) of clipped *S. lanata* was 67 %. No regrowth occurred in the group completely defoliated at the end of summer, although tiny buds were breaking in the fall but no leaves grew. When clipping occurred either after snowmelt or in early summer, the impact of defoliation was independent of defoliation intensity. The impact of these defoliation regimes had a carry-over effect the following year as spring and early summer defoliation groups had a lower net production in 1991, although no clipping took place that year. The relative net production of treated *Salix* was 66 % in 1991.

The response of *S. lanata* during the treatment year resulted partly from buds found on non-primary stems. Buds found on primary twigs (1 year old) produced 99 % of the biomass of unclipped plants. However, for plants clipped at an intensity of 50 %, 93 % of the biomass was produced by primary stems. This percentage decreased further to 73 % for plants clipped at an intensity of 100 %. In a few cases, individuals clipped the previous year responded by growing new and vigourous shoots, at the base of the main stem. Clipped (all treatments) *S. lanata* had significantly fewer leaves per individual (mean of 165 for clipped plants vs 314 for unclipped plants; $P < 0.05$) and a lower mean weight per leaf (0.007 g vs 0.011 g; $P < 0.05$) than unclipped plants. In the following year (1991), clipped individuals had a lower number of leaves (318 vs 504; $P < 0.05$). Mean weight per leaf was not significantly different in 1991 between clipped and unclipped individuals (0.008 g vs 0.008 g; $P > 0.05$). However, in 1991 leaves growing on new shoots (see above) were much heavier than leaves found on controls (0.015 g vs 0.008 g; $P < 0.05$).

Different defoliation treatments had no significant impact on the net production of *D. integrifolia* during the treatment year (Table 5-3). However, the impact was more apparent the second year; 100 % removal of the photosynthetic tissue after snowmelt and in early summer induced a lower net production. In 1990 and 1991, clipped *D. integrifolia* attained 93 % and 75 % of the net production achieved by the respective control groups.

During the treatment year, individual *C. tetragona* shoots clipped in the spring or early in summer at 100 % intensity showed significantly lower net production (Table 5-4). Clipped *C. tetragona* showed a mean relative net production of 49 %. However, the impact was more pronounced the second season. Relative net production reached only 7 %, and all the treatment groups had significantly lower tissue production.

The impacts of defoliation treatments on wet meadow graminoids are presented in Table 5-5. The comparisons between the different treatments and the control group demonstrate that net production was significantly lower only during the treatment year for plants that were clipped repeatedly. Indeed, plots subjected to repeated clipping had a relative net production of 73 % in 1990. However, the net production of individuals subjected to repeated defoliation was restored the following year. Treated graminoids had net production of 90% and 85 % of controls in 1990 and in 1991, respectively. In 1991, the only year in which it was quantified, the ratio of live to dead matter (above ground) was significantly lower for all treated groups relative to the control group (0.59 vs 1.30; $P < 0.05$). For *C. sc[illegible]pidea*, the different defoliation treatments had no significant ($P < 0.05$) effe[illegible] net production during either the treatment year or the recovery year.

Changes in vegetation cover following different clipping and removal treatments to lichens are presented in Figures 5-4. Vegetation cover did not change for the control group during the two sampling intervals. Consequently, there was no measurable net production of lichens during these two years. However, following clipping and thinning, cover of lichens decreased in the subsequent year by a mean value of 6 % in all treatment plots. This reduction in cover of lichens represented 14 % of the lichen biomass removed at the onset of the experiment. Conversely, the combined values of the dead matter, bare ground, and crustose lichens increased by a mean value of 11 %. Changes in this category were primarily the result of an increase in dead matter. In the second year, except for plots clipped at an intensity of 50 %, cover of lichens "increased" slightly (1 %). This small increase in cover of lichens during the second year was not enough to compensate for losses that occurred during the first year. The net production of clipped and thinned lichens were consequently negative.

When all the lichens or all the vegetation were removed, cover of lichens increased rapidly during the first and second year, attaining 4 % and 9 % of ground cover, respectively. However, the increase was from lichen fragments blown onto the plots. Although the vegetation cover was relatively low in the plots that were totally denuded, plants species belonging to all five vegetation categories were found after one or two years (Figure 5-4).

Chemical composition

The impacts of defoliation on the chemical composition of the different forage types are presented in Tables 5-2, 5-3, 5-4 and 5-5. The different clipping regimes did not have a major impact on the chemical composition of *C. tetragona* (Table 5-4). However, the other forage types responded more strongly. Individual *S. lanata* that were totally defoliated in the spring had a higher content of nitrogen and phosphorus, and a lower concentration of total nonstructural carbohydrates relative to controls (Table 5-2). Nitrogen and calcium content increased for *D. integrifolia* clipped in the spring or early in summer (Table 5-3a). *D. integrifolia* individuals that were totally defoliated in the spring also showed an increase in potassium and phosphorus content. Clipped wet meadow graminoids had higher nitrogen, magnesium, potassium, phosphorus and cellulose and lower levels of total nonstructural carbohydrates than unclipped controls (Table 5-5a). However, those graminoids clipped in the spring had a chemical composition similar to the control group. For all the forage types, the chemical composition of the individuals that were clipped the previous season was similar to those which were left unclipped in the subsequent year (Tables 5-2b, 5-3b, 5-5b).

Graminoids were also clipped repeatedly. Consequently, the influence of the these defoliations can be determined over time. Repeated defoliation enhanced the levels of nitrogen, magnesium, potassium, phosphorus and cellulose in wet meadow graminoids (Figures 5-6, 5-7 and 5-8). The same trend exhibited by the wet meadow graminoids was observed for nitrogen content in *C. scirpoidea* (Figure 5-7b). Repeated defoliation also generated a decrease in the concentration of the total nonstructural carbohydrates (Figure 5-7a). The impact of repeated defoliation on the chemical composition of graminoids was noticeable early in the growing season.

Discussion

The impact of defoliation on the net production of shrubs differed among species for the growing season during which the various clipping regimes were applied (Table 5-6). The differential impact of simulated grazing on the net production of shrubs can be explained partially by differences existing between the seasonal pattern of growth among the shrubs. In fact, based on seasonal changes in biomass, each shrub species was at a different phenological stage when treatments were applied. *D. integrifolia* and *C. tetragona* produced a greater proportion of their biomass early in the season, relative to *S. lanata*. Consequently, net production of species showing an early growth pattern were least likely to be affected by simulated grazing. Thus, the timing of defoliation in relation to the phenology of each species influenced net production. The intensity of defoliation was also determinant. Shrubs totally defoliated generally showed reduced net production relative to individuals which were clipped at a lower intensity. Net production was also influenced in the year following treatment suggesting that grazing had a carry-over effect. Timing and intensity of defoliation influenced net production. The carry-over impact of simulated grazing on *C. tetragona*, an evergreen shrub, was particularly severe relative to the other types of shrubs. Clipped *C. tetragona* attained only a small fraction of the net production achieved by the control group. This influence of grazing on net production can be attributed, in part, to its effect on nutrient reserves (Chapin *et al.* 1980). Forage plants having a greater proportion of their nutrient pool in the leaves, such as *C. tetragona*, are consequently more likely to be affected. Similarly, deciduous shrubs move a large proportion of their nutrient capital to leaves immediately following snow-melt (Chapin *et al.* 1980). Indeed, *Salix* individuals that showed lower net production where those clipped early in the growing season. Therefore, patterns of nutrient movement and allocation, that differ between forage types, influenced the response to defoliation.

Findings support Archer & Tieszen's (1980) classification of shrubs in terms of their ability to recover from defoliation. Evergreen shrubs have a poor ability to recover from grazing, whereas deciduous shrubs show a moderate capacity to do so. However, Henry and Gunn (1991) proposed that *Salix* is resilient to grazing. Their results suggested that compensatory growth occurred in the year following an episode of overgrazing on Rideout Island, Bathurst Inlet, N.W.T., Canada. This study confirms the results of Henry & Gunn (1991), but only when individuals are clipped late in the growing season. When *S. lanata* was clipped earlier in the growing season, little compensatory growth occurred.

Among graminoids, *C. scirpoidea* showed compensatory growth for all treatment groups during the treatment year, as well as the following year. Only repeated clipping caused a lower net production for the wet meadow graminoids, but this effect did not carry over to the following year. As with shrubs, it is possible that the differential ability to acheive maximum net production after clipping can be attributed to their different growth pattern; *C. scirpoidea* had acheived a larger proportion of its final standing biomass early in the season relative to wet meadow graminoids. Consequenlty, the timing of defoliation in relation to the phenology of growth may be an important factor in determining whether or not graminoids, subjected to repeated defoliation, achieve total compensation. Graminoids possess several features that make them resilient to grazing (Archer & Tieszen 1980; McNaughton 1979; Jonsdottir 1991), and results from this study support this claim, as compensatory growth was achieved in most instances.

Lichens in control sites did not show any changes in standing biomass (net production of zero) during the two years of the study, indicating that they had reached maximum standing crop. However, net production of clipped lichens was negative during the same period of time. The reduction in standing biomass of lichens was due to the fact that some lichens, likely those dismantled from the mat during the process of extracting, rotted following removal and were consequently classified as dead matter in the subsequent year. However, in the second year a slight positive response was measured, indicating that net production of lichens might be enhanced after the initial phase of decline. These findings confirm the low resilience of foliose and fruticose lichens to grazing (e.g. Henry & Gunn 1991; Klein 1968,1987; Palmer & Rouse 1945). Klein (1987) reported that graminoids and willows increased in abundance some 20 years after reindeer removed most of the lichen mat. Such a response was not found in this study, nor one year after a dramatic episode of overgrazing on Rideout Island (Henry & Gunn 1991).

Absolute values of nitrogen, calcium, magnesium, potassium, and phosphorus contents were generally comparable to values obtained for similar forage types in other studies (Chapin 1980a,1980b; Chapin *et al.* 1980; Chapin & Shaver 1988; Klein 1990: studies conducted in the western arctic). However, results for total nonstructural carbohydrate concentrations are slightly higher than those reported by Klein (1990), whereas cellulose and lignin contents are slightly lower. But, results of this study were in concordance with those presented in the studies conducted by Chapin (see above). Seasonal changes in the chemical composition were also generally consistent with other reports (Chapin 1980a, 1980b; Chapin *et al.* 1980, 1986; Klein 1990).

Preference and digestibility of caribou summer foods are correlated positively with nitrogen and phosphorus levels and negatively with fiber content (Chapin *et al.* 1986; Klein 1990; Kuropat & Bryant 1983). However, total nonstructural carbohydrates is positively correlated with digestibility (Klein 1990) but negatively correlated with food preference ranking (Chapin *et al.* 1986). This led Chapin *et al.* (1986) to suggest that nitrogen and minerals are more likely to limit tundra herbivores during summer, than is energy. However, there is potentially an optimal protein:energy ratio for maximum utilization efficiency of both dietary protein and energy (Allaye-Chan 1991). Nevertheless, observed changes in the chemical composition of the various forage types over the course of the growing season indicate that food quality peaked early in summer and declined gradually therafter. The seasonal decline in food quality might be further exacerbated by a concomitant increase in protein complexing leaf phenols that reduce digestibility (Kuropat & Bryant 1983), at least in deciduous shrubs (Bryant *et al.* 1983; Harkioja *et al.* 1978). Generally forage plants are of better quality in the early stages of growth than later in the growing season (Klein 1990). Results of this study indicated that the timing of this peak in food quality differed slightly between forage types. This was partly a reflection of different seasonal patterns of growth observed among forage types.

The nutritional value also differed among forage types. *S. lanata* and the graminoids had lower values of cellulose, lignin, and higher concentrations of nitrogen, potassium, and phosphorus relative to *C. tetragona* and *D. integrifolia*. Consequenlty, these forage types (*S. lanata* and graminoids) likely represent higher food quality and should be preferred by caribou. Although no preference trial was conducted, these two forage types composed a large proportion of the summer diet of caribou on the island (unpub. data). The chemical composition of *C. tetragona* indicates that this species is of low nutritive value, and accordingly was not abundant in the caribou diet (Unpub. data). Henry & Gunn (1991) reported that *C. tetragona* was generally avoided by caribou except when severe food limitation takes place. It is also known that evergreen shrubs contain high resin concentrations which play an anti-herbivore role (Chapin & Shaver 1988). The presence of such anti-herbivore compounds in *C. tetragona* suggests that it may receive little grazing pressure, explaining its low resilience to simulated grazing.

The chemical composition of most forage types was modified by defoliation during the treatment year. Clipped wet meadow graminoids attained nitrogen, magnesium, potassium and phosphorus levels beyond the maximum concentration obtained by controls at any point during the growing season. Within 15 days the chemical composition of new growth was altered in wet meadow graminoids. But the effect of grazing on the chemical composition is attenuated after a certain period of time, likely between 1 and 1.5 months after clipping. Nitrogen content of *C. scirpoidea*, the only nutrient considered for this species, was modified by simulated grazing in the same manner as the wet meadow graminoids. Consequently, it is likely that the observed changes in the chemical composition of wet meadow graminoids also occurred in *C. scirpoidea* . The effect of defoliation on the chemical composition was less marked for *S. lanata* and *D. integrifolia* than for graminoids. Nutrient values of these shrubs did not reach levels beyond those attained by control groups earlier in the season. Chapin (1980a) suggested that grazing caused a delay of about a month in the phenology of clipped *S. pulchra* relative to controls. This might explain why the greatest responses were observed in *S. lanata* and *D. integrifolia* clipped early in the season. During the recovery year, new growth of clipped individuals of all forage types had a chemical composition not significantly different from controls.

A positive effect of grazing on the nutritive value of the vegetation has been demonstrated in some studies. For example, grazing by geese in the subarctic (Ydenberg & Prins 1981; Cargill & Jefferies 1984) and by ungulates in Africa (McNaughton 1985) enhances nitrogen content of forage plants. This grazing-related process, that could be referred to as resource regulation (Price 1991), might be particularly important for caribou. Caribou alter their diet in the winter to rely heavily on lichens as food, and are in a negative phosphorus balance and probably a negative nitrogen balance during this period (Boertje 1990). Consequently, they have to replenish nitrogen and phosphorus during the growing season. Moreover, caribou populations located on isolated islands cannot effectively use the asynchrony of plant phenology (i.e. forage quality is higher in early stages of plant growth), as suggested by Klein (1970), because they cannot migrate long distances. Northern caribou populations also experience a very short growing season, and physical growth, and body reserves repletion must take place in summer (Chapter 3). For example, during the peak of calving season (early June) on Southampton Island, almost no new growth is available to caribou. The growth pattern of two dominant forage types, *S. lanata* and wet meadow graminoids, suggests that during the month following calving the biomass of live tissue was very limited. In fact, *Salix* buds broke early in July and wet meadow graminoids had produced only a small fraction of their total production of photosynthetic tissue by then. Plant senescence began in mid-August, when calves were only 2.5 months old. Enhancement of forage quality through grazing might also be relevant for gravid females of continental herds that aggregate on calving grounds in treeless habitat.

There are two obvious interrelated consequences of forage quality enhancement through grazing, the vegetation is subjected to repeated defoliation, and it may favor the aggregation of herbivores (see Fryxell 1991). Some level of compensatory growth is necessary in the vegetation for the herbivore to benifit from regrazing plants that have been grazed previously. Recently, Murray (1991) showed that bite size is a key component of food selection by ruminants. Although, regrowth can be substantial (e.g. wet meadow graminoids; see Table 5-5), it remains to be tested if grazed forage would be selected by caribou. White & Trudell (1980) indicated that caribou tend to regraze plants that have been previously grazed (see also White 1983). Moreover, as shown earlier, repeated defoliation may be detrimental to the vegetation and may ultimately decrease the abundance of plant species, such as deciduous shrubs. On the other hand, repeated grazing and aggregation imply increased herbivore activities within an area. This may prove to be beneficial to the vegetation. In Africa, it has been shown that level of nutrient contents of the vegetation was related to soil nutrients (McNaughton 1988). The sources of those nutrients appear to be waste products (e.g. urine, feces) or carcasses of the herbivores themselves. Therefore, increased herbivore activities speeds up the rate of nutrient recycling, and may prove ultimately, to be beneficial to both vegetation and herbivores. Predation pressure and optimal foraging might not be opposing hypotheses (see Jakimchuk *et al.* 1987; Bergerud & Heard, unpub. data; Klein 1970) explaining caribou migration and aggregation on calving grounds located in the tundra. It is possible that these two forces might be acting in concert to favor the movements and aggregation patterns observed (Fryxell 1991; Fancy & Whitten 1991).

In summary, simulated grazing influenced plant net production. Plant growth after grazing likely differs among forage types and within forage types depending on the timing and intensity of defoliation. In most cases maximum net production of plants was not restored during the following year, although grazing pressure was lifted. This carry-over effect of simulated grazing on plant net production suggests that consequences might be additive from year to year. Finally, grazing modified forage quality and potentially favors repeated grazing and aggregation of herbivores. Modelling of plant-herbivore interactions should consider the effect of grazing on net production and chemical composition of plants. A step in that direction has been done in a recent paper by Fryxell (1991) who constructed a model of plant-herbivore interactions that integrates forage digestibility and its changes resulting from grazing (see also Hobbs & Swift 1988). This model suggests that aggregation may be favored when forage quality is enhanced by grazing.

Table 5-1. Description of the various clipping regimes applied to the different forage types during the 1990 growing season.

A) Shrubs (*Salix lanata, Dryas integrifolia, Cassiope tetragona*)

Treatments

Period	Intensity
After snowmelt	50 %
	100 %
Early summer	50 %
	100 %
Late summer	50 %
	100 %
Control	

B) Graminoids (Wet meadow graminoids, *C. scirpoidea*)

Treatments

Period	Intensity
After snow melt	100%
Early summer	100%
Late summer	100%
3 times	100%
Control	

C) Lichens (species belonging to the genera *Cetraria* and *Alectoria*)

Treatments

Type	Intensity
Thinned	33 %
	50 %
Clipped	33 %
	50 %
Removal of all lichens	100 %
Removal of all the vegetation	100 %
Control	

Note: For shrubs and graminoids, treatments applied after snowmelt, early in summer, and late in summer were initiated at the end of June (30th), mid-July (15th), and the end of July 1990 (30th), respectively. Plant material, was harvested in mid August 1990 (15th) and 1991 (15th). For lichens, treatments were applied at the end of July 1989.

Table 5-2. Impact of different simulated grazing regimes on the nutritional value of current leaves of *Salix lanata*

Treatment		Net Production[1] (g [dry wt] / year)	Cellulose (%)	Lignin (%)	TNC (%)	N (%)	Ca (%)	Mg (%)	K (%)	P (%)
A) 1990 (treatment year)										
After snowmelt:	50%	2.1* [2.0][2] (0.3)	12.4 (0.3)	5.9 (0.6)	9.9 (0.4)	2.8 (0.1)	1.89 (0.08)	0.23 (0.02)	1.43 (0.06)	0.23 (0.02)
	100%	2.3* [2.0] (0.3)	2.0 (1.0)	5.3 (0.2)	9.1* (0.5)	3.2* (0.2)	1.56 (0.16)	0.22 (0.02)	1.67 (0.17)	0.29* (0.01)
Early summer:	50%	2.2* [1.4] (0.2)	3.3 (0.4)	6.1 (0.4)	7.3* (0.3)	3.0 (0.1)	2.10* (0.10)	0.27 (0.04)	1.36 (0.03)	0.25 (0.02)
	100%	2.1* [0.1] (0.3)	-	-	8.9	3.8	0.66	0.12	2.10	0.40
Late summer:	50%	3.1 [1.6] (0.3)	12.4 (0.4)	5.8 (0.3)	9.6 (0.7)	2.9 (0.1)	2.07* (0.13)	0.25 (0.03)	1.47 (0.11)	0.24 (0.03)
	100%	2.6* [0.0] (0.3)	-	-	-	-	-	-	-	-
Control:		3.6 (0.3)	11.7 (0.7)	5.4 (0.5)	10.6 (0.3)	2.8 (0.1)	1.72 (0.08)	0.25 (0.03)	1.38 (0.10)	0.21 (0.03)
B) 1991 (recovery year)										
After snowmelt:	50%	1.6* (0.3)	10.2 (0.3)	4.2 (0.2)	7.6 (0.9)	2.1 (0.1)	2.20 (0.08)	0.27 (0.02)	1.66 (0.13)	0.14 (0.01)
	100%	1.6* (0.3)	10.3 (0.7)	4.4 (0.5)	8.2 (0.7)	2.2 (0.1)	2.11 (0.11)	0.24 (0.02)	1.93 (0.33)	0.16 (0.01)
Early summer:	50%	2.1 (0.2)	11.6 (0.3)	4.6 (0.2)	7.9 (0.6)	2.0 (0.1)	2.15 (0.17)	0.29 (0.04)	1.86 (0.08)	0.15 (0.01)
	100%	1.8* (0.2)	10.6 (0.2)	3.7 (0.3)	7.7 (1.2)	2.0 (0.1)	2.32 (0.14)	0.26 (0.03)	1.96 (0.18)	0.12 (0.01)
Late summer:	50%	2.0 (0.2)	10.6 (0.3)	3.9 (0.2)	8.3 (0.6)	2.0 (0.1)	2.22 (0.09)	0.24 (0.03)	1.90 (0.16)	0.13 (0.01)
	100%	2.1 (0.2)	10.7 (0.1)	4.1 (0.1)	8.5 (0.4)	2.0 (0.1)	2.31 (0.20)	0.29 (0.03)	1.86 (0.15)	0.14 (0.01)
Control:	1990	2.8 (0.3)	10.5 (0.5)	3.7 (0.2)	8.2 (0.5)	2.0 (0.1)	2.22 (0.13)	0.28 (0.03)	1.71 (0.13)	0.14 (0.01)
	1991	2.8 (0.3)	11.5 (0.6)	4.4 (0.4)	7.4 (0.5)	2.1 (0.1)	2.12 (0.12)	0.26 (0.04)	1.41 (0.12)	0.14 (0.02)

Note: Mean value (S.E. in brackets) of leaves from 4 individuals, except for net production (n=9); * Significantly different ($P<0.05$) from the control group. - Analysis not conducted due to the lack of plant material. Values without standard error shown are based on a single lumped sample of nine individuals; those values were not considered in the statistical analyses. 1: Net production for the entire summer; 2: biomass produced during the post treatment period.

Table 5-3. Impact of different simulated grazing regimes on the nutritional value of current leaves of *Dryas integrifolia*.

Treatment		Net Production[1] (g [dry wt] / year)	Cellulose (%)	Lignin (%)	TNC (%)	N (%)	Ca (%)	Mg (%)	K (%)	P (%)
A) 1990 (treatment year)										
After snowmelt:	50%	4.1 [3.0][2]	13.2	8.8	14.9*	1.6 *	1.97*	0.07	0.52	0.12
		(0.2)	(0.6)	(0.3)	(0.3)	(0.1)	(0.02)	(0.02)	(0.02)	(0.01)
	100%	3.6 [1.7]	13.5	8.6	13.7	1.9*	2.02*	0.09	0.66*	0.15*
		(0.4)	(0.5)	(0.3)	(0.2)	(0.1)	(0.05)	(0.02)	(0.03)	(0.01)
Early summer:	50%	4.1 [2.4]	13.3	8.7	13.2	1.6*	2.19*	0.10	0.49	0.12
		(0.3)	(0.5)	(0.2)	(0.1)	(0.1)	(0.06)	(0.02)	(0.02)	(0.01)
	100%	3.2 [0.2]	13.5	8.8	11.7*	2.1	2.21	0.09	0.56	0.13
		(0.2)		(0.2)						
Late summer:	50%	3.9 [2.9]	13.4	8.7	13.1	1.5	2.19*	0.08	0.48	0.10
		(0.2)	(0.4)	(0.3)	(0.1)	(0.1)	(0.05)	(0.02)	(0.05)	(0.01)
	100%	3.8 [<0.1]	-	-	15.4	2.2	-	-	-	-
		(0.2)								
Control:		4.1	13.7	8.9	13.4	1.4	1.87	0.10	0.49	0.10
		(0.2)	(0.5)	(0.2)	(0.3)	(0.1)	(0.03)	(0.01)	(0.05)	(0.01)
B) 1991 (recovery year)										
After snowmelt:	50%	1.9	13.3	8.4	9.4	1.3	2.20	0.09	0.61	0.12
		(0.2)	(0.4)	(0.3)	(0.7)	(0.1)	(0.04)	(0.01)	(0.07)	(0.01)
	100%	1.7*	12.9	8.0	8.6	1.3	2.17	0.10	0.63	0.11
		(0.1)	(0.6)	(0.2)	(0.3)	(0.1)	(0.03)	(0.01)	(0.04)	(0.01)
Early summer:	50%	2.2	13.7	8.6	8.1	1.3	2.31	0.11	0.64	0.12
		(0.2)	(0.3)	(0.2)	(0.2)	(0.1)	(0.12)	(0.01)	(0.04)	(0.01)
	100%	1.7*	13.8	8.8	8.3	1.4	2.44	0.11	0.67	0.15
		(0.2)	(0.6)	(0.3)	(0.6)	(0.1)	(0.05)	(0.01)	(0.02)	(0.01)
Late summer:	50%	2.1	13.0	8.2	7.9	1.3	2.41	0.09	0.61	0.13
		(0.1)	(0.5)	(0.2)	(0.3)	(0.1)	(0.12)	(0.01)	(0.03)	(0.01)
	100%	2.6	13.3	8.5	7.8	1.5	2.67	0.10	0.62	0.14
		(0.2)	(0.7)	(0.4)	(0.3)	(0.1)	(0.14)	(0.01)	(0.04)	(0.01)
Control:	1990	2.0	13.7	8.7	8.4	1.4	2.21	0.09	0.65	0.11
		(0.2)	(0.6)	(0.3)	(0.3)	(0.1)	(0.03)	(0.01)	(0.02)	(0.01)
	1991	2.7	13.5	8.6	8.3	1.4	2.42	0.10	0.63	0.11
		(0.3)	(0.6)	(0.2)	(0.3)	(0.1)	(0.08)	(0.01)	(0.03)	(0.01)

Note: Mean value (S.E. in brackets) of leaves from 4 individuals, except for net productivity (n=10); * Significantly different ($P < 0.05$) from the corresponding control group. - Analysis not conducted due to the lack of plant material. Values without standard error shown are based on a single lumped sample of 10 individuals; those values were not considered in the statistical analyses. 1: Net production for the entire summer; 2: biomass produced during the post treatment period.

Table 5-4. Impact of different simulated grazing regimes on the nutritional value of current leaves of *Cassiope tetragona.*

Treatment		Net Production^1 (g [dry wt] / year)	Cellulose (%)	Lignin (%)	TNC (%)	N (%)	Ca (%)	Mg (%)	K (%)	P (%)
1990 (treatment year)										
After snowmelt:	50%	1.8 [1.0]^2 (0.4)	12.6 (0.8)	15.5 (0.7)	12.0 (0.3)	1.4 (0.1)	0.72 (0.03)	0.10 (0.01)	0.37 (0.01)	0.09 (0.01)
	100%	0.7* [<0.1] (0.2)	-	-	11.1	1.8	-	-	-	-
Early summer:	50%	2.9 [1.5] (0.6)	12.5 (0.6)	15.3 (0.7)	12.0 (0.4)	1.4 (0.1)	0.69 (0.05)	0.11 (0.01)	0.35 (0.01)	0.08 (0.01)
	100%	1.6* [<0.1] (0.3)	-	-	-	1.5	-	-	-	-
Late summer:	50%	2.1 [1.1] (0.3)	12.4 (0.7)	15.5 (0.7)	11.9 (0.5)	1.3 (0.1)	0.91* (0.06)	0.11 (0.01)	0.36 (0.02)	0.08 (0.01)
	100%	2.6 [<0.1] (0.6)	-	-	9.5	1.4	-	-	-	-
Control:		3.0 (0.5)	12.7 (0.9)	15.6 (0.8)	12.7 (0.2)	1.3 (0.1)	0.66 (0.07)	0.11 (0.01)	0.36 (0.01)	0.07 (0.01)

Note: Mean value (S.E. in brackets) of leaves from 4 individuals, except for net production (n=10); * Significantly different (*P* <0.05) from the control group. - Analysis not conducted due to the lack of plant material. Values without standard error shown are based on a single lumped sample of 10 individuals; those values were not considered in the statistical analyses. Refer to the text for the 1991 net production data (due to low growth no chemical analyses were conducted). 1: Net production for the entire summer; 2: biomass produced during the post treatment period.

Table 5-5. Impact of different simulated grazing regimes on the nutritional value of wet meadow graminoids.

Treatment	Net Production[1] (g [dry wt] / year)	Cellulose (%)	Lignin (%)	TNC (%)	N (%)	Ca (%)	Mg (%)	K (%)	P (%)
A) 1990 (treatment year)									
After snowmelt	9.6 [6.6][2] (0.6)	18.7 (0.5)	3.1 (0.5)	11.1 (0.2)	2.9 (0.1)	0.70 (0.03)	0.10 (0.01)	2.02 (0.07)	0.19 (0.01)
Early summer	10.1 [2.3] (0.6)	21.3* (0.3)	2.2 (0.1)	8.4* (0.3)	3.4* (0.1)	0.63 (0.04)	0.18* (0.02)	2.39* (0.08)	0.32* (0.02)
Late summer	12.5 [1.0] (0.9)	22.6* (0.5)	2.9 (0.4)	6.8* (0.1)	2.9 (0.1)	0.49* (0.03)	0.18* (0.01)	1.99 (0.24)	0.29* (0.01)
3X defoliated	8.6* [0.8] (0.7)	22.7* (0.3)	1.6 (0.3)	7.3* (0.4)	3.5* (0.1)	0.59 (0.01)	0.18* (0.01)	2.28* (0.07)	0.39* (0.01)
Control	11.9 (0.8)	20.1 (0.3)	2.3 (0.1)	11.6 (0.2)	2.7 (0.1)	0.62 (0.04)	0.12 (0.01)	1.71 (0.12)	0.19 (0.01)
B) 1991 (recovery year)									
After snowmelt	4.9 (0.4)	19.5 (0.5)	2.6 (0.1)	6.7 (0.5)	1.8 (0.1)	0.74 (0.05)	0.12 (0.01)	1.36 (0.06)	0.14 (0.01)
Early summer	4.0	19.2	2.4*	7.0	1.9	0.84	0.12	1.32	0.14
	(0.3)	(0.2)	(0.2)	(0.6)	(0.1)	(0.03)	(0.01)	(0.08)	(0.01)
Late summer	4.6 (0.4)	19.2 (0.2)	2.7 (0.1)	7.4 (0.7)	1.7 (0.1)	0.76 (0.06)	0.11 (0.01)	1.37 (0.07)	0.14 (0.01)
3X defoliated	3.8 (0.3)	18.8 (0.5)	2.9 (0.3)	7.6 (0.3)	1.8 (0.1)	0.72 (0.02)	0.13 (0.01)	1.22 (0.03)	0.12 (0.01)
Control 1990	5.6 (0.4)	19.6 (0.3)	2.8 (0.1)	7.2 (0.7)	1.9 (0.1)	0.75 (0.07)	0.11 (0.01)	1.30 (0.05)	0.14 (0.01)
Control 1991	5.6 (0.4)	19.9 (0.2)	3.1 (0.1)	7.0 (0.5)	1.7 (0.1)	0.72 (0.02)	0.12 (0.01)	1.16 (0.09)	0.11 (0.01)

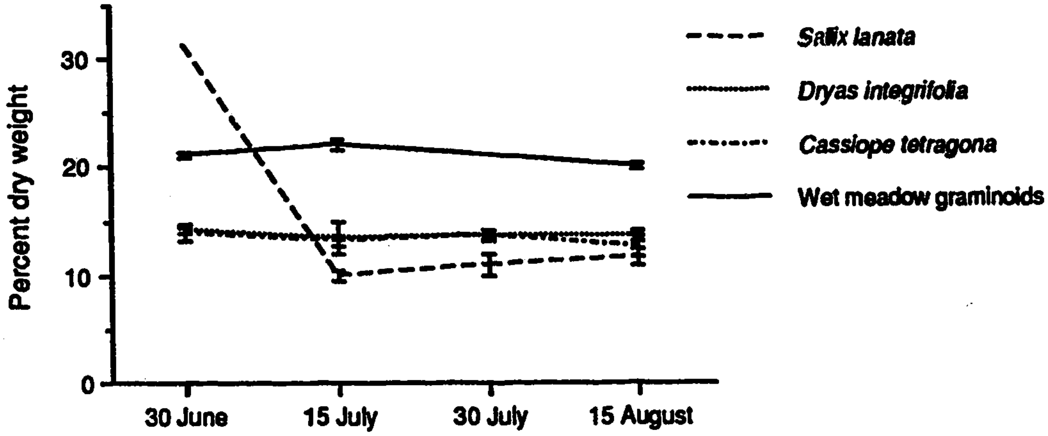
Note: Mean value (S.E. in brackets) of green tissue from 4 quadrats, except for net production (n=17 quadrats). * Significantly different ($P < 0.05$) from the corresponding control group. 1: Net production for the entire summer; 2: biomass produced during the post treatment period.

Table 5-6. Summary of the biomass response relative to controls of different forage types subjected to various clipping regimes.

Forage types (Treatments)		Impact on net production	
Period	Intensity	Treatment year	Recovery year
A) Shrubs			
S. lanata			
After snowmelt	50 %	-	-
	100 %	-	-
Early summer	50 %	-	
	100 %	-	-
Late summer	50 %		
	100 %	-	
D. integrifolia			
After snowmelt	50 %		
	100 %		-
Early summer	50 %		
	100 %		-
Late summer	50 %		
	100 %		
C. tetragona			
After snowmelt	50 %		-
	100 %	-	-
Early summer	50 %		-
	100 %		-
Late summer	50 %		-
	100 %		-
B) Graminoids			
Wet meadow graminoids			
After snowmelt	100%		
Early summer	100%		
Late summer	100%		
3 times	100%	-	
C. scirpoidea			
After snowmelt	100%		
Early summer	100%		
Late summer	100%		
3 times	100%		
C) Lichens			
Thinned	33 %	-	+ (?)
	50 %	-	
Clipped	33 %	-	+ (?)
	50 %	-	
Denuded	100 %		+ (?)
Denuded +	100 %		+ (?)

Note: Lower (-) or higher (+) net production relative to controls; no results means that the net production was not significantly different from controls (see results for more details). Denuded, removal of all lichens; Denuded +, removal of all the vegetation.

A) Cellulose



B) Lignin

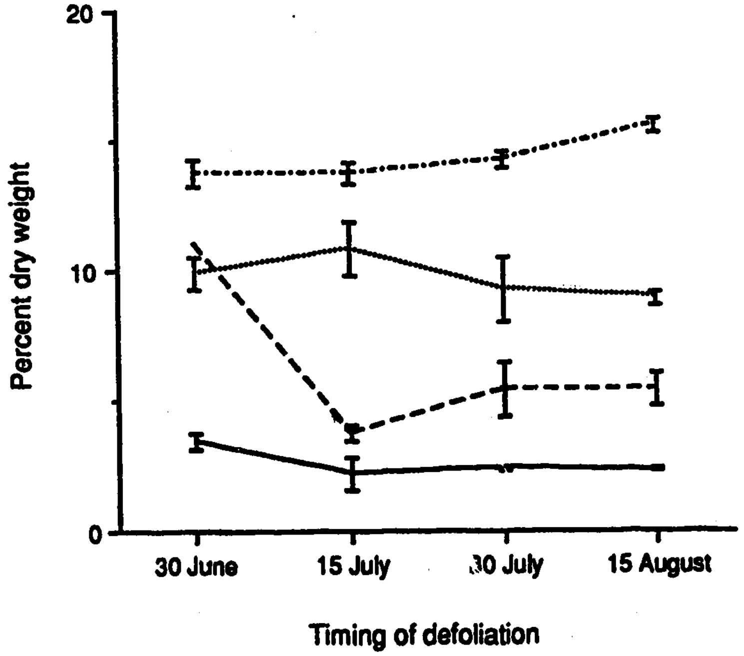


Figure 5-1. Seasonal change in percent dry weight (n=4; mean ± 1 SE) in current leaves of (a) cellulose and (b) lignin contents for *S. lanata* (June 30th result is based on a single lumped sample of nine individuals), *D. integrifolia*, *C. tetragona*, and wet meadow graminoids for 1990 growing season.

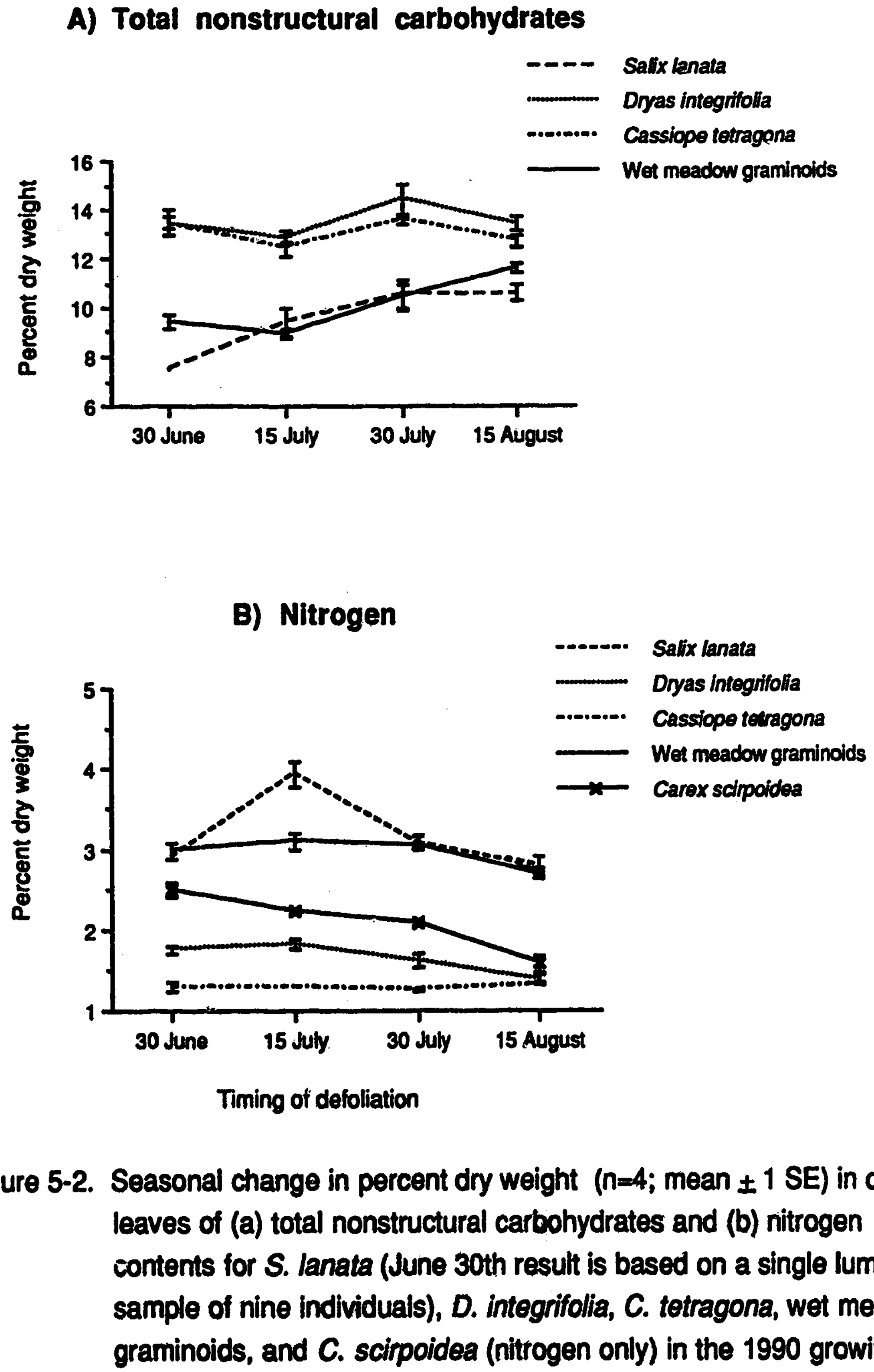


Figure 5-2. Seasonal change in percent dry weight (n=4; mean ± 1 SE) in current leaves of (a) total nonstructural carbohydrates and (b) nitrogen contents for *S. lanata* (June 30th result is based on a single lumped sample of nine individuals), *D. integrifolia*, *C. tetragona*, wet meadow graminoids, and *C. scirpoidea* (nitrogen only) in the 1990 growing season.

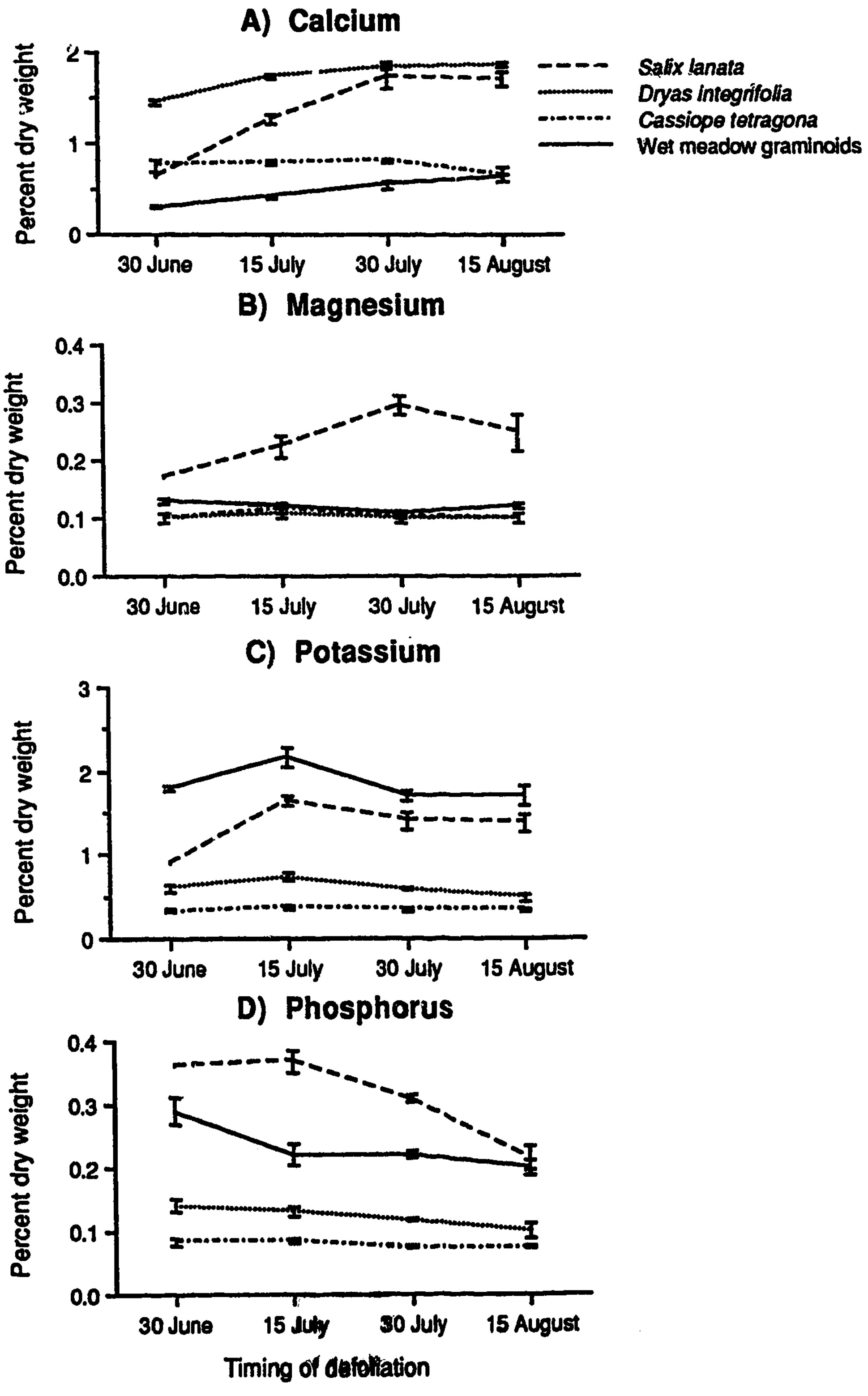


Figure 5-3. Seasonal change in percent dry weight (n=4; mean ± 1 SE) in current leaves of (a) calcium, (b) magnesium, (c) potassium, and (d) phosphorus contents for *S. lanata* (June 30th result is based on a single lumped sample of nine individuals), *D. integrifolia*, *C. tetragona*, and wet meadow graminoids in the 1990 growing season.

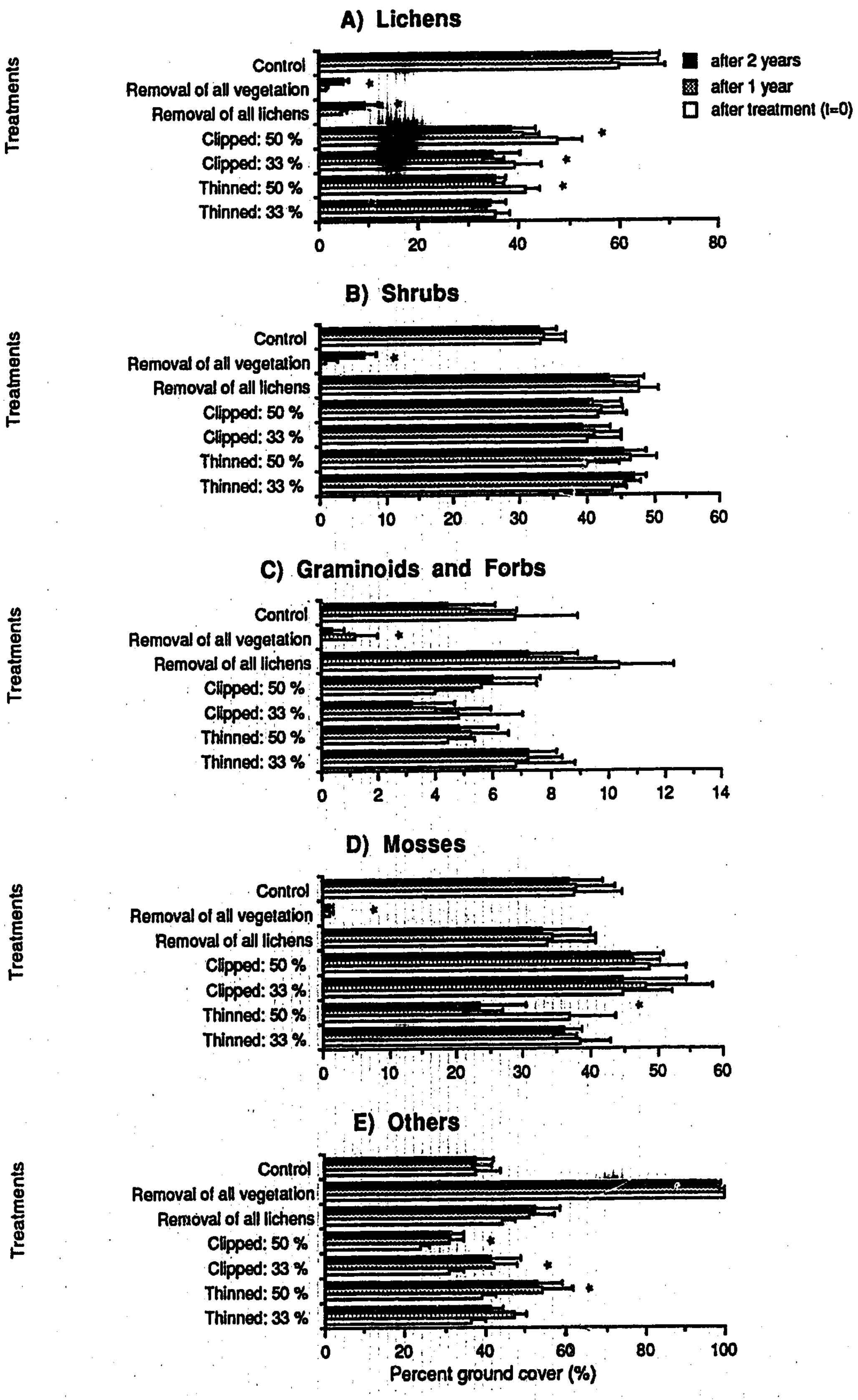


Figure 5-4 Consequence of various simulated grazing regimes applied to lichens on vegetation cover (n=5; mean ± 1 SE) of (a) lichens, (b) shrubs, (c) graminoids and forbs, (d) mosses, and (e) other categories. (* indicates means are significantly different (*P*<0.05), Anova for repeated measures).

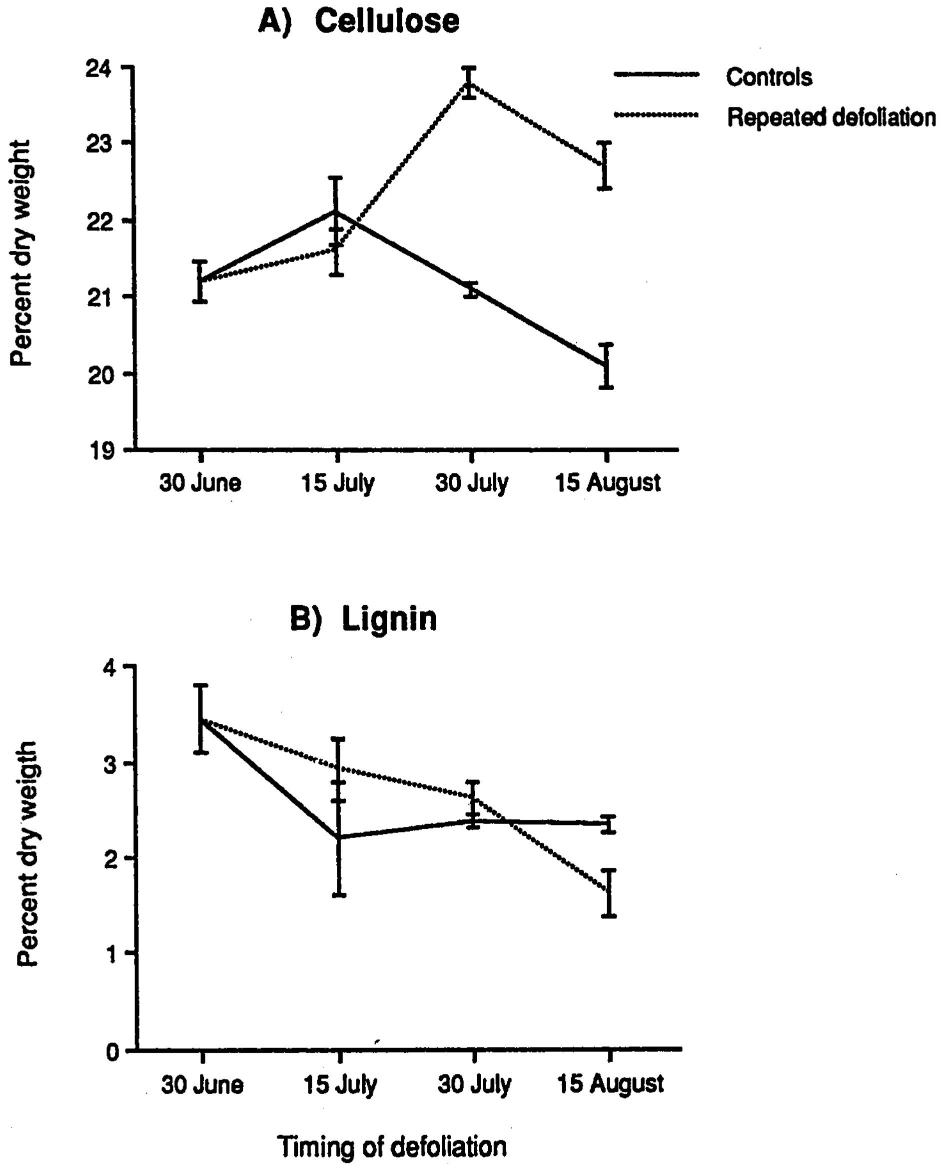
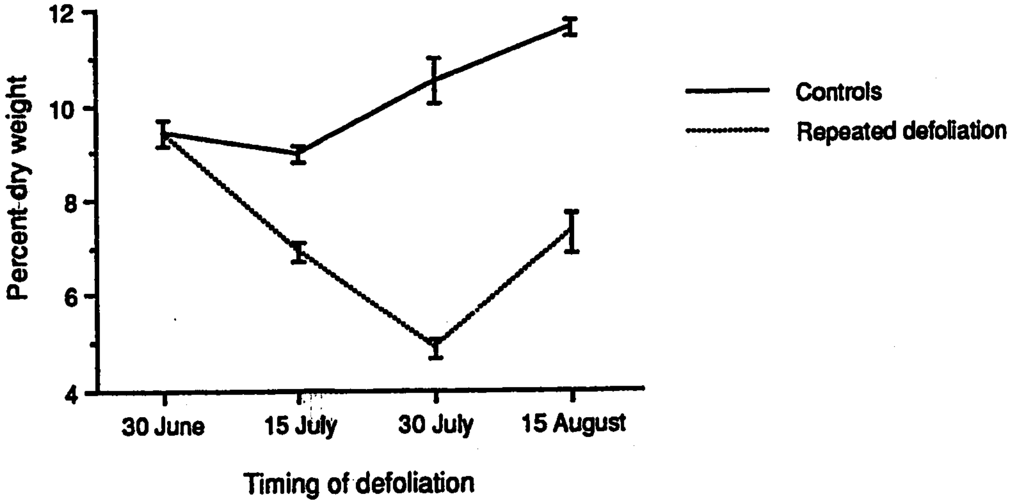


Figure 5-5. Consequence of repeated simulated grazing in percent dry weight (n=4; mean ± 1 SE) on (a) cellulose and (b) lignin contents of shoots of wet meadow graminoids in the 1990 growing season.

A) Total nonstructural carbohydrates



B) Nitrogen

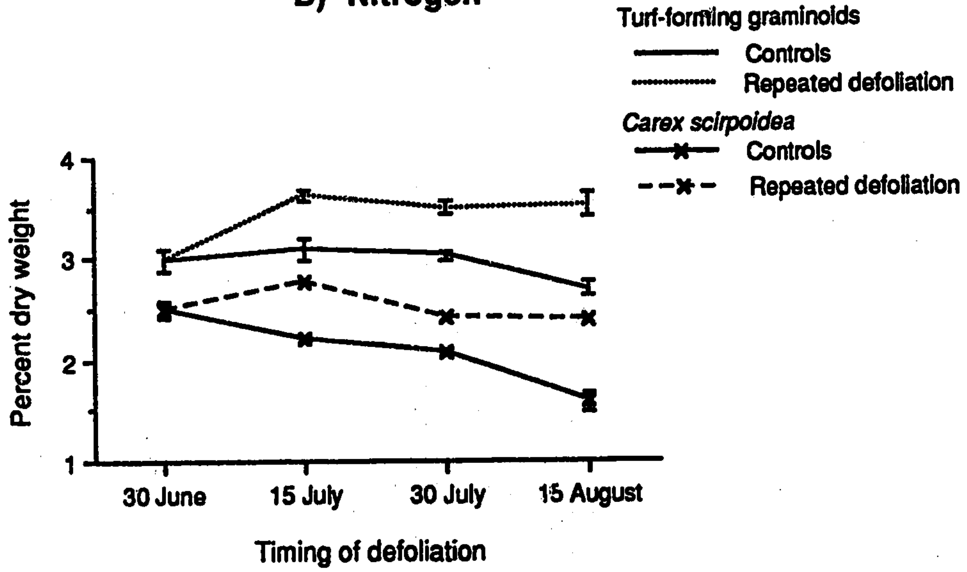


Figure 5-6. Consequence of repeated simulated grazing in percent dry weight (n=4; mean ± 1 SE) on (a) total nonstructural carbohydrates and (b) nitrogen contents of shoots of wet meadow graminoids and *C. scirpoidea* (nitrogen only) in the 1990 growing season.

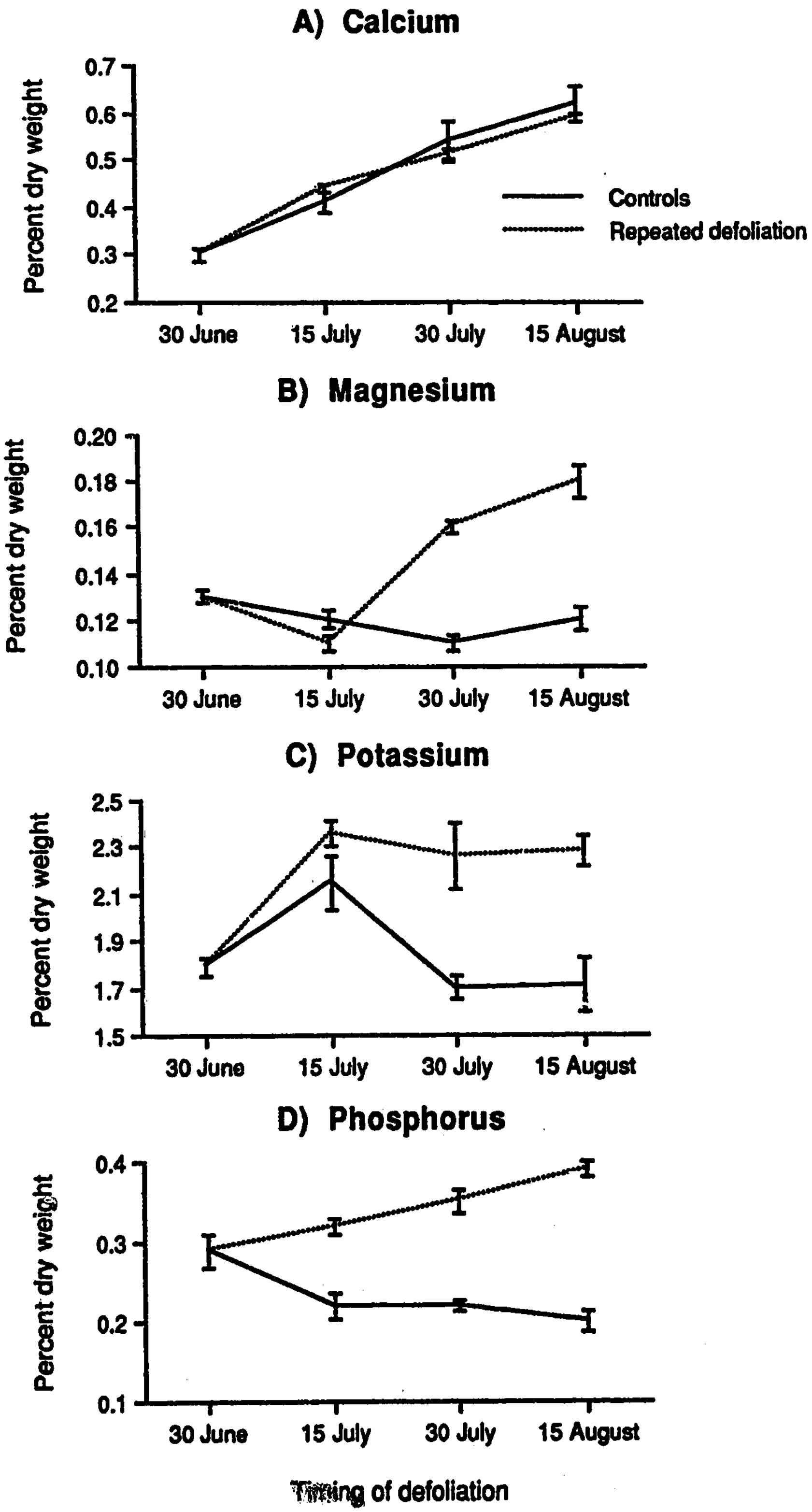


Figure 5-7. Consequence of repeated simulated grazing in percent dry weight (n=4; mean ± 1 SE) on (a) calcium, (b) magnesium, (c) potassium, and (d) phosphorus contents of shoots of wet meadow graminoids in the 1990 growing season.

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Chapter 6.

General discussion

This study provided an opportunity to examine some basic assumptions relevant to the ecology of ungulates. The Southampton island caribou herd (N.W.T.) has increased at a rapid and steady rate since its introduction in 1967 (Chapter 2). *Per capita* food availability was high and it has not regulate population growth. This contrast sharply with neighboring Coats island where caribou have much lower *per capita* winter food availability (Adamczewski *et al.* 1988; Chapter 3; Chapter 4; Chapter 5).

Male and female caribou on Southampton Island were in exceptional physical condition based on several indicators (e.g. growth, reproduction, body reserves) relative to previous reports for other caribou populations (Adamczewski 1987; Couturier *et al.* 1989; Dauphiné 1976; Thomas 1982). For example, Southampton Island caribou were the most sexual dimorphic of all caribou populations based on jaw length (Chapter 3). This observation supports the view that male caribou are adapted to take maximum advantage of changes in food availability possibly because their reproductive success is enhanced by large body size to a greater extent than females (Clutton-Brock *et al.* 1984). My results, along with those of other studies, suggest that growth (i.e. size at physical maturity, sexual dimorphism), body condition (i.e. spring body condition), and reproduction (i.e. yearling pregnancy rate) react in a density-dependent manner (Chapter 3). This study also showed the degree of flexibility in the pattern of depletion of body reserves in caribou (Chapter 3). For example, body reserves (and body weight) in the fall appeared to reflect requirements for winter conditions rather than simply being a response to summer conditions, as generally assumed for reindeer and caribou (Reimers 1983).

The comparison between Southampton Island and Coats Island populations helped to understand the population dynamics of northern predator-free herds. High winter mortalities of calves were recorded on Coats Island in 1975 and 1980 (Gates *et al.* 1986). This was attributed to adverse snow conditions, and appeared to be density-independent (Gates *et al.* 1986). But in a solely density-independent world, any level of stochasticity, however slight, will ultimately cause population extinction (Schaefer & Messier 1991).

Whereas important mortalities were recorded on Coats Island, mortalities must have been low and stable over time on Southampton Island considering the rapid and steady rate of growth of the population since introduction (Chapter 2). Therefore, the effect of snow conditions may be related to density-dependent resource limitation. On Coats Island, the rate of growth of the population during recovery years was lower (r=0.21, theorically this rate could have been much higher because the population was composed of a high proportion [83 %] of cows; Gates *et al.* 1986) than the rate of increase recorded on Southampton Island (r=0.24; Chapter 2). Further, despite the fact that the population was possibly increasing, Coats Island calves (11 months old) were in particularly poor body condition in the spring relative to Southampton Island calves (Adamczewski *et al.* 1987; see Chapter 3). The impact of adverse snow conditions may increase under resource limitation (Skogland 1985). It is suggested that the rate of growth of northern predator-free caribou populations may be predicted by winter food availability which is influenced by climatic conditions and grazing. This is consistent with the observation that dramatic declines observed in two reindeer populations, on two islands off the coast of Alaska, were attributed to adverse climatic conditions (ground ice in winter) following overgrazing of the lichens (Klein 1968; Scheffer 1951).

This study showed that caribou-plant interactions are complex and go beyond a simple relationship between caribou numbers and plant biomass (Chapter 5). Grazing can modify productivity and chemical composition of forage plants. Defoliation can reduce net productivity but increased forage quality. For example, clipped wet meadow graminoids had nitrogen, magnesium, potassium and phosphorus levels above the maximum concentration obtained by controls at any point during the growing season. This grazing-related effect may be particularly important for caribou. Caribou alter their diet to rely heavily on lichens as winter food and are in a negative phosphorus balance and probably a negative nitrogen balance during winter (Boertje 1990). Consequently, they have to replenish nitrogen and phosphorus during the remaining time. Moreover, caribou populations located on isolated islands cannot effectively use the asynchrony of plant phenology (Klein 1970). It might also be relevant for gravid females of continental herds that aggregate on calving ground in treeless habitat. Northern caribou populations also experience a very short growing season and physical growth and body reserve repletion must take place in summer. Finally, the positive impact of defoliation on forage quality suggests that predation pressure and optimal foraging might not be two opposing hypotheses (see Bergerud 1988; Bergerud & Heard Unpub. data; Klein 1970) explaining caribou migration and aggregation on calving ground located in the tundra but it is possible that these two forces might be acting in concert to favor such movement and aggregation pattern (Fryxell 1991).

Management implications

At the present rate of increase, the number of caribou on Southampton Island is doubling every three years. If the herd continues to increase geometrically then it will reach the island's predicted carrying capacity (Parker 1975) of 40 000 within 5 years.

Some introduced *Rangifer* populations increased geometrically before crashing and remaining at very low levels because grazing reduced available food (Leader-Williams 1988). Range damage is least likely to occur where graminoids are the staple food and most likely where the major food is lichens as is the case on Southampton Island. Associated with the increase in caribou density, there has been a decrease in lichen standing crop (Chapter 4). Already, the impact of grazing on lichens is obvious in certain areas of the island (Chapter 4). As the lichens are not resilient to grazing (Chapter 5) and under the present hunting regime, it is likely that the Southampton Island caribou herd is on its way to a population peak and subsequent dramatic crash similar to those observed for other insular populations (e.g. St Matthew, Klein 1968). The potential for a severe crash is accentuated by the fact that the population is growing at a fast rate. Indeed, model simulations suggested that the amplitude of a decline is related to the rate of growth of the population (Messier *et al.* 1988). To prevent overgrazing on Southamption Island and its potential consequences on the dynamics of the caribou population, the more appropriate way to manage the herd is by changing hunting quotas. Hunting quotas have been increased to 300 males and 100 females in 1989. Even when considering errors in sex identification from hunters, those kills would only slightly reduce herd growth rate. As there are only about 475 residents on Southampton Island, it will be important to restrain the growth of the population at a level at which it can be controlled effectively. A selective harvest in favor of females could be considered knowing its greater impact on the rate of growth.

Another potential way to restrain herd growth would be to let wolves recolonize Southampton Island. Wolves were once part of the Southampton ecosystem but they disappeared before the caribou were exterminated in the 1950's. Southampton Island is the only area in the Northwest Territories where wolves do not occupy their natural range (Heard 1983). In December 1979, a wolf was shot on Southampton Island but none have been reported since. That wolf may have followed men across Roes Welcome Sound who were returning from hunting caribou on the mainland. Roes Welcome Sound freezes in some winters but there is no evidence that caribou have ever moved across it. For example, there was no natural recolonization of the island after caribou became extinct. It is likely that wolves will again attempt to colonize the island. If they do, wolves could be protected from hunting until they become established. On one hand a viable wolf population would limit the growth of the herd and provide wolf hunting opportunities and income for the residents of Coral Harbour. On the other hand, those benefits could be outweighted by the fact that a wolf population would likely reduce the sustained yield of caribou, would result in a more complex system (plant-herbivore-predator) to deal with, and would force managers to consider two populations rather than one, to secure long-term stability of the caribou herd. Further, considering actual rate of growth and hunting quota, a wolf introduction would not be enough to stop the growth of the herd rapidly enough to avoid overgrazing of the range. Therefore, careful thought will need to be given to this management option.

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