



NATIONAL COUNCIL FOR AIR AND STREAM IMPROVEMENT

**A REVIEW OF UNGULATE NUTRITION
AND THE ROLE OF TOP-DOWN AND
BOTTOM-UP FORCES IN WOODLAND
CARIBOU POPULATION DYNAMICS**

TECHNICAL BULLETIN NO. 934

JUNE 2007

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PRESIDENT'S NOTE

Caribou live in tundra, taiga, and forest habitats at high latitudes in the northern hemisphere. They are closely related to other North American deer species such as reindeer, moose, elk, white-tailed deer and mule deer. In Canada, the majority of caribou live in the open tundra and taiga, where they congregate in large herds and migrate long distances. A smaller portion of caribou live in boreal and montane woodlands where they tend to exist in much smaller herds.

Biologists differentiate between various subgroups of woodland caribou based on geographic region and seasonal behaviour. Each subgroup has its own unique set of seasonal habitat requirements and ecological threats. In the southern mountains of British Columbia, for example, it is thought that human recreational activities are disrupting caribou behaviour during the breeding season. In several parts of their range, caribou are affected by expanding populations of deer and moose, which bring with them predators such as wolves and bears, and parasites and diseases that caribou are ill-equipped to handle. There is concern that caribou are more vulnerable to predators where forests are disturbed by human activities including timber harvesting and exploration for oil and gas.

Woodland caribou populations are declining in some areas, and most populations are listed as *threatened* under Canada's Species at Risk Act. Caribou habitat overlaps with planned and previous forest management activities in several provinces, so it is important for forest industry to be engaged in caribou research and conservation planning.

Research has demonstrated that predation and other factors can have important effects on woodland caribou populations, but there is still much to be learned about these rare and elusive animals. For example, there have been few studies of forage quality and quantity in woodland caribou habitats. Studies of other deer species have shown that food supply and animal nutrition can have important effects on breeding dynamics and female pregnancy rates; timing of birth; birth weight of calves; rate of calf growth and development; and survival probability of juveniles and adults.

This report reviews available literature on the relationship between seasonal diet and population dynamics of forest-dwelling caribou, with an emphasis on vascular plants and the effects of habitat selection, climate, disturbance, and forest succession on the relative availability and dietary quality of various forage species. Published studies provide little evidence to support or refute hypotheses about possible effects of food supply and nutrition on woodland caribou populations. The authors of this report suggest priorities for research, including detailed studies of summer foraging ecology and experiments to better define effects of forestry practices on winter and summer forage.

A handwritten signature in black ink, appearing to read 'Ron Yeske', is positioned above the printed name.

Ronald A. Yeske

June 2007

MOT DU PRÉSIDENT

Le caribou vit dans la toundra, la taïga et dans les habitats forestiers situés à des latitudes élevées de l'hémisphère nord. Il est le proche cousin d'autres espèces nord américaines de cervidés comme le renne, l'orignal, le wapiti, le cerf de Virginie (chevreuil) et le cerf mulet (cerf à queue noire). Au Canada, la majorité des caribous vit dans les grands espaces ouverts de la toundra et de la taïga, dans lesquels les individus se rassemblent en très grands troupeaux et migrent sur de longues distances. Une petite portion des caribous vit dans les forêts boréales et montagneuses où ils ont tendance à évoluer en troupeaux beaucoup plus petits.

Les biologistes établissent la distinction entre les divers sous groupes de caribous des bois selon la région géographique et les comportements saisonniers. Chaque sous groupe possède ses propres exigences en matière d'habitat saisonnier et ses propres menaces écologiques. Par exemple, dans les montagnes du sud de la Colombie Britannique, les activités récréatives humaines semblent perturber les comportements du caribou lors de la saison de reproduction. Dans plusieurs sections de leur territoire, les caribous sont affectés par l'expansion des populations de cerfs et d'orniaux, qui entraînent avec eux les prédateurs comme les loups et les ours, de même que les parasites et les maladies contre lesquels les caribous ne sont pas en mesure de combattre efficacement. La vulnérabilité du caribou envers ses prédateurs est plus importante dans les forêts affectées par les activités humaines telles que la récolte forestière et l'exploration pour le pétrole et le gaz naturel.

Les populations de caribou des bois sont en déclin dans certaines régions et la plupart des populations sont considérées comme « menacées » en vertu de la Loi sur les espèces en péril du Canada. Dans plusieurs provinces, l'habitat du caribou chevauche les régions où des activités d'aménagement forestiers ont eu lieu ou sont planifiées. Il est donc important, pour l'industrie forestière, de s'engager dans la recherche sur le caribou et dans la planification de la conservation.

Les recherches ont démontré que la prédation ainsi que d'autres facteurs peuvent générer des effets importants sur les populations de caribous des bois mais d'autres efforts de recherche doivent être déployés pour en connaître plus sur ces animaux rares et fuyants. Par exemple, il existe peu d'études portant sur la qualité et la quantité de nourriture dans les habitats fréquentés par le caribou des bois. Les études portant sur d'autres espèces de cerfs ont montré que la nourriture et la nutrition animale peuvent avoir un effet important sur : les dynamiques de reproduction et les taux de gestation des femelles, la période de mise bas, la masse à la naissance des jeunes, le taux de croissance et de développement des jeunes et les chances de survie des individus juvéniles et adultes.

Ce rapport fait la revue de la littérature disponible sur la relation entre les régimes alimentaires saisonniers et les dynamiques des populations de caribous, en mettant l'accent sur les plantes vasculaires et les effets de la sélection de l'habitat, du climat, des perturbations et des stades de succession des peuplements forestiers sur la disponibilité relative et la qualité diététique de plusieurs espèces de ressources alimentaires. Les études publiées à ce jour fournissent peu de preuves pour

soutenir ou réfuter les hypothèses reliées aux effets possibles des ressources alimentaires et de la nutrition sur les populations de caribous des bois. Les auteurs de ce rapport proposent certaines priorités pour la recherche future telles que des études détaillées de l'écologie des aires d'alimentation estivales et des expériences permettant de mieux définir les effets des pratiques forestières sur les aires d'alimentation hivernales et estivales.



Ronald A. Yeske

Juin 2007

A REVIEW OF UNGULATE NUTRITION AND THE ROLE OF TOP-DOWN AND BOTTOM-UP FORCES IN WOODLAND CARIBOU POPULATION DYNAMICS

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ABSTRACT

Management strategies to conserve populations of woodland caribou *Rangifer tarandus caribou* frequently emphasize the importance of predator-prey relationships and availability of lichen-rich late seral forests, yet the importance of summer diet and forage availability to caribou survival is poorly understood. We synthesized published information on the diet and nutritional needs of *Rangifer* populations to evaluate the importance of vascular forage, as well as potential interactions among forage and climate, disturbance, and predation in affecting caribou survival and reproduction. We also reviewed studies on the population dynamics of woodland caribou in North America to assess the relative importance of top-down and bottom-up factors in the decline of woodland caribou populations. Populations of forest-dwelling woodland caribou that share range with predators and alternate ungulate prey typically occur at low densities and evidence of density-dependent food limitation is not apparent. Predation is generally considered an important proximal factor limiting woodland caribou populations; however, our review suggests that methodological limitations in existing studies prohibit proper evaluation of the mechanism of decline and fail to elucidate potential interactions between top-down and bottom-up effects on populations. Our review of caribou dietary needs highlights the importance of vascular summer forage in the growth and reproduction of caribou. Diet may be seasonally important in relation to snow accumulation, reproduction, and landscape-scale disturbances that change the availability of preferred food items. Based on current knowledge, forest management is expected to have a greater potential to affect the availability of winter forage than summer forage. In light of our findings, we offer management recommendations that could aid in developing effective landscape- and stand-level harvesting and silvicultural practices for maintaining caribou foraging habitat.

KEYWORDS

diet, density-dependent, forage, limiting factors, *Rangifer tarandus caribou*, silviculture, timber harvesting, vascular plants

RELATED NCASI PUBLICATIONS

Technical Bulletin No. 893 (December 2004). *Ecological interactions among caribou, moose, and wolves: Literature review.*

REVUE DES EFFETS DU RÉGIME ALIMENTAIRE SAISONNIER SUR LES DYNAMIQUES DE POPULATIONS DE CARIBOUS DES BOIS

BULLETIN TECHNIQUE N^o 934
JUN 2007

RÉSUMÉ

Les stratégies de gestion pour préserver la population boréale de caribous des bois (*Rangifer tarandus caribou*) mettent fréquemment l'accent sur l'importance des relations prédateur-proie et sur la disponibilité des peuplements que l'on retrouve souvent en fin de succession. Par contre, on comprend moins bien l'importance du régime alimentaire estival et de la disponibilité des aires d'alimentation pour la survie du caribou. Nous avons fait la synthèse de l'information disponible portant sur le régime alimentaire et les besoins nutritionnels des populations de *Rangifer* afin d'évaluer si les sites d'alimentation composés de plantes vasculaires et les interactions potentielles entre ces sites et le climat, les perturbations naturelles et la prédation affectent de façon importante la survie du caribou ainsi que sa reproduction. Nous avons également fait la revue des études traitant des dynamiques de population de caribous des bois en Amérique du Nord afin d'évaluer l'importance relative des facteurs relevant de la prédation (*top-down factors*) et ceux relevant de la qualité de la nourriture (*bottom-up factors*) pour expliquer le déclin des populations de caribous. Les populations de caribous des bois qui partagent l'habitat avec des prédateurs et d'autres proies alternatives pour ces prédateurs restent typiquement à de faibles densités et l'évidence d'une relation de cause à effet entre l'abondance de la nourriture et la densité de population ne semble pas apparente. On considère généralement la prédation comme étant un facteur proximal important, régulant les populations de caribous des bois. Toutefois, notre revue soutient que les limites de la méthodologie empêchent l'évaluation adéquate du mécanisme de déclin et elles ne permettent pas d'élucider les interactions potentielles entre les facteurs relevant de la prédation et ceux relevant de la qualité de la nourriture sur les populations. Notre revue des besoins alimentaires du caribou met l'emphase sur l'importance des aires d'alimentation estivales composées de plantes vasculaires pour ce qui est de la croissance et la reproduction du caribou. Le régime alimentaire saisonnier peut s'avérer important selon l'accumulation de neige, la reproduction et les perturbations à l'échelle du paysage car ces facteurs modifient la disponibilité des sources de nourriture préférées. On croit que l'aménagement des forêts aura un plus grand potentiel d'affecter la disponibilité des aires d'alimentation hivernales, comparativement aux aires d'alimentation estivales. À la lumière de nos résultats, nous offrons des recommandations d'aménagement qui peuvent aider à développer des pratiques de récolte et de sylviculture (à l'échelle du paysage et des peuplements) efficaces pour le maintien des aires d'alimentation composant l'habitat du caribou.

MOTS CLÉS

régime alimentaire, densité-dépendance, aire d'alimentation, facteurs limitants, *Rangifer tarandus caribou*, sylviculture, récolte forestière, plantes vasculaires

AUTRES PUBLICATIONS DE NCASI DANS CE DOMAINE

Bulletin technique n^o 893 (décembre 2004). *Ecological interactions among caribou, moose, and wolves: Literature review.*

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A REVIEW OF UNGULATE NUTRITION AND THE ROLE OF TOP-DOWN AND BOTTOM-UP FORCES IN WOODLAND CARIBOU POPULATION DYNAMICS

1.0 INTRODUCTION

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) lists forest-dwelling woodland caribou *Rangifer tarandus caribou* as a threatened species. Research to date suggests that caribou range has receded across the boreal forest due to habitat loss and fragmentation, human disturbance, and increased predation (Thomas and Gray 2002). Managers attempting to conserve populations of woodland caribou while allowing sustainable resource development require an understanding of the importance of dietary quality and forage availability to caribou survival. Although predation is generally considered the most important proximal factor limiting caribou populations, factors that negatively affect an animal's ability to obtain adequate food of suitable quality, avoid predation, and reproduce may be cumulative in their effects on individual fitness and population dynamics. Diet may be seasonally important in relation to snow accumulation, reproduction, and landscape-scale disturbances that change the availability of preferred food items. Lichens are widely considered to be an important winter food item; however, the value of vascular plants to caribou in other seasons is less understood. The summer diet of caribou is often more diverse than during winter and consists of forbs, deciduous leaves, lichens, grasses, and sedges (Bergerud 1972). A better understanding of caribou dietary needs and nutritional ecology could allow managers to develop more effective stand-level harvesting and silvicultural practices for maintaining caribou habitat.

In systems where predators have a substantial influence on prey survival, the activity budgets of foraging species reflect a balance between the need to gain sufficient energy intake and meet other daily requirements, such as rumination, resting, caring for young, avoiding predators or insect harassment. Interactions among factors may be important. For example, predation can affect large-scale habitat selection, which may influence nutrient intake rate. The role of bottom-up (e.g., primary productivity) and top-down (e.g., predation) forces in the dynamics of caribou populations has been debated in the literature and previous studies have focused on the importance of one or the other factor. Rettie and Messier (2000) found that woodland caribou show strong selection at coarse scales for habitat that reduces predation risk; however, some authors have suggested that food availability may replace predation as a limiting factor for caribou that migrate or inhabit predator-free areas (Messier et al. 1988; Bergerud, Ferguson, and Butler 1990; Mallory and Hillis 1998). Female reproductive success of many polygamous ungulates is limited by the ability of females to acquire adequate food resources for lactation and calf development (Clutton-Brock, Albon, and Guinness 1989). Post et al. (2003) found that parturition (birthing of young) by depredated and non-depredated caribou populations was highly synchronized with plant phenology, suggesting strong long-term evolutionary pressures of food on fitness, and inadequate food supply is associated with poor survival and reduced reproduction in ungulates (Knight 1970; Thomas 1982; Kojola and Helle 1993).

Growing evidence for diverse food webs suggests that both top-down and bottom-up forces affect herbivore populations and that interaction effects may occur among limiting factors (Gratton and Denno 2003; Jiang and Morin 2005). Vegetation can affect herbivores directly by influencing their performance and survival, and indirectly by mediating the effects of predators (Bender et al. in press). For example, Gratton and Denno (2003) attributed the top-down control of planthopper populations (*Prokelisia* spp.) to the greater availability of alternative prey and concurrent aggregation of predators in more productive, complex-structured habitats. The relative importance of bottom-up and top-down regulation of prey assemblages may also depend on the identity and diet breadth of predators (Jiang and Morin 2005). The primary predator of most caribou populations is the wolf, a generalist predator,

and research to date suggests that predation risk to caribou may be greater where moose *Alces alces* and caribou populations overlap (Seip 1992). If predator diet breadth and primary productivity play important roles in caribou trophic interactions and prey species diversity, one might expect greater prey diversity, and therefore predation pressure on caribou, in more species diverse and productive habitats. However, this hypothesis has yet to be tested with empirical data.

Natural and human-induced disturbances, such as forest management, can alter via direct physical manipulation and secondary succession the nutritive value of plant communities to foraging caribou by changing species composition, forage abundance, and structure and chemistry of vegetation. Disturbance may also affect forage availability or energy budgets of caribou by altering movement patterns or causing range abandonment. Caribou preferences among vegetation communities and forage items may vary both spatially and temporally in relation to soil type, climate, and seral changes in vegetation composition and structure. Important differences may exist between natural disturbances (e.g., fire intensity) and human-related industrial disturbances (e.g., surface treatment and restocking methods) that may have meaningful implications for caribou forage availability.

Our objectives were threefold:

- (1) to review available literature and synthesize information on the extent to which nutritional resources influence dynamics of caribou populations, with specific emphasis on landscape-scale studies of population-level responses of free-ranging herds;
- (2) to assess the relative importance of top-down and bottom-up factors in the decline of woodland caribou populations and the adequacy of existing research to decipher important interactions among limiting factors, including the consequences to fitness that result from habitat selection; and
- (3) to identify potentially important information gaps regarding nutritional influences where new research is needed to clarify nutritional influences on caribou populations.

We provide recommendations for management measures expected to minimize negative disturbance-related effects on forage availability and quality and identify key scientific information gaps related to seasonal diet selection, forage quality, and the importance of top-down and bottom-up effects on woodland caribou trophic interactions.

2.0 METHODS

We define several nutrition-related terms to help reduce potential for uncertainty. First, although widely used in a variety of ways, “nutrition” was formally defined as “rate of ingestion of assimilable energy and nutrients” (Harder and Kirkpatrick 1994). Second, “nutritional condition” was formally defined, also by Harder and Kirkpatrick (1994), as the “...state of body components controlled by nutrition and which, in turn, influence an animal’s fitness”. Saltz, White, and Bartmann (1996) altered this definition by replacing “fitness” with “future fitness”. We emphasize that nutrition is a “rate” variable, denoting amount consumed across time (i.e., per minute, per day, and so forth) whereas nutritional condition is a state variable, and denotes the status of the animal at any point in time. Many terms have been used in the literature to denote nutritional condition, including body condition, physiological condition, condition, nutritional condition, and others. Herein, we restrict our use to either nutritional condition or condition. In practice, measures of nutritional condition nearly always involved fat or energy stores in the body (although total body protein and calcium stores have been used rarely [Harder and Kirkpatrick 1994]). Moreover, many different approaches involving a variety of fat indices (e.g., kidney fat, femur fat, weight) have been used to measure nutritional condition; some of these are valuable whereas others are exceedingly unreliable (Harder and Kirkpatrick 1994; Cook et al. 2001a).

Both “nutritional plane” and “nutritional status” are used throughout this report, and are intended to be equivalent. Following Cook (2002), we define both as the level of intake of assimilable nutrients in relation to the daily nutrient requirements of the animal, independent of the animal’s nutritional condition. Gross energy refers to the total amount of energy contained in food, much of which is typically unavailable to the animal and lost in feces. The energy in food available to the animal is referred to here as digestible energy (DE). Within DE, energy not lost to urine and methane production in the rumen is referred to as metabolizable energy (ME).

We reviewed available literature from peer-reviewed journals, government reports, and unpublished reports and synthesized information on ungulate nutrition, with emphasis on the nutritional requirements and diet composition of caribou. Dietary information was evaluated in relation to seasonal patterns in caribou energetic constraints (e.g., reproductive status) and the availability and quality of different food items. Studies were scrutinized as to whether they included measures of forage intake requirement, forage availability, relevant population parameters, and whether assessments were qualitative or quantitative in nature. Although we were primarily interested in the importance of forage to the ecotypes of woodland caribou *Rangifer tarandus caribou* (Thomas and Gray 2002), relevant research pertaining to other subspecies of caribou and reindeer were also reviewed. Preliminary review of the literature revealed that a substantially greater number of forage-related studies have been conducted for reindeer and barren-ground caribou than woodland caribou and these studies were expected to provide considerable insight into caribou foraging ecology and information gaps in the woodland caribou literature. Notably, a substantial amount of research on caribou and reindeer nutrition has been conducted for populations in Alaska. All caribou in Alaska are currently classified as barren-ground caribou *R. t. granti*; however, many of these populations inhabit taiga and alpine regions and Thomas and Gray (2002) suggested mountain caribou in British Columbia and Yukon might be more closely related to Alaskan barren-ground caribou than woodland caribou.

To evaluate the relative importance of predation and forage as limiting factors for woodland caribou populations, we reviewed available literature and synthesized trends in population parameters in relation to the presence or absence of predators in the system, population trend, and stated conclusions as to the relative importance of limiting factors. We also reviewed published evidence of the importance of predation risk and forage availability to caribou habitat selection.

3.0 FORAGE-RELATED STUDIES OF CARIBOU: LITERATURE SURVEY RESULTS

We consulted approximately 320 publications in the preparation of this review, of which approximately 100 were research-oriented and reported on empirical data collected from one or more woodland caribou populations. The following section provides a broad overview of the range and focus of forage- and population-limitation related studies of woodland caribou. Documents that provided context for discussion, but did not provide empirically derived information on woodland caribou forage, nutrition, or population dynamics were not included in this component of our overview.

Foraging and dietary studies of woodland caribou were generally rare in the published literature and we found a greater number of papers on mountain caribou than other woodland ecotypes (Figure 3.1). A number of studies focused exclusively on autumn or winter foraging or only examined caribou foraging on lichens and did not consider other plant groups (Table 5.3). The total number of studies available for woodland caribou was small in comparison to studies on foraging and diet in barren-ground caribou and reindeer. Although our review did not permit an accurate census of all forage-related studies for all *Rangifer* spp., we identified at least 28 forage-related papers for barren-ground caribou and reindeer when conducting our review on woodland caribou. In contrast to the abundance

of nutritional studies for barren-ground caribou and reindeer, there was an absence of empirical studies on the effects of dietary quality and nutrition on reproduction and nutritional condition in wild populations of woodland caribou.

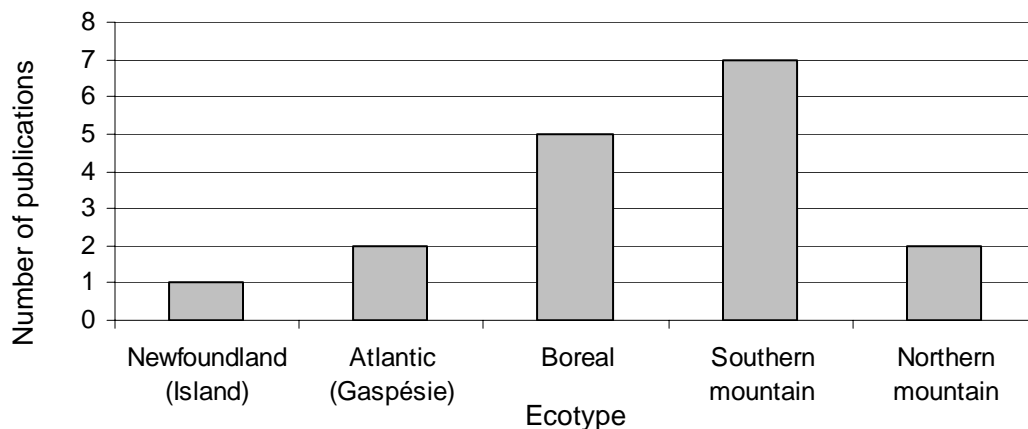


Figure 3.1 Research Publications Consulted in the Preparation of This Review That Provided Information on the Diet Content or Foraging Behaviour of Woodland Caribou

Several empirical studies described the effects of disturbances (natural or anthropogenic) on caribou forage availability (Bergerud 1971a; Schaefer and Pruitt 1991; Harris 1996; Webb 1998; Rominger et al. 2000; Metsaranta, Mallory, and Cross 2003; Miège et al. 2001a, 2001b; Proceviat 2003; Proceviat, Mallory, and Rettie 2003; Stevenson and Coxson 2003); however, only Proceviat (2003) examined changes in availability of vascular plants eaten in summer in relation to forest harvesting. Most studies focused on arboreal and terrestrial lichens and no studies measured changes in caribou diet quality, nutrition, or fitness in relation to forage-related effects of disturbances. An exception was Rominger et al. (2000) who measured forage intake rates of captive animals in harvested and unharvested portions of pens during autumn.

We found two studies that compared forage availability in relation to predator avoidance strategies in woodland caribou (Ferguson, Bergerud, and Ferguson 1988; Bergerud, Ferguson, and Butler 1990) and no studies were found that quantitatively tested for an interaction between the nutritional status of woodland caribou and susceptibility to predation.

All 14 studies (Figure 3.2) that quantitatively measured population dynamics of woodland caribou implicated predation as an important limiting factor (Table 6.1). Only one of these studies, an unpublished report, implicated an interaction among forage, predation, and extreme winter weather in the decline of a woodland caribou population (Farnell and Gardner 2002) and this was one of only a few studies that attempted to assess diet quality or availability. Bergerud (1971a) measured forage abundance on winter range and Hayes et al. (2003) measured snowmelt phenology as well as the percentage of lichens in the diet of caribou. Two studies implicated interactions between predation and disease (Bergerud 1971b) and predation and emigration (Schaefer et al. 1999) as factors in caribou declines. None of these studies measured caribou nutritional status or forage intake rates in relation to summer and winter forage availability. Although Cringan (1957) concluded that lichen availability was critically important to caribou survival on the Slate Islands, Lake Superior, where predators were absent, his methodology did not permit evaluation of population limitation.

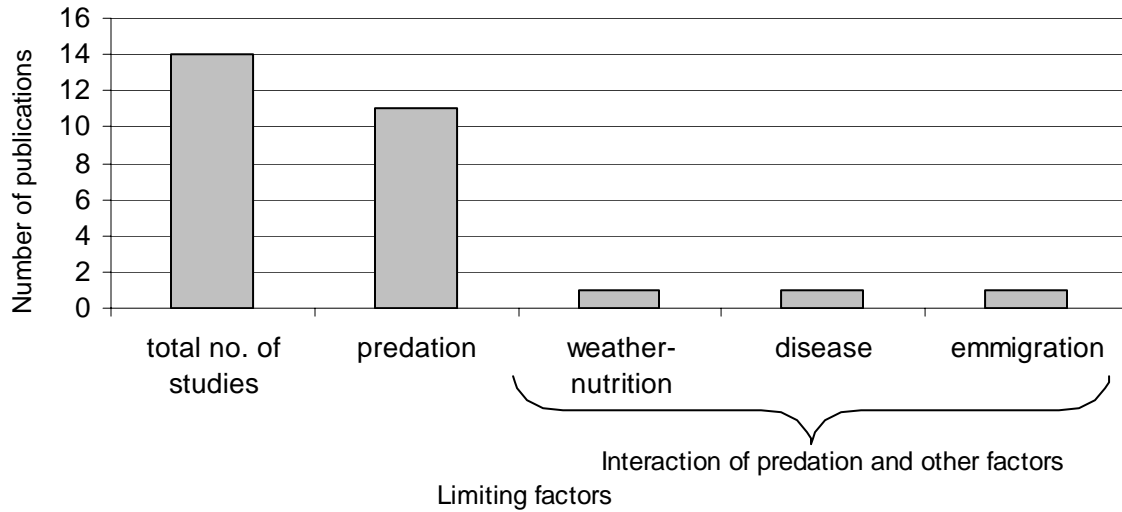


Figure 3.2 Research Publications Consulted in the Preparation of This Review That Quantitatively Measured Population Dynamics of Woodland Caribou and Drew Conclusions as to Important Limiting Factors

4.0 CARIBOU BIOLOGY: REPRODUCTION AND SEASONAL MOVEMENTS

Caribou exhibit local synchrony in breeding and calving and the timing of reproduction may vary among different populations (Thomas and Gray 2002). The breeding season, or rut, typically occurs between late September and mid-October (Bergerud 1975; Edmonds 1988) and the gestation period is 227-229 days (Bergerud 1975; Dzus 2001). Synchronized breeding tends to result in approximately 90% of calves being born in a 12-day period in mid-May or early June (Bergerud 1975; Fuller and Keith 1981; Bergerud, Butler, and Miller 1984; Rettie and Messier 2001).

The seasonal movement patterns of both mountain and boreal ecotypes of woodland caribou range from sedentary use of an annual home range (Darby and Pruitt 1984; Seip 1992; Ouellet, Ferron, and Sirois 1996; Rettie and Messier 1998) to migratory movements between distinct seasonal ranges (Fuller and Keith 1981; Edmonds 1988; Seip 1992; Brown, Mallory, and Rettie 2003). *Rangifer* show considerable behavioural plasticity and Schaefer et al. (1999) documented the emigration of caribou from the sedentary Red Wine Mountains Herd of central Labrador to the migratory George River Herd where portions of their respective ranges overlapped. Caribou movement patterns may be influenced by seasonal habitat requirements, predators, snow cover, and forage quality and availability (Thomas and Gray 2002). Large-scale movements typically occur in spring before calving and in autumn before or after the rut (Edmonds 1988; Thomas and Gray 2002). Spring migration typically occurs in a 2-4 week period between late April and early June (Edmonds 1988; Saher 2005). Snow cover influences the timing of both spring and autumn migrations, with movements occurring later in spring, when snowmelt is delayed, and later in autumn if snow cover is shallow or late to arrive (Edmonds 1988). Woodland caribou are widely dispersed at calving, with calves often born on the females' summer range (Bergerud, Butler, and Miller 1984; Cumming and Beange 1987; Edmonds 1988; Bergerud, Ferguson, and Butler 1990).

5.0 NUTRITION AND FOOD HABITS

5.1 Nutrition Effects among Large Ungulates

Very few studies have been conducted to evaluate the effects of nutrition on woodland caribou. Nevertheless, nutrient content of forage and nutrition levels that foraging ungulates can obtain from plant communities can vary significantly across different ecological settings, and, based on extensive literature on barren ground caribou, elk, red deer, and deer, it is clear that nutrition can and does have a wide variety of influences on their performance. In fact, habitat's greatest *direct* influence on large ungulate populations very well may operate primarily through nutritional mechanisms in many ecological settings (Cook et al. 2004). Hence, understanding the direct effects of habitat change, either via plant succession or natural or anthropomorphic disturbance, on woodland caribou populations may require a good understanding of how habitat influences the nutrition of these ungulates. Here, we summarize literature that generically describes ways in which nutrition affects performance of large ungulates.

5.1.1 Nutrition and Pregnancy

Perhaps one of the most frequently documented effects of nutrition is its effect on pregnancy rates. Among caribou, studies have reported significant relationships between pregnancy and nutritional condition in autumn (which in turn reflects nutrition in summer) in barren-ground caribou (Dauphiné 1976; White 1983; Cameron et al. 1993) and reindeer (Reimers 1983a). Dauphiné (1976) found that body weight (dressed weight) during early gestation (November–December) was significantly greater for pregnant (N = 38) than non-pregnant (N = 7) adult females harvested from the Kaminuriak Herd. Gerhart et al. (1997a) found that body weight (live weight), body fat, and body protein (all measured in November) were significantly lower in non-pregnant (N = 24) females than pregnant (N = 78) females of the Porcupine Herd. Reimers (1983a) found that pregnancy rates of wild female reindeer in Norway were significantly correlated to weight of animals harvested during the autumn rut. Conception data support the hypothesis that a critical body fat or weight threshold must be met for a female to conceive. Crête et al. (1993) suggested that a threshold of approximately 7 kg of fat reserves (or 7.8% ingesta-free body mass) in late autumn or early winter was necessary for successful conception in the subspecies *R. t. caribou*. Russell et al. (1998) demonstrated strong relations between autumn body fat and pregnancy, and provided first-time evidence that embryo survival soon after breeding also was correlated to fat levels. Significant relations between body fat levels and pregnancy rates are well documented across a variety of other ungulate species (e.g., Heard et al. 1997; Testa and Adams 1998; Kohlmann 1999; Cook et al. 2001b, 2004).

Some evidence indicates that the interplay among pregnancy, lactation, and nutrition on nutritional condition may “carry-over” across years. On ranges that offer marginally adequate or inadequate nutrition, nutritional condition of females that successfully raise a calf one year may decline to the point where pregnancy fails and no calf is raised the subsequent year. These failures are called reproductive pauses (or sometimes “alternate” year breeding). In caribou, decline of nutritional condition each year the female successfully gives birth and raises a calf was estimated to be 10-13% per year (Reimers 1983a) until reproduction fails (Cameron 1994). With elk, Cook et al. (2004) demonstrated that reproductive pauses occur when summer nutrition relative to requirements was low. When nutrition was adequate, females had no difficulty providing milk for their calves and replenishing their reserves in time to breed successfully and early in the breeding season.

Finally, inadequate nutrition in the months preceding the breeding season may delay the timing of breeding, and this in turn might delay birthing and desynchronize the birth pulse the following spring. Nutrition-mediated delays in ovulation/breeding have been documented for red deer (Mitchell and Lincoln 1973; Guinness, Clutton-Brock, and Albon 1978), elk (Kohlmann 1999; Cook et al. 2004), white-tailed deer (Verme 1969), and reindeer (Reimers 1983b).

How nutrition explicitly affects pregnancy is very complex physiologically and is poorly understood (National Research Council 1985; Bronson and Manning 1991; Gerhart et al. 1997a). Because of this complexity, the use of herd-level pregnancy data as an indicator of habitat's nutritional adequacy is problematic for at least 4 reasons. First, two components of nutrition's contribution to ovulation evidently exist, a "static" component (i.e., body fat levels) resulting from nutrition 2 to 3 months prior to breeding, and a "dynamic" component involving short-term nutrition ranging from 4 days to 3 weeks prior to the normal breeding time (National Research Council 1985; Molle et al. 1995; Martin et al. 2004). Variation in either may independently or interactively affect ovulation, e.g., a pulse of high quality forage available at or near the time of breeding may increase the chance of pregnancy for lean animals that survived on inadequate nutrition earlier in the season (Gerhart et al. 1997a).

Second, lactation prior to or ongoing during the breeding season may confound the relation between nutrition and pregnancy in two ways: (1) the strongly elevated nutritional demands required to support lactation can greatly hinder fat accretion and produce very lean females at the time of breeding (the static component) (Cook et al. 2004), and (2) at any given level of body fat during breeding, the physical stimulus of being nursed may alter reproductive hormones that reduce probability of ovulation (i.e., lactational infertility as described for red deer [Loudon, McNeilly, and Milne 1983] and caribou [Gerhart et al. 1997a]). In addition, Russell et al. (1998) found that caribou may successfully breed, but that the embryo may die in the few weeks after breeding, and that this effect can be substantial for lean females. They hypothesized that relatively lean female caribou, particularly if they are lactating during the breeding season, may "conceive a calf in October, yet 're-evaluate' in November" and might terminate the pregnancy if nutritional conditions are unfavourable. The frequency and practical relevance of this early embryonic mortality is poorly understood.

Whatever the case, in herds where calf mortality is high (e.g., due to high predation) particularly during the months prior to breeding, a high proportion of mothers are "released" from the high nutritional demands of raising a calf, such that their nutritional condition improves to the point where she can breed and maintain pregnancy. In this situation, herd-level pregnancy rates may be high, thereby masking the nutritional inadequacy of their environment (Verme 1962; Verme and Ullrey 1984; Gerhart et al. 1997b).

Third, the relation between body fat (the static component) and pregnancy evidently is indirect; no strong causal physiological relation between body fat and pregnancy has been found in *any* species (Bronson and Manning 1991). (However, recent research of the hormone leptin which is primarily produced in fat tissue does play an important role in signalling nutritional status to the central reproductive axis of mammals and "appears to be at least a permissive factor" for ovulation [Zieba, Amstalden, and Williams 2005]). Evidently, plasma levels of important metabolic substrates such as glucose, triglycerides, and/or certain amino acids play a direct causal role (Bronson and Manning 1991; Molle et al. 1995; Scaramuzzi et al. 2006). Thus, quantitative relations among nutrition levels in the summer, resultant body fat levels in late summer and autumn, and probability of pregnancy are imperfect and might be inconsistent across space and time (Gerhart et al. 1997a). Additionally, the oft-cited relation between pregnancy and body weight in *adult* females is probably spurious and occurs primarily because weight and body fat are intercorrelated, not because weight per se controls ovulation (Cook 2002; p. 296).

Fourth, nutrition levels just adequate to maintain high pregnancy rates are inadequate to support optimal performance in other ways, such as juvenile growth and adult fat accretion rates (Table 1 in Cook et al. 2004). It is possible to have high pregnancy rates yet slow growth of calves and subadults, delayed breeding, and other nutrition-related problems.

Thus, for the purpose of evaluating nutritional adequacy of the habitat, comparisons of pregnancy rates among herds may be misleading. For elk, Cook et al. (2001b) indicated that high pregnancy

rates do not necessarily mean that overall nutrition is good, but that even a moderate depression in pregnancy rates indicates relatively strong nutritional limitations most likely during the 2-3 months prior to breeding.

5.1.2 Nutrition, Fetal Development, and Neonatal Viability

While little studied, extreme under-nutrition in winter or spring can induce fetal death (Thorne, Dean, and Hepworth 1976), but these events evidently are rare in elk (Kohlmann 1999; Cook et al. 2004), white-tailed deer (Verme 1962), and caribou (Cameron et al. 1993). Inadequate nutrition in winter and spring also can reduce fetal growth and development, and may be a relatively common occurrence. Nutritional deprivation in spring has greater potential to affect fetal development than nutritional deprivation in winter, simply because fetal development occurs much more rapidly in the third trimester of spring (Verme 1962; Clutton-Brock, Guinness, and Albon 1982; Oldemeyer, Robbins, and Smith 1993). However, severe nutritional deficiencies during harsh winters likely affect birth weight regardless of spring nutrition (Verme 1962, 1977).

Females have some capability to buffer inadequate winter/spring nutrition by mobilizing body stores of protein and energy to support fetal growth (Holland and Odde 1992), but ability to do so may depend on their own levels of protein and energy, and these may be depleted by late winter (Keech et al. 2000; Parker, Barboza, and Stephenson 2005). Additionally, mothers can extend the length of gestation in late spring thus providing a period for the fetus to “catch up” until it reaches some critical threshold in size. Delayed parturition as a result of inadequate nutrition in winter/spring has been reported for caribou (Skogland 1983; Cameron et al. 1993), white-tailed deer (Verme 1965), moose (Schwartz and Hundertmark 1993), and elk (Cook et al. 2004).

Such adaptive responses of mothers may not always compensate for harsh winter/spring nutritional conditions, however, and death of the juvenile may occur just before, during, or very soon after birth (Verme 1962; Wegge 1975; Thorne, Dean, and Hepworth 1976; Holland and Odde 1992). Alternatively, inadequate nutrition may reduce birth weight (Keech et al. 2000), and low birth weight in turn can reduce neonatal survival, growth, resistance to disease, and ability to overcome inclement weather (Holland and Odde 1992; Thorne, Dean, and Hepworth 1976; Verme 1977, Guinness, Clutton-Brock, and Albon 1978; Clutton-Brock, Guinness, and Albon 1982; Fairbanks 1993). Delays in birthing to allow calves to “catch up” while *in utero* might desynchronize the birthing pulse and thus increase susceptibility to predation.

Bergerud (1975) suggested that nutritional condition (as indexed through body size) and nutrition of wild female woodland caribou (*R. t. caribou*) in Newfoundland affected gestation length and parturition date. The birth weight of 46 calves was positively correlated with maternal body size (measured as the sum of total length + chest girth + hind foot length) and negatively correlated with winter snowfall. In addition, the weight of newborn calves declined significantly in relation to date of birth for both males (N = 121) and females (N = 153). McEwan and Whitehead (1972) found that the mean duration of gestation (216 ± 1.7 days, N = 15) in captive barren-ground caribou was shorter than the mean duration (227 days, min.-max.: 210-238) reported for wild reindeer (Schmitt 1936 and Steen 1968, cited in McEwan and Whitehead 1972). The authors speculated that the longer duration of gestation of wild populations might be due to prenatal undernourishment, caused by the relatively low energy consumption and greater maintenance requirements of caribou foraging on winter range, compared to captive animals maintained on a pellet ration.

5.1.3 Nutrition, Lactation and Juvenile Growth

Lactation is the most nutrient-demanding life process of adult ungulates. For species giving birth to a single young per year, total annual metabolizable energy requirements for lactation exceed by 3.5

times the total energy requirements for gestation (Ofteidal 1985, p. 233). On a daily basis, lactation by mid-summer increases ME requirement over gestation about 60% and over maintenance (i.e., of non-lactating females) about 1.5 times (Cook 2002). Milk production peaks 3-4 weeks after parturition in caribou and gradually declines thereafter (Ofteidal 1985), and caribou may maintain lactation through autumn breeding into early winter (Russell et al. 1998). Inadequate nutrition can greatly reduce milk output even in animals in good condition at the time of parturition (Barnicoat, Logan, and Grant 1949 and Peart 1968 with sheep; Loudon, Darroch, and Milne 1984 and Landete-Castillejos et al. 2003 with red deer). For mammals such as ruminant herbivores that produce milk mainly from food they ingest each day (rather than from body reserves), inadequate nutrition has rapid and marked impacts on milk production (Landete-Castillejos et al. 2003).

For juveniles, supporting high levels of growth is their most nutrient-demanding life process. High levels of growth fundamentally require good nutrition, a relation that has been well demonstrated for a variety of ungulate species (Holter and Hayes 1977; Verme and Ozoga 1980a, 1980b; Cook et al. 1996, 2004). Moreover, Holter and Hayes (1977) and Verme and Ozoga (1980a, 1980b) demonstrated the crucial role of digestible/metabolizable energy for maintaining high growth rates in deer fawns (see also Parker et al. 1999; Cook 2002; Cook et al. 2004). Juveniles are nearly completely dependent on mother's milk during the first 6-8 weeks post partum, and thus nutritional effects on milk yields can affect growth rates of juveniles during this time (Landete-Castillejos et al. 2003). However, nutritive value of forage declines rapidly after mid-summer in many ecological settings (Cook 2002, p. 324). Under these conditions, milk yields in late summer and early autumn may be depressed, forcing calves to compensate by using forage that may be inadequate to support high rates of growth. Forage quality levels inadequate to support normal milk yields also may not support rapid growth of calves. These effects, in combination, can greatly reduce juvenile growth after mid-summer (Cook et al. 2004).

Although infrequently studied, nutritional requirement to maintain a high level of growth in subadults (such as yearlings) remains as high as that for juveniles, when adjusted for body weight. Sensitivity of growth rate to nutrition also evidently remains high during at least their second summer of life (Cook et al. 2004). Among caribou, Crête and Huot (1993) found that cows on poor summer range were unable to sustain lactation in the first month post-parturition during peak milk production. Post-lactation, growth of calves on poor summer range was 30% to 40% below calves ranging on high quality summer range and those raised in captivity.

5.1.4 Nutrition and Age of First Reproduction

For wild ungulates, explicit relations between nutrition and achievement of sexual maturity (i.e., age of first breeding or primiparity) have infrequently been studied. Maturation must be adequately advanced before successful breeding occurs, and Hudson et al. (1991) indicated that subadults must achieve 65-70% of their adult weight before they will breed (see also White 1983, p. 381). Thus, nutrition's strong effect on growth probably translates to important effects on primiparity. For a large-bodied ungulate genetically capable of breeding as yearlings (such as elk), Cook et al. (2004) reported that high nutrition levels during the first and second summer of life were required to provide a high probability of breeding as a yearling. They also showed that, under conditions of good nutrition, yearling cohorts are capable of nearly 100% pregnancy (for comparison, yearling elk pregnancy rates of 0-25% are common in the wild [Taber, Raedeke, and McCaughan 1982], and that in some herds, sexual maturity of most individuals in a cohort may not occur until ages of 2.5 or even 3.5 years old [Stussy 1993]).

A number of studies confirm a general threshold of body weight across species required to initiate breeding, including that for red deer (Hamilton and Blaxter 1980), reindeer (Reimers 1983b) white-tailed deer (Verme and Ullrey 1984), moose (Sæther and Haagenrud 1983, Sæther and Heim 1993)

and elk (Cook et al. 2004). In barren-ground caribou, Dauphiné (1976) found that the size and fatness of females of the Kaminuriak Herd affected age of first conception but not first ovulation.

5.1.5 Nutrition and Calf Summer Survival

Juvenile mortality between birth and prior to winter due to inadequate nutrition can be partitioned into two general categories: (1) mortality due to lingering effects of low birth weight, and (2) mortality due to inadequate summer nutrition. Maternal nutrition in winter/spring may strongly affect survival at or near birthing by inducing low birth weight and the cascade of problems noted above. The extent to which low birth weight affects survival well after the birthing period is unclear. Low birth weight calves may have immature digestive tracts, digestion and assimilation of milk thus may be retarded for months after birthing (Lyford 1988), and low birth weight effects on growth and weight linger for years (Schultz and Johnson 1995; Keech et al. 1999; Festa-Bianchet, Jorgenson, and Reale 2000). Further, Keech et al. (2000) for moose and Singer et al. (1997) for elk reported significant relations between birth weight of calves and their survival across summer in predator-rich environments.

The effect of summer/early autumn nutrition's effect on calf survival also is poorly understood, and probably depends on the extent to which nutrition might predispose to various mortality factors such as predation and disease. For example, strong links exist between nutrition and immuno-competence in juveniles (e.g., Ogra 1984), and significant relations among summer nutrition, disease, and juvenile mortality have been reported for bighorn sheep (Cook 1990), white-tailed deer (Sams et al. 1996), and mule deer (Tollefson 2007). Further, if low birth weight predisposes to mortality across summer in predator-rich environments (Singer et al. 1997; Keech et al. 2000), it follows that substantial nutritional deficiencies in summer also might increase summer mortality of calves in predator rich environments, but this hypothesis is largely untested.

Among caribou, forage quality and availability have been found to influence nutritional condition of female caribou, which in turn affects production and survivorship of calves (Cameron et al. 1993; Crête et al. 1993; Dauphiné 1976; Gerhart et al. 1997a). In a study of 12 wild reindeer herds in Norway, Skogland (1983, 1986) observed a decrease in adult female body size and recruitment rate in response to increasing population density and winter food limitation. Inadequate nutrition in autumn, winter, and/or spring might retard fetal development and reduce fetal survival, reduce birth mass, and delay parturition (Skogland 1983; Couturier et al. 1990; Cameron et al. 1993).

Finally, either by causing delays in breeding and/or retarding fetal development, nutrition may influence summer survival of juveniles indirectly by affecting timing and synchrony of parturition. Desynchronized birthing may facilitate predation by reducing predator "swamping," and delayed birthing reduces the synchrony of high nutritional demands of mother and calf with the peak in forage quality (Keech et al. 2000). Clutton-Brock, Guinness, and Albon (1982) reported links between red deer calf summer survival and birth date; however, others have found no significant relation (e.g., Guinness, Clutton-Brock, and Albon 1978; Fairbanks 1993; Singer et al. 1997). Evidently, the magnitude of the delay in birthing greatly affects birth date's influence on calf performance and survival. Delays of a few weeks from the normal birth peak may have little effect (Cook et al. 2004; Landete-Castillejos et al. 2005), whereas delays of several months can have marked negative effects on calves and their mothers (Landete-Castillejos et al. 2004). Guinness, Clutton-Brock, and Albon (1978) reported that the combination of late birth and low birth weight was especially detrimental to red deer calves.

5.1.6 Nutrition and Over-Winter Survival

The relationship between nutrition and over-winter survival for both juveniles and adults is well recognized, in part because substantial die-offs are highly visible and are not uncommon (e.g.,

Houston 1982; Hobbs 1989). Winter-range forage for ungulates in temperate/arctic ecosystems is marginal, and either insufficient quantity or quality of forage, particularly in combination with periods of harsh weather, threatens over-winter survival (Wallmo et al. 1977; Hobbs et al. 1982; Hobbs 1989). Nutritional studies of reindeer and barren-ground caribou suggest that spring and summer diet is essential for growth, whereas the protein-poor winter diet provides maintenance energetic requirements and does not contribute to growth (Dauphiné 1976; Reimers, Klein, and Sørungård 1983).

Body fat levels accumulated prior to winter also affect over-winter survival (Mautz 1978; Hobbs 1989). In wild settings, studying the effect of summer nutrition on autumn body fat and subsequent winter survival has been a difficult challenge and rarely attempted. In a captive setting using 57 adult female elk, Cook et al. (2004) demonstrated that summer-autumn nutrition significantly affected autumn fat levels, and these fat levels in turn significantly affected their ability to survive under simulated harsh winter nutritional conditions. Similarly, body size in calves greatly affected their ability to survive over winter. Small calves were particularly susceptible and tended to succumb surprisingly early in winter, probably because of triple challenges: (1) low endogenous energy reserves; (2) elevated thermodynamic susceptibility (higher surface area:volume ratio in smaller calves increases heat loss—see Parker and Robbins [1985]); and (3) shorter stature that impedes predator avoidance and movement in deep snow.

5.1.7 Nutrition and Body Fat Accretion Dynamics

Adequate fat in adult females serves three crucial functions: (1) it enhances over-winter survival; (2) it increases the probability of becoming pregnant; and (3) it enhances foetal/juvenile development and survival probability by serving as an energy “buffer” during periods of inadequate nutrition. In temperate and arctic regions, large herbivores lose fat in winter and gain fat in summer. Over time, amount of fat lost and gained must balance. If a negative fat balance persists sequentially over multiple years, the animal must forego reproduction to interrupt the downward fat trend (Cameron 1994), or it will eventually die. The further north, or the harsher the environment, the more crucial the role of fat becomes, yet the more difficult it may be for animals to accrue adequate fat due to long winters and short growing seasons.

Despite the pivotal role of fat, detailed studies of nutrition’s influences on fat levels are rare. The amount of energy animals should consume over summer for fat accretion depends on how much fat they lost during the previous winter, and how much fat they will need over the coming winter. Jiang and Hudson (1992) reported that 9.3 kcal of ME are required per gram of gain in subadult elk cows. Using this as a general approximation, Cook (2002) calculated that the total summer metabolizable energy requirement to replenish a 10% weight loss the previous winter (presumed to represent a mild to normal winter) is about 30% of ME needed for 4 months of lactation. For cows that lose 25% of weight in winter (representing a harsh winter), the replenishment ME requirement is about 65% of the ME needed for lactation. The energy costs of lactation plus those of recovering from the previous winter can therefore more than double daily ME requirements compared to those of non-lactating, non-compensating females in summer/autumn (Cook 2002).

These calculations of ME requirements for lactation and recovery of winter weight loss indicate an important interaction between lactation status and fat accretion rates. In some environments, it may be difficult for lactating females to support their calves and simultaneously restore body fat levels, and under these conditions, total ME requirements may be unsatisfied and occasional reproductive pauses would be expected. In contrast, non-lactating females would face substantially less difficulty developing fat under these conditions. Results from captive animal studies support this hypothesis—Cook et al. (2004) found that fat accretion in lactating elk is remarkably sensitive to digestible energy content of food, but that fat accretion in non-lactating females is insensitive to DE content. For

example, a 15 to 20% difference in DE content resulted in a three- to fivefold difference in body fat levels in lactating females in early autumn, a difference that developed in merely 3 months of controlled feeding (July through September). Lactating cows on the lower diet (2.51-2.54 kcal of DE/g of food) had very low fat levels of 2-5% by early autumn, failed to breed, and their calves were markedly stunted. Non-lactating cows on this same lower diet had body fat of 15-20%, equivalent to lactating cows on high nutrition (2.9-3.0 kcal of DE/g of food).

As noted above for pregnancy, this interaction complicates the use of body fat, and a host of nutritional condition indices, as a direct index of nutritional adequacy of caribou range, because autumn body fat levels for the herd will be sensitive to the proportion of females that successfully raise a calf. However, nutrition-fat relations are less complex than nutrition-pregnancy relations; simply stratifying body fat levels by lactation status and focusing on fat levels only of lactating females largely solves this confounding problem (e.g., Gerhart et al. 1997a; Cook et al. 2004; Cook, Cook, and Mech 2004).

5.2 Nutritional Requirements

Estimates of nutritional requirements are a key data type important for modeling nutritional effects on ungulates and understanding or evaluating the nutritional adequacy of habitat. Such an effort was a major focus of livestock research in past decades (e.g., National Research Council 1984, 1985). For wild ungulates, such a concerted effort has not been undertaken, probably due in large part to the need for controlled experiments with captive animals (see Verme and Ozoga 1980a, 1980b; Verme and Ullrey 1984; Haigh and Hudson 1993; Cook et al. 2004 for summaries of estimated requirements or examples of nutritional requirements studies).

Nutritional requirements are usually expressed in one of two general formats: as nutrient intake required per unit time, usually per day (e.g., total daily requirement in units of kcal of digestible energy (DE) per kg of weight per day), or in terms of concentration in the food (e.g., kcal of DE per g of food). Sufficient information exists about nutritional needs for various life stages (e.g., maintenance, gestation, lactation) that total daily requirements can be calculated with reasonable accuracy using a “factorial” approach (e.g., Parker et al. 1999; Cook 2002). Very complex versions have been integrated into simulation models for deer (Hobbs 1989), moose (Moen, Pastor, and Cohen 1997), and caribou (Boertje 1985a; Russell, White, and Daniel 2005). The caribou model of Russell, White, and Daniel resulted from long-term caribou studies, evidently is being updated continually, and probably represents the “state of the art” for estimating caribou nutritional requirements.

Requirement in units of nutrient concentration in food is more difficult to estimate, yet such estimates have important practical applications such as for calculating carrying capacity (Hobbs and Swift 1985; Hanley and Rogers 1989) and for evaluating the nutritional adequacy of vegetation samples from standard forage quality surveys (Schwartz and Hobbs 1985). Uncertainty in estimating requirements in units of concentration arises mainly because how much food animals eat each day and the animal’s total daily requirement must be known (e.g., required nutrient content in food = total daily nutrient requirement ÷ daily dry matter food intake). In turn, how much food animals eat each day depends on complex interactions among (1) animal attributes, e.g., production stage, age, season, current nutritional condition relative to target condition (i.e., the set point concept of Renecker and Samuel 1991) and anatomical constraints to intake (Ketelaars and Tolkamp 1991; Shipley and Spalinger 1992; Romsos 1998; Cook et al. 2004); and (2) plant community characteristics, such as distribution of nutrients among plant parts and species (Hobbs and Swift 1985), bite mass offered by plant taxa actually in the diet (Hobbs et al. 2003), plant toxins (Hanley 1997), and plant structure and distribution patterns (Hobbs et al. 2003). Additionally, in ruminants, forage passage rates through the gut slow as nutrient content of food declines, and thus the amount of food ruminants can consume each day also declines as nutrient content of food declines (Spalinger, Robbins, and Hanley 1986;

Minson and Wilson 1994; Grey and Servello 1995; Cook et al. 2004) (sometimes called “bulk” limitation to intake [Robbins 1983]). In practice, small differences particularly in DE, ME, protein, or even mineral content (Minson and Wilson 1994) can have large effects on daily intake, and thus can strongly influence nutritional plane and performance of the animal (Cook et al. 2004). This is the “multiplier” effect described by White (1983). Considerable experimental work has addressed several of these confounding variables associated with food intake (e.g., Hobbs and Swift 1985; Gross et al. 1993; Shipley et al. 1999; Hobbs et al. 2003). Nevertheless, predicting nutrient acquisition rates remains problematic across the huge variety of plant community types that exist in nature.

Research has incompletely identified requirements in the context of multiple variables, such as protein, energy, and minerals, and their potential interactions, even for livestock (National Research Council 1984). For wild ungulates, most research has focused on protein and energy requirements. Very early work tended to focus on protein (French et al. 1956; Smith et al. 1975; Ullrey et al. 1967), whereas recent work suggests that digestible/metabolizable energy can be more limiting in settings where vascular plants are the primary food (Holter and Hayes 1977; Verme and Ozoga 1980b; Parker et al. 1999; Cook 2002). Available evidence from published literature on diet composition and nutrient utilization suggests that caribou sometimes may be more influenced by energetic constraints than protein balance. In a study of the effects of nutrient intake on fat/protein deposition and milk production in captive caribou and reindeer, Chan-McLeod, White, and Holleman (1994) found that energy intake was the only significant variable in affecting body mass changes in lactating or non-lactating adult females during summer. Protein intake, dietary protein:energy ratio, date, and nutritional condition did not have significant explanatory power. Production of milk lactose correlated with maternal energy intake, while production of milk protein correlated with the maternal dietary protein:energy ratio. Syrjälä-Qvist and Salonen (1983) examined the effects of protein and energy supply on nitrogen utilization in captive reindeer and found that when the digestible crude protein content of the feed was increased, reindeer were able to use only 12% of the increased protein, but when the energy supply was increased at the same time, animals were able to use 62% of the protein increase.

Nevertheless, protein levels also may be limiting, and many of the effects of inadequate energy on ungulates described in the above sections also have been identified for protein deficiencies (see Parker, Barboza, and Stephenson 2005). Clarifying the relative importance of the two is complicated by the fact that in vascular plants, protein and energy are strongly intercorrelated (when one is high, so is the other), so careful research designs are required to separate their relative effects. For juvenile growth, protein generally becomes more limiting when the ratio of digestible protein falls below about 30 mg/kcal of digestible energy (Lyford and Huber 1988). Moreover, diets of caribou in many environments may be largely restricted to lichens in some seasons, a food source with protein levels normally inadequate for large ungulates yet often with high digestible energy levels (Parker, Barboza, and Stephenson 2005). Parker, Barboza, and Stephenson (2005) indicated that the primary source for fetal protein may be maternal protein, not dietary protein, and indicated that fetal development in winter may be more sensitive to levels of maternal protein than maternal fat. Particularly for caribou, more understanding of the role of protein and energy is clearly needed (Parker, Barboza, and Stephenson 2005). And, it is likely that understanding of nutrition effects on caribou populations will require integration of both, as does the simulation model of Russell, White, and Daniel (2005).

5.3 Nutritional Requirements in *Rangifer*

Reliable estimates of the nutritional requirements of woodland caribou (Northern Mountain, Southern Mountain, Boreal, Newfoundland (Island), Atlantic (Gaspésie)) are virtually absent from the published literature. Given similar environmental settings, research on other subspecies of *R. tarandus* (e.g., barren-ground caribou, reindeer, and the forest-tundra ecotype of woodland caribou)

can aid in identifying the nutritional needs of *R. t. caribou*; however, they should be interpreted with caution. Activity patterns and energy expenditure may vary among different populations, due to differences in forage availability, climate, and level of insect harassment. In spite of these problems, woodland caribou share a common evolutionary history with other cervids and similarities should exist among diverse ruminants in their nutritional requirements for reproduction, growth, and development.

Due to the vast array of constraints that influence the fitness of wild ungulates (e.g., competition, predation, weather), isolating the relative importance of one or the other factor requires experimental conditions involving controlled diets. In a study of captive female elk, Cook et al. (2004) identified important indicators of nutritional stress and thresholds in the digestible energy content of summer forage corresponding to those indicators (Table 5.1). We could not find similar indicator thresholds for *Rangifer* in the literature we reviewed and such information could provide a useful tool for evaluating nutritional stress in wild woodland caribou populations. Although captive studies allow for measurement of nutritional requirements and energy expenditure under controlled conditions, such estimates are expected to be conservative due to the lower activity of captive animals. Energetic requirements may be lower for captive animals due to differences in forage accessibility, climate, costs of locomotion through variable terrain, and level of insect harassment.

Table 5.1 Indicators of Summer/Autumn Nutritional Stress for Elk (based on Cook et al. 2004)

Indicator	Sensitivity	Threshold for decline (DE in summer forage) kJ/g (kcal/g)
Probability of winter starvation	Variable ^a	Linear w/out thresholds
Calf and yearling growth and development	High	12.56-13.40 (3.00-3.20)
Yearling breeding probability (age of primiparity)	High	12.56-13.40 (3.00-3.20)
Body fat accretion rates of lactating cows	High	11.93 (2.85)
Timing of adult breeding	High	11.72-11.93 (2.80-2.85)
Timing of birthing	Moderate ^b	11.72-11.93 (2.80-2.85)
Breeding probability of adult lactators	Moderate	11.10-11.30 (2.65-2.70)

^a Dependent on winter severity and age class, in addition to summer nutrition and autumn body fat levels.

^b Strong delays in breeding can translate to delays in birthing, but the effect may be modified by weather and nutrition in winter and spring.

5.3.1 Annual and Seasonal Requirements

The total metabolizable energy requirement of an adult female barren-ground caribou in Denali National Park, Alaska was estimated to be 9 870 MJ/year (2 357 Mcal/year)(1 MJ = 1000 kJ, 1 Mcal = 1000 kcal), including costs of pregnancy (368.6 MJ, 88 Mcal) and lactation (560.3 MJ, 134 Mcal) (Boertje 1985a). Boertje (1985a) used factorial modeling to estimate the annual energy requirements (Table 5.2) of adult female caribou (*R. t. granti*), and estimates of activity budgets and the energy costs of resting, activity, and productive processes were acquired from available literature. His findings were comparable to studies of food energy requirements of penned caribou, considering the relative inactivity of penned animals (McEwan 1970). Boertje's (1985a) model prediction of the

average metabolizable energy intake requirements of free-ranging caribou during the entire gestation period was approximately $683 \text{ kJ} * \text{kg}^{-0.75}$ per day ($163 \text{ kcal} * \text{kg}^{-0.75}$)($1.79 * \text{winter basal metabolic rate}$), including pregnancy costs. This estimate was comparable to McEwan and Whitehead's (1972) estimate of $571 \text{ kJ} * \text{kg}^{-0.75}$ per day ($136 \text{ kcal} * \text{kg}^{-0.75}$) ($1.50 * \text{winter basal metabolic rate}$) for 11 pregnant reindeer and caribou fed *ad libitum* over the same period. Similar studies have not been published on the energetic requirements of forest-dwelling woodland caribou. The above estimates for barren-ground caribou included the energy costs of large-scale travel between seasonal ranges and may overestimate the annual energy requirements of sedentary caribou populations.

Rangifer exhibit a cyclic pattern of reduced energetic requirements in winter compared to summer (Boertje 1985a), concurrent with reduced voluntary food intake (McEwan 1968; Crête et al. 1993) and weight loss in winter (McEwan 1968; Dauphiné 1976; Reimers, Klein, and Sørungård 1983). Boertje (1985a) estimated that the metabolizable energy requirements were 46% lower in mid-winter (20.5 MJ/day, 4.9 Mcal/day) than summer (38.2 MJ/day, 9.1 Mcal/day), concurrent with a reduction in estimated food intake and metabolizable energy requirement in food during winter (Table 5.2). This difference was attributed to a 21% reduction in resting metabolic rate, fat catabolism in winter, and high summer costs of lactation, fat deposition, and activity. Boertje's (1990) summary of the Denali herd's nutritional regime (Table 5.2) describe a well nourished free-ranging caribou herd and may provide a framework for comparison of the nutritional status of other populations. His estimates incorporated empirical data on the diet quality, activity budgets, and energy costs of different activities as previously published for the herd (Boertje 1981, 1984, 1985a, 1985b).

Table 5.2 Estimates of Daily Metabolizable Energy and Dry Matter Intake Requirements of Free-Ranging Adult Female Caribou *R.t. granti* (with a calf) of the Denali Herd, Alaska for Different Seasons and Life Processes

Life process /activity	Season ^a				Reference
	Spring	Summer	Autumn	Winter	
Total energy requirements for all activities ^b $\text{kJ} * \text{kg}^{-0.75} * \text{day}^{-1}$ ($\text{kcal} * \text{kg}^{-0.75} * \text{day}^{-1}$)	926 (221)	1 163 (278)	939 (224)	617 (147)	Boertje (1985a)
Pregnancy $\text{kJ} * \text{kg}^{-0.75} * \text{day}^{-1}$ ($\text{kcal} * \text{kg}^{-0.75} * \text{day}^{-1}$)	0	0	4 (1)	29 (7)	Boertje (1985a)
Lactation $\text{kJ} * \text{kg}^{-0.75} * \text{day}^{-1}$ ($\text{kcal} * \text{kg}^{-0.75} * \text{day}^{-1}$)	202 (48)	112 (27)	16 (4)	0	Boertje (1985a)
Fattening $\text{kJ} * \text{kg}^{-0.75} * \text{day}^{-1}$ ($\text{kcal} * \text{kg}^{-0.75} * \text{day}^{-1}$)	-36 (-9)	165 (39)	165 (39)	-55 (-13)	Boertje (1985a)
Metabolizable energy requirements in food $\text{KJ} * \text{g}^{-1}$ ($\text{kcal} * \text{g}^{-1}$)	10.76 (2.57)	11.01 (2.63)	9.64 (2.30)	9.10 (2.17)	Boertje (1990)
Digestible energy requirements in food $\text{KJ} * \text{g}^{-1}$ ($\text{kcal} * \text{g}^{-1}$)	13.12 (3.13)	13.43 (3.21)	11.76 (2.81)	11.10 (2.65)	Boertje (1990)
Estimated dry matter intake ($\text{g} * \text{kg}^{-0.75}$ per day)	86	104	104	74	Boertje (1990)

^a Boertje 1985a: spring (May-June), summer (July – August), autumn (September – October), winter (January – February).

Boertje 1990: spring (22 May – 30 June), summer (1 July – 20 August), autumn (21 August – 15 October), winter (16 October – 21 May).

^b activities incorporated in the model included lying, standing, feeding, walking, trotting/galloping, ruminating, lying to standing and return, ascent, descent, lactation, pregnancy, fattening, and hair growth (Boertje 1985a).

5.3.2 Lactation

No estimates of the energetic costs of lactation for ecotypes of woodland caribou could be found in the published literature; however, they are assumed to be similar among different subspecies of *R. tarandus*. In an experimental study of captive caribou (*R. t. granti*) and reindeer (*R. t. tarandus*), Chan-McLeod, White, and Holleman (1994) found that the maintenance requirement for lactating females [$457 \text{ kJ} * \text{kg}^{-0.75}$ ($109 \text{ kcal} * \text{kg}^{-0.75}$) per day, net energy intake] was twice that for non-lactating individuals [$232 \text{ kJ} * \text{kg}^{-0.75}$ ($55 \text{ kcal} * \text{kg}^{-0.75}$) per day]. For free-ranging female caribou of the Denali Herd, Alaska, Boertje (1985a) estimated a total daily metabolizable energy requirement of [$926 \text{ kJ} * \text{kg}^{-0.75}$ ($221 \text{ kcal} * \text{kg}^{-0.75}$)] for lactating females during the calving/post-calving season. Lactation accounted for $202 \text{ kJ} * \text{kg}^{-0.75}$ ($48 \text{ kcal} * \text{kg}^{-0.75}$) in the daily energy requirement. He concluded that the estimated energy requirements for lactation totalled 560 MJ (134 Mcal) per calf.

The energy content and composition of milk appear to be more closely related to diet quality during lactation than pregnancy (i.e., winter diet). Rognmo et al. (1983) found that the energy content of milk during lactation was similar for captive female reindeer fed a typical winter diet of lichen (N = 18) and females fed an improved winter diet, rich in protein and minerals (N = 14). Both groups received the same high quality diet following parturition and growth rates of calves born to young females (2-3 years old) did not differ between the two groups.

5.3.3 Juvenile Growth and Development

McEwan (1968) estimated the growth curves of minimum body weight from birth to maturity for captive barren-ground caribou (1 male and 1 female) fed *ad libitum*. The mean daily feed intake of a single male caribou in its first three summers of growth (June to mid-September) increased from 2 100 to 4 000, 2 500 to 4 000, and 3 000 to 5 500 g, reflecting a digestible energy intake of approximately 30.3 to 57.8, 36.1 to 57.8, and 43.3 to 79.4 MJ (7.2 to 13.8, 8.6 to 13.8, and 10.3 to 19.0 Mcal) of digestible energy. A similar trend, but with slightly lower feed intake, was reported for the female caribou.

McEwan and Whitehead (1970) estimated the energy and nitrogen requirements during the first two years of growth in captive reindeer and barren-ground caribou. The estimated metabolizable energy requirement for maintenance in winter was $837 \text{ kJ} * \text{kg}^{-0.75}$ ($200 \text{ kcal} * \text{kg}^{-0.75}$) and body fat accretion was high during the phase of rapid growth. The energy retention of the calves in August was approximately 13.8 MJ (3.3 Mcal) per day, (75% in fat). In both male and female caribou, nitrogen retention was greater during the summer growth phase than during winter and the amount of digestible nitrogen required for N equilibrium was $0.462 \text{ g N/W kg}^{0.75}$ per day. Parker et al. (1990) measured the daily energy expenditure of two captive caribou calves *R. t. granti* using a doubly labelled isotope tracer. Daily energy costs were highly variable and ranged between 450 and 650 kJ/kg (107 and 155 kcal) per day during the first 60 days of life. Between 20 and 40 days of age, the daily existence metabolism averaged $439 \pm 1 \text{ kJ/kg}$ per day or $923 \pm 70 \text{ kJ} * \text{kg}^{-0.75}$ ($220 \pm 17 \text{ kcal} * \text{kg}^{-0.75}$).

5.3.4 Over-Winter Survival

McEwan (1970) reported that the maintenance digestible energy intake (DEI) in 2 penned, adult female barren-ground caribou averaged approximately $665 \pm 18 \text{ kJ} * \text{kg}^{-0.75}$ ($159 \pm 4 \text{ kcal} * \text{kg}^{-0.75}$) per day from February to May. Energy metabolism was measured using a closed-circuit respiration chamber and captive animals were fed a voluntary intake diet of approximately 1 260 – 1 440 g of dry matter, sufficient for maintenance of body weight. Boertje (1985a) converted this value to metabolizable energy intake (MEI = $0.82 * \text{DEI}$, Agricultural Research Council 1965), indicating a value of $545 \text{ kJ} * \text{kg}^{-0.75}$ ($130 \text{ kcal} * \text{kg}^{-0.75}$) per day ($1.43 * \text{winter basal metabolic rate}$). Boertje's (1985a) model gave a value of approximately $652 \text{ kJ} * \text{kg}^{-0.75}$ ($156 \text{ kcal} * \text{kg}^{-0.75}$) per day ($1.71 * \text{winter basal metabolic rate}$).

winter basal metabolic rate) for free-ranging caribou during the same period. In both studies, caribou were assumed to not be pregnant and to be feeding on a maintenance diet.

Gotaas et al. (2000) used a doubly labelled water method to measure total energy expenditure of three free-ranging male reindeer *R. t. tarandus* in winter. This methodology involved estimating CO₂ production using feces and isotope analysis and permitted the study of subjects living unrestricted in their natural environment. The mean specific total daily energy expenditure in the three animals was 16.0 MJ (4 Mcal) per day or, assuming 70 kg body weight, 764 kJ * kg^{-0.75} (182 kcal * kg^{-0.75}). This value was 64% greater than the total energy expenditure of three captive, non-pregnant female reindeer *R. t. tarandus* in winter (Gotaas et al. 1997) and was speculated to reflect the greater locomotory requirements of free-ranging animals. Fancy (1986) used factorial models to estimate the total daily energy expenditure of wild adult female woodland caribou *R. t. caribou* (reproductive status unknown) between March and April and found similar values (759 kJ * kg^{-0.75} (181 kcal * kg^{-0.75})) to the estimates of Gotaas et al. (2000).

5.4 Seasonal Food Habits

Plant phenology and seasonal weather patterns (e.g., snow accumulation) greatly affect caribou forage availability and plant nutrient content. Although the actual species content may vary across geographic regions, ecotypes of woodland caribou exhibit similar seasonal patterns in forage utilization (Table 5.3). In spring, caribou seek rapidly growing green plants and intake of lichens is relatively low (Figure 5.1) (Bergerud 1972). Selection of forage plants appears to be opportunistic and based on the timing of emergence of new green growth. Summer diet in caribou is the most diverse of any season and all major plant groups are eaten, including forbs, graminoids, and leaves of shrubs (Figure 5.1) (Simkin 1965; Bergerud 1972; Darby and Pruitt 1984; Ferguson, Bergerud, and Ferguson 1988; Smith and Ouellet 2004). In autumn, the dropping of deciduous leaves and lack of snow cover results in a relatively high usage of terrestrial lichens. Although terrestrial lichens and vascular plants may be eaten year-round (Bergerud 1972; Darby and Pruitt 1984; Smith and Ouellet 2004), snow accumulation greatly affects plant availability in winter and arboreal lichens and evergreen shrubs may increase in importance where snow depth prohibits cratering for forage (Rominger and Oldemeyer 1990; Kinley 2000; Rominger et al. 2000; Johnson, Parker, and Heard 2001). Stardom (1975) found that woodland caribou in Manitoba shifted their feeding areas from open bogs to lichen-rock ridges, when snow accumulation approached 60 cm and Pruitt (1959) found that barren-ground caribou may avoid cratering through snow for ground lichens when snow depths exceed 50 cm.

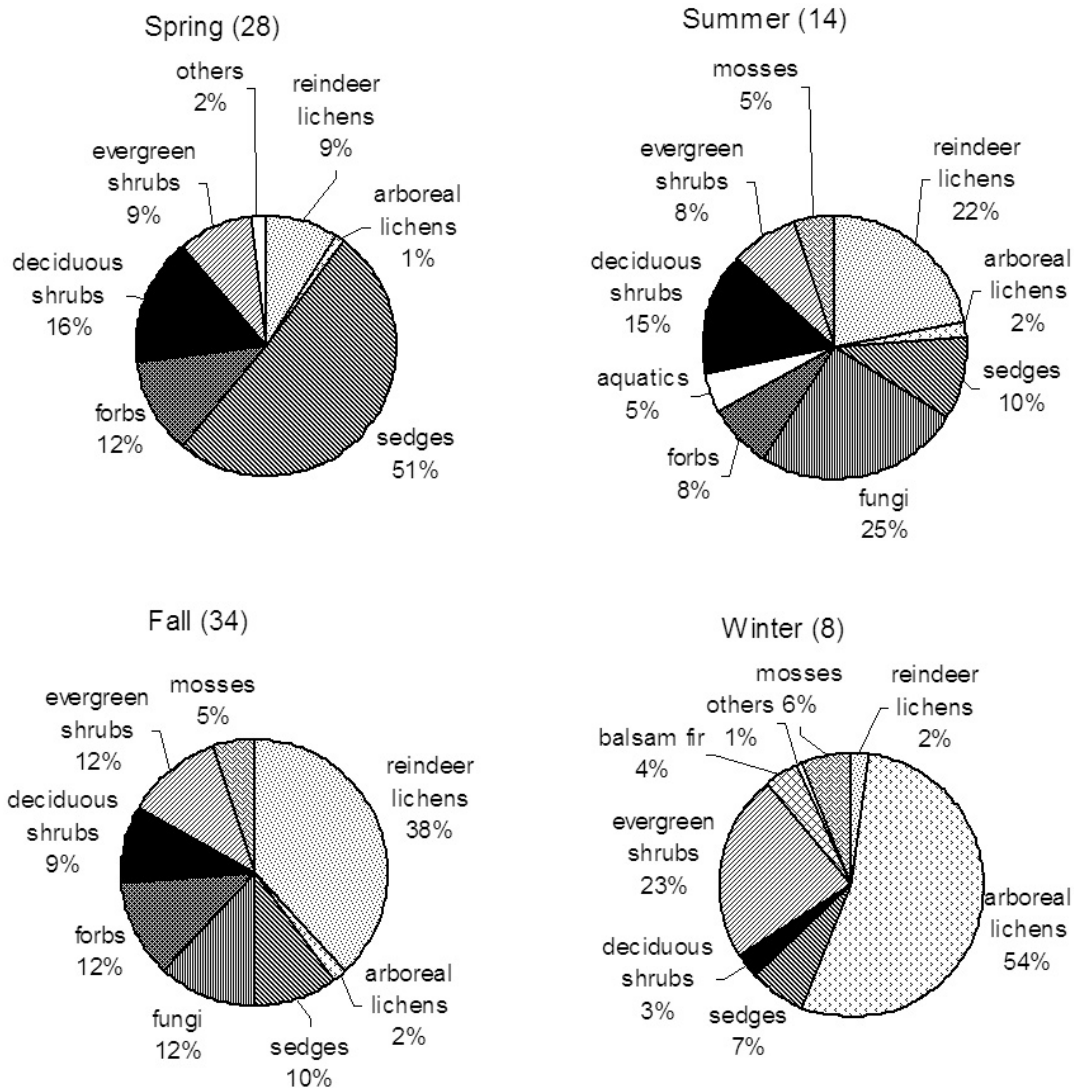


Figure 5.1 Seasonal Diet of Woodland Caribou in Newfoundland as Estimated from the Percentage of Plant Groups Identified in the Contents of 84 Caribou Rumina (reproduced from Fig. 1 in Bergerud 1972).

Table 5.3 Summary of Selected Studies That Describe the Seasonal Diet of Woodland Caribou

Study/ Caribou Ecotype	Diet	Notes on Methodology	Comments
<p>Bergerud 1972 Newfoundland (Island)</p>	<p>Spring: sedges (<i>Scirpus cespitosus</i>, <i>Carex</i> spp.) 51%, deciduous shrubs 16%, forbs 12%, broadleaved evergreen shrubs 9%, reindeer lichens 2%, other 2%, arboreal lichens 1%. Calves ate more bryophytes than adults</p> <p>Summer: reindeer lichen (<i>Cladonia</i> spp.) 22%, fungi 25%, deciduous shrubs (<i>Betula pumila</i>, <i>B. glandulosa</i>, <i>Vaccinium angustifolium</i>, <i>Amelanchier bartramiana</i>) 15%, sedges 10%, forbs 8%, evergreen shrubs 8%, aquatics 5%, mosses 5%, arboreal lichens 2%.</p> <p>Autumn: reindeer lichen 38%, fungi 12%, evergreen shrubs 12%, forbs 12%, sedges 10%, deciduous shrubs 9%, mosses 5%, arboreal lichens 2%.</p> <p>Winter: arboreal lichens (<i>Cetraria ciliaris</i>, <i>Parmelia physodes</i>, and <i>P. sulcata</i>) 54%, evergreen shrubs 23%, sedges 7%, mosses 6%, balsam fir 4%, deciduous shrubs 3%, reindeer lichens 2%, other 1%.</p>	<p>Rumen samples (N = 28 spring, 14 summer, 34 autumn, and 8 winter)</p> <p>Identification of plant fragments that were separated by a 0.078 inch screen opening. Diet composition reported as the percentage of the plant groups identified, rather than the percentage of the entire rumen contents.</p> <p>Time of plant sampling for nutrient content analysis reflected seasonal patterns in use by caribou.</p> <p>No measure of use relative to availability</p>	<p>Differences in digestibility of plant species limit ability to detect differences in the relative abundance of each species in the diet.</p>
<p>Smith and Ouellet 2004 Atlantic (Gaspésie)</p>	<p>Summer: moss 41%, lichens 22.2%, deciduous shrubs 14.5%, forbs 13.5%, graminoids 6.9%, conifer 1.5%</p> <p>Winter: moss 14.2%, lichens 55.5%, deciduous shrubs 20.2%, forbs 1.2%, graminoids 4.5%, conifer 3.3%</p>	<p>Microhistological analysis of fresh fecal samples (N = 151) collected in February – April, 2000 and June – August 1999, 2000. Samples were predominantly taken from alpine areas, although both alpine and boreal vegetation types are used by caribou</p>	<p>The authors speculated that moss was over-represented in fecal samples, compared to more digestible forage, and may have been ingested incidentally with other food. The</p>

Study/ Caribou Ecotype	Diet	Notes on Methodology	Comments
	Significantly more forbs and graminoids in summer than winter ($P < 0.05$) and less lichen, deciduous shrubs, and conifers during summer than during winter ($P < 0.01$).	No measure of use relative to availability	increased use of lichens and decreased use of moss in winter was assumed to be a result of selection for arboreal lichens in winter that would greatly reduce the incidental intake of moss.
Mosnier et al. 2003 Atlantic (Gaspésie)	Winter habitat along foraging tracks: Biomass of accessible arboreal lichens (<i>Alectoria</i> , <i>Usnea</i> , <i>Bryoria</i>) was significantly higher in foraging tracks than along adjacent available transects within the same stands where foraging tracks occurred ($P < 0.001$).	Examined the habitat characteristics along winter foraging tracks (N = 23 foraging tracks, 23 adjacent available tracks). Due to other study objectives, the collected data does not permit assessment of the relative importance of different forage items, as only evidence of lichen foraging was used to identify foraging tracks for sampling.	
Thomas and Armbruster 1996 Boreal	Summer: terrestrial lichens 22 – 69%, shrubs 5 – 27%, <i>Equisetum</i> spp. 8 – 18%, mosses 6 – 16%, forbs 1 – 8%, graminoids 2 – 4% Winter: lichens, shrubs, and <i>Equisetum</i> spp. dominated diet in winter. Labrador tea was the most common shrub species consumed. We pooled winter data provided in Thomas and Armbruster (1996) among seven sampling sites (N = 19) and estimated that lichens, shrubs, and <i>Equisetum</i> spp. represented approximately 50, 19, and 17%, respectively, of the identifiable plant	Microhistological analysis of plant fragments in fecal samples. The low sample size (N = 4 summer) does not permit generalization of the relative importance of each species in caribou diet.	Differences in digestibility of plant species limit ability to detect differences in the relative abundance of each species in the diet.

Study/ Caribou Ecotype	Diet	Notes on Methodology	Comments
<p>Ferguson, Bergerud, and Ferguson 1988</p> <p>Boreal</p>	<p>fragments.</p> <p>Summer:</p> <p>Systematic surveys: Ferns <i>Dryopteris</i> spp., <i>Rubus</i> spp., and <i>Vaccinium</i> spp. dominated caribou diet, representing 46%, 12%, and 6% of the total diet composition, respectively.</p> <p>Monthly plot surveys: usage of ferns <i>Dryopteris</i> spp. was greatest during late May, the utilization of forbs was greatest in July, and use of <i>Rubus</i> spp. peaked in October. <i>Populus tremuloides</i>, <i>Salix</i> spp., and <i>Acer spicatum</i> were the most highly preferred shrub species in spring and summer.</p>	<p>Study area: Pic Island, Lake Superior (1138 ha)</p> <p>Summer food preference in July determined using systematic surveys of island and measurements of the number of bites eaten and available for utilized forage plants within 4 m² plots (N = 219).</p> <p>Monthly plot surveys (N = 8) conducted between April and November.</p>	
<p>Simkin 1965</p> <p>Boreal</p>	<p>Western Ontario: caribou fed opportunistically on the succulent leaves of trees, shrubs and herbs as they became available in early spring and summer.</p> <p>Prior to the emergence of green vegetation, caribou fed on Labrador tea <i>Ledum groenlandicum</i>, club mosses <i>Lycopodium</i> spp., the coarse stocks of dwarf elder <i>Aralia hispida</i>, and the buds and twigs of shrubs.</p> <p>Spring: caribou fed heavily on ground lichens (42.5%) and shrubs and herbs (39.6%), and ate arboreal lichens (17.9%) less frequently.</p> <p>Summer: shrubs and herbs 64.8%, ground lichens 24.8%, arboreal lichens 10.4%</p> <p>The most frequently eaten species included <i>Cladonia rangiferina</i>, <i>C. unctatis</i>, and <i>C. metis</i></p>	<p>Spring (May-June) and summer (July) diet: based on field observations of feeding in free-roaming wild caribou. No systematic sampling was conducted and the species eaten at observed feeding sites were recorded. Relative importance of each plant group was based on the percentage of feeding observations (N = 124 spring, 125 summer observations) for each group.</p> <p>Winter diet: qualitative assessment based on 10 days of observing a group of approximately 40 animals in March, 1958.</p>	

Study/ Caribou Ecotype	Diet	Notes on Methodology	Comments
Darby and Pruitt 1984 Boreal	<p>(ground lichens); <i>Usnea comosa</i>, and <i>Evernia mesomorpha</i> (arboreal lichens); and <i>Betula papyrifera</i>, <i>Populus tremuloides</i>, and <i>Prunus pensylvanica</i> (shrubs).</p> <p>Winter: ground lichens (<i>Cladonia</i> spp.) were concluded to be the most common food item and arboreal lichens were used less frequently. Deciduous browse (willow and mountain alder <i>Alnus crispa</i>) was speculated to represented a considerable portion of caribou diet, and where caribou dug through snow for ground lichens, species such as sweet gale <i>Myrica gale</i>, leatherleaf <i>Chamaedaphne calyculata</i>, Labrador tea, and bog rosemary <i>Andromeda glaucophylla</i> were also eaten.</p> <p>Early spring: caribou fed on lichens (<i>Cladonia</i> spp. and <i>Parmelia</i> spp.) and twig tips of willow <i>Salix</i> spp. and alder <i>Alnus</i> spp.</p> <p>Late spring and summer: caribou were observed feeding on forbs, deciduous foliage and arboreal and ground lichens.</p> <p>Autumn: caribou fed on ground lichens, arboreal lichens, sedges, and bog ericoids (<i>Andromeda glaucophylla</i>, <i>Chamaedaphne c.</i>, <i>Kalmia polifolia</i>, and <i>Ledum</i> g.) near semi-open and open bogs.</p> <p>Winter: snow accumulation restricted travel in open bogs and caribou fed on <i>Cladonia</i> spp. and <i>Vaccinium myrtilloides</i> on Jack Pine-rock ridges where snow accumulation was relatively low.</p> <p>Spring and summer: roots and shoots of herbs,</p>		
Cringan 1957		Qualitative descriptions of the seasonal diet of woodland caribou in southeastern Manitoba (boreal population), based on observations of feeding caribou during aerial and ground surveys.	
		Study area: Slate Islands, Lake	

Study/ Caribou Ecotype	Diet	Notes on Methodology	Comments
Boreal	<p>mosses, lichens, and fungi. Frequently eaten items in spring included large-leaved aster <i>Aster ciliolatus</i>, bunchberry <i>Cornus canadensis</i>, mosses, and lichens.</p> <p>Summer: deciduous shrubs, herbs, lichens, and aquatic plants. Herbs and shrubs in the summer diet included large-leaved aster, sarsaparilla <i>Aralia nudicaulis</i>, ferns, fireweed <i>Epilobium angustifolium</i>, high bush cranberry, mountain ash, mountain maple and bush honeysuckle <i>Diervilla lonicera</i>.</p> <p>Winter diet: no quantitative measures were available to contrast the relative usage among plant species; however Cringan (1957) concluded that utilization of woody browse was low in winter, while usage of arboreal and terrestrial lichens was critically important. There was evidence of heavy grazing in most lichen-rich stands (mainly <i>Cladonia rangiferina</i> and <i>C. alpestris</i>) on the islands.</p> <p>Utilization of woody browse species, relative to their availability, was greatest for mountain maple <i>Acer spicatum</i> (41% of woody browse eaten), followed by mountain ash <i>Pyrus americana</i>, willows <i>Salix</i> spp., red-osier dogwood <i>Cornus stolonifera</i>, and highbush cranberry <i>Viburnum rafinesquiana</i>.</p>	<p>Superior.</p> <p>Winter diet: estimated by measuring the percentages of use and availability of woody browse, arboreal lichens, and ground lichens within sample plots (N = 495) in 1949. Additional information on the grazing of herbs and leaf-browsing of shrubs was assessed using field observations of wild caribou engaged in feeding.</p> <p>Cringan's (1957) conclusion that arboreal lichens were more important than ground lichens in the winter diet of caribou is not substantiated by quantitative data, as the conclusion was based on a greater availability of arboreal lichens.</p> <p>Spring and summer diet: qualitative observations of feeding caribou.</p>	
Thomas 1999 Southern Mountain	<p>Terrestrial lichens, primarily <i>Cladonia</i> spp., and <i>Cladonia</i> spp. and lesser amounts of <i>Cetraria</i> spp., <i>Stereocaulon</i> spp., and <i>Peltigera</i> spp., averaged 67-85% of fragments in winter, spring,</p>	<p>Microhistological analysis of plant fragments in fecal samples (N = 127) collected in Jasper National Park, Alberta. Percentage composition of the</p>	

Study/ Caribou Ecotype	Diet	Notes on Methodology	Comments
(Alberta)	<p>and autumn and 34-55% of fragments in summer (June-August)(Thomas 1999).</p> <p>Summer: terrestrial lichens (29 – 55%), graminoids (10 – 26%), and <i>Salix</i> spp. (16 – 45%) dominated fecal samples and their relative importance varied according to month. The percentage of terrestrial lichens declined from June (55%, N = 3) to July (29%, N = 10), <i>Salix</i> spp. increased from June (16%) to July (45%) and usage of graminoids was greatest in August (26%).</p> <p>Winter: Snow accumulation and compaction were suspected to reduce accessibility of ground-level forage and affect diet selection. Statistical comparisons were not conducted; however percentage of terrestrial lichens and <i>Equisetum</i> spp. generally declined from early winter (EW: October – January) to late winter (LW: February – April) (terrestrial lichen: EW = 77 – 83%, LW = 46 – 72%; <i>Equisetum</i> spp.: EW = 2 – 5%, LW = 0 – 3%), whereas, conifers (EW = 3 – 7%, LW = 10 – 18%), <i>Ledum</i> spp. (EW = 3 – 4%, LW = 4 – 16%), and mosses (EW = 2 – 5%, LW = 3 – 18%) increased in percent abundance.</p> <p>Diet during the early winter transition period was influenced by snow accumulation.</p> <p>Caribou shifted to an arboreal lichen – conifer diet (98 – 99% of the diet) during years of rapid snow accumulation and ate myrtle boxwood (65 - 90%), evergreen shrubs (32 – 66%), and other vascular plants during years of slower snow accumulation.</p>	<p>diet reflected relative species abundances among identifiable plants fragments and forbs were suspected to be greatly underestimated in caribou diet due to their high digestibility.</p>	
Rominger and Oldemeyer 1990 Southern mountain		<p>Microhistological analysis of fresh fecal samples. Diet composition was expressed as a percent frequency and converted to a percent relative cover and feces sample sizes ranged between 1 and 12, depending on sampling period.</p> <p>Without any measure of the availability</p>	

Study/ Caribou Ecotype	Diet	Notes on Methodology	Comments
	<p>Their data indicated that caribou shifted to an arboreal lichen diet when snow depths reached 50 cm.</p> <p>Nutritional role of conifer needles was uncertain and authors and speculated that conifer may provide marginally higher protein intake than lichens, depending on digestibility by caribou, or that it may be incidental to the ingestion of arboreal lichens.</p>	<p>of each food item, the data do not provide evidence of their relative selective value or whether or not usage was in proportion to each species' availability.</p>	
Rominger et al. 2000 Southern mountain	<p>Arboreal lichen was a more important dietary component in early autumn than previously reported.</p> <p>Autumn diet: Forested portion of control pens: arboreal lichens 28%, myrtle boxwood < 0.4%. Forested portion of all pens: vascular plants 33% (coolwort foamflower <i>Tiarella trifolia</i>, 23%; rattlesnake plantain <i>Goodyera oblongifolia</i>, 6%; and strawberry bramble <i>Rubus pedatus</i>, 4%).</p> <p>Treatment effect: caribou had a significantly greater dry matter intake rate and crude protein intake rate when in the control pens than when placed in the treatment pens. This was primarily due to increased foraging on arboreal lichens that provided a significantly larger bite than vascular species. Although foraging bite rate did not differ between the two treatments, eating bite rate was greater in the treatment pens and was significantly slower when caribou fed on arboreal lichens than when eating vascular species.</p>	<p>Autumn foraging behaviour of three tame woodland caribou (2 castrate males and one reproductively intact female) in the Selkirk Mountains. Animals were maintained in pens containing natural vegetation features. To determine the influence of lichen bearing windthrown trees and extant myrtle boxwood on the foraging dynamics of woodland caribou, all lichen bearing windthrown trees and extant myrtle boxwood plants were removed from treatment pens (N = 3) and retained in control pens (N = 3). All pens were located such that half of the area was mature climax forest and half was an adjacent clearcut.</p> <p>Autumn diet: expressed as the percentage of the total dry matter intake.</p>	
Edwards and	Summer: diet was diverse and included arboreal	Qualitative descriptions of the diet of	

Study/ Caribou Ecotype	Diet	Notes on Methodology	Comments
Ritcey 1960 Southern mountain	<p>lichens, ground lichens, mosses, sedges, grasses and other seasonally available vascular plants (e.g., slide lily <i>Erythronium graniflorum</i>, <i>Valerina</i> spp., Elephant head <i>Pedicularis groenlandicum</i>).</p> <p>Autumn: observations of feeding on arboreal lichen (36%), myrtle boxwood <i>Pachistima myrsinites</i> (16%) and coolwart foamflower <i>Tiarella trifolia</i> (13%) were most common. Other plants in the diet included bunchberry <i>Cornus canadensis</i>, twinflower <i>Linnaea borealis</i>, horsetail <i>Equisetum arvense</i>, grasses, bracken fern <i>Pteridium aquilinum</i>, ground lichens, sedges, willow <i>Salix</i> spp., and trailing rubus <i>Rubus pedatus</i>.</p> <p>Winter: caribou fed primarily on arboreal lichens (N = 11 of 12 observations) and minimal amounts of myrtle boxwood (N = 1 of 12 observations).</p> <p>Autumn-winter transition: Mean snow depth (32 cm) and snow lift (snow depth – sinking depth = 9 cm) were significantly lower between November 11 – 19 than November 20 – January 6 (Mean snow depth = 143 cm; mean lift = 109 cm).</p> <p>Diet during period of lower snow depth and lift: primarily arboreal lichens (50.8% of feeding sites) and shrubs (29.5%). In all but 1 of the shrub or shrub-combination feeding sites, caribou fed on the evergreen grouseberry (<i>Vaccinium scoparium</i>). Minimal amounts of heather (<i>Cassiope mertensiana</i>, <i>Phyllodoce empetriformis</i>, or <i>P. glanduliflora</i>) were eaten in combination</p>	<p>woodland caribou in Wells Gray Park, British Columbia. No systematic sampling methodology was employed and findings were based on incidental field observations of feeding animals (N = 11 summer (May-August), 70 autumn (October-December), 12 winter (January-April)).</p> <p>Although informative of the inclusion of vascular plants in caribou diet, the data did not permit determination of the relative importance of different plant groups.</p>	
Kinley 2000 Southern mountain	<p>Autumn-winter transition: Mean snow depth (32 cm) and snow lift (snow depth – sinking depth = 9 cm) were significantly lower between November 11 – 19 than November 20 – January 6 (Mean snow depth = 143 cm; mean lift = 109 cm).</p> <p>Diet during period of lower snow depth and lift: primarily arboreal lichens (50.8% of feeding sites) and shrubs (29.5%). In all but 1 of the shrub or shrub-combination feeding sites, caribou fed on the evergreen grouseberry (<i>Vaccinium scoparium</i>). Minimal amounts of heather (<i>Cassiope mertensiana</i>, <i>Phyllodoce empetriformis</i>, or <i>P. glanduliflora</i>) were eaten in combination</p>	<p>Foraging behaviour of woodland caribou in the Southern Purcell Mountains, British Columbia during the autumn-winter transition period.</p> <p>Caribou feeding trails were located using radio-collared caribou (N = 10) and each feeding site (N = 816) was classified based on the plant groups eaten (terrestrial lichen, arboreal lichen, shrubs, forbs, or some combination).</p> <p>Radio-collared caribou occurred in groups and feeding sites were not differentiated according to animal. In</p>	

Study/ Caribou Ecotype	Diet	Notes on Methodology	Comments
	<p>with <i>Cladonia</i> or grouseberry (1% of early period feeding sites).</p> <p>Diet during the later period of greater snow depth and lift: exclusive feeding on arboreal lichens (100% of 426 feeding sites), primarily <i>Bryoria</i> spp.</p>	<p>addition, data for each feeding site did not appear to be pooled according to animal feeding trail or day, suggesting pseudo-replication could potentially be a problem.</p>	
<p>Johnson, Parker, and Heard 2001</p> <p>Southern mountain</p>	<p>Winter: In both alpine and forested habitats caribou selected feeding sites with lower snow depths and greater biomass of lichens. Food abundance and accessibility, in relation to snow accumulation, influenced foraging behaviour and caribou increased usage of arboreal feeding sites as snow accumulation and hardness increased.</p>	<p>Winter foraging behaviour of woodland caribou in British Columbia</p> <p>Measurement of the abundance of lichens and mosses at feeding sites in forested and alpine habitats (Forest - terrestrial sites: N = 206 feeding, 255 random; Forest – arboreal sites: N = 102 feeding, 251 random; Alpine – terrestrial only: N = 70 feeding, 66 random).</p> <p>As no attempts were made to measure the intake of plants other than lichens and mosses, the data do not permit assessment of the relative utilization of vascular plants in winter.</p>	
<p>Terry, McLellan, and Watts 2000</p> <p>Southern mountain</p>	<p>Winter: Biomass of accessible arboreal lichens was significantly greater along foraging paths than along random paths.</p>	<p>Examination of the habitat characteristics along winter foraging paths (N = 23) of woodland caribou in the northern Caribou Mountains, British Columbia.</p> <p>Due to study objectives, the collected data does not permit assessment of the relative importance of different forage items.</p>	
<p>Fischer and Gates 2005</p>	<p>Winter: Feeding craters were dominated by ground lichens</p>	<p>Winter diet of woodland caribou in southwestern Yukon determined from</p>	

Study/ Caribou Ecotype	Diet	Notes on Methodology	Comments
Northern mountain	(58 % of vegetation cover). Fecal analysis: lichens 65.3%, shrubs 6.4%, sedges and rushes 4.5%, forbs 4.1%, grasses 2.9%, mosses 2.7%, and conifer < 1%.	vegetation composition of feeding craters (N = 19) and a microhistological analysis of plant fragments in caribou feces (N = 14).	
Farnell and Gardner 2002 Northern mountain	Winter diet (Chisana herd): lichen 39.7%, moss 38.4%, evergreen shrubs 10.1%, forbs 6.0%, graminoids 3.1 %, horsetails 3.0%, deciduous shrubs 0.7%, and other 0.1%. Other Yukon herds: diet was predominantly lichen (74.94%, SD = 6.22, range = 59.67 - 86.34) and moss (3.57 %, SD = 2.12, range = 1.33 - 8.09) was a minor component of fecal plant fragments. Authors speculated that the high usage of mosses by Chisana caribou may have reflected a limited availability of lichens.	Winter diet composition of the Chisana caribou herd, Yukon determined from microhistological analysis of plant fragments in feces (N = 20 samples collected from the herd range in March of 1994, 1995, 2000, and 2001). Diet composition compared to that of 13 other Yukon woodland caribou herds for which fecal samples (N = 95 samples) were collected between 1981 and 2001 (R. Farnell, unpublished data, cited in Farnell and Gardner 2002).	
Boertje 1984 Barren-ground (Alaska) Included due to relevance to Yukon herds	Spring: deciduous shrubs 45%, lichen 25%, forbs 16%, graminoids 12%, berries 2% Summer: deciduous shrubs 48%, lichen 17%, mushrooms 12%, forbs 10%, graminoids 10%, berries, 2%, evergreen shrubs 1% Autumn: lichen 43%, deciduous shrubs 14%, graminoids 14%, mushrooms 10%, forbs 9%, mosses 5%, berries 3%, evergreen shrubs 2% Winter: lichen 62%, graminoids 11%, mosses 10%, forbs 7%, evergreen shrubs 7%, mushrooms 2%, deciduous shrubs 1%	Combination of fecal analysis (N = 27 samples) and field observations of foraging caribou (N = 190 different days) were used to derive approximate percentages of different foods in the seasonal diets of female caribou (1978 – 1979).	

Arboreal lichens may have heightened importance for caribou inhabiting the high-snowpack ecosystems common in mountainous regions (Rominger and Oldemeyer 1990; Kinley 2000; Rominger et al. 2000; Terry, McLellan, and Watts 2000). Food abundance and accessibility, in relation to snow accumulation, influence foraging behaviour and caribou increase usage of arboreal feeding sites as snow accumulation and hardness increase (Kinley 2000; Johnson, Parker, and Heard 2001). Woodland caribou in the Selkirk Mountains (Rominger and Oldemeyer 1990) and Southern Purcell Mountains (Kinley 2000) of British Columbia (southern mountain population) were found to use a mixed diet of arboreal lichens and vascular shrub species during periods of low snow accumulation and either an arboreal lichen–conifer diet or pure arboreal lichen diet during periods of high snow accumulation. Species of arboreal lichen that are commonly eaten by caribou include *Bryoria* spp., *Alectoria* spp., and *Usnea* spp.

Mountain caribou in Alberta exhibit different seasonal habitat selection patterns than is typical of mountain caribou in British Columbia. In Alberta, mountain caribou spend the summer in alpine areas and migrate to lower elevation mixed conifer forests when snow accumulates in the mountains (Edmonds and Smith 1991; Saher 2005). In contrast to the importance of arboreal lichens as winter forage for mountain caribou in British Columbia, terrestrial lichens are the primary winter food of caribou in Alberta (Thomas 1999; Dzus 2001).

Available studies of caribou foraging behaviour in alpine areas have focused primarily on autumn and winter foraging. Although these studies often suggested the importance of vascular plants during the growing season, no studies were available that provided quantitative assessment of the selective (use versus availability) or nutritional value of forage items in spring or summer. Arboreal lichens are often more abundant on mature trees, and woodland caribou habitat management in British Columbia has focused primarily on the protection of old-growth forests; however, experimental studies were lacking that quantitatively compared the explanatory power of multiple factors that may affect reproductive parameters (e.g., energy or nutrient balance in summer, predation).

Methodology used to identify forage species of ungulates can greatly influence conclusions made about diet content and forage preference. Studies that estimate diet composition of caribou using rumen contents or fecal analysis, without supporting data from esophageal fistula samples or observations of foraging behaviour, should be interpreted with caution. Such methodology may underestimate utilization of easily digestible forage selected by caribou in spring and summer. In addition, plant digestibility may vary among species and decrease during the course of a growing season as fibre content increases (Cote 1998). Bergerud (1964) evaluated the potential bias of rumen food analysis for Newfoundland caribou using captive caribou (N = 4) fed known diets prior to being sacrificed. Ingested plant groups were not proportionally represented in the rumen plant fragments due to differences in their digestibility and deciduous leaves were under-represented. Boertje (1984) compared the dietary intake of a single tame reindeer during feeding trials in Denali National Park, Alaska, to the plant composition of its feces and found that the percent composition of forbs and mushrooms was underestimated and *Salix* spp. and lichens overestimated from the fecal analysis.

Our review of available literature revealed that most studies of diet selection in woodland caribou involved examination of feces or rumen contents or qualitative observations of feeding. In addition to the bias associated with differential digestibility of plant material using rumen or fecal analysis, evidence of utilization does not provide insight into the selective value of different plants. As a result, it is difficult to ascertain whether caribou foraging reflects the availability of food items or selective foraging to maximize, for example, nutrient content or digestibility. White and Trudell (1980) examined the foraging behaviour of reindeer and caribou using a combination of direct field observations, rumen or esophageal fistula samples, as well as quantitative measures of preference (usage relative to availability) of different plant groups. Although lichen dominated the diet of tethered reindeer, they were used in proportion to availability and animals exhibited a strong

preference for deciduous shrubs (*Salix* spp. and *Betula* spp.) and herbaceous dicotyledons. Dicotyledons represented a small proportion of the diet due to their low availability and wide dispersal in foraging areas. Even use/availability studies may not reflect optimal foraging as estimates of selection or preference change as availability changes through range degradation from disturbance or over-grazing by caribou.

In general, winter foraging and habitat selection studies were much more common in the literature than studies that examined summer diet or seasonal patterns in foraging behaviour. This trend likely stems from the general contention that suggests winter is the most limiting season for caribou populations and lichens are a critical food source in winter. This emphasis on winter constraints and diet may undermine progress in understanding woodland caribou nutritional needs and the importance of vascular plants in caribou diet. Although studies that describe the chemical composition of selected forage items (Bergerud 1972; Scotter 1972) provide some general insight into seasonal forage quality, they do not establish the nutritional status of free-ranging caribou populations. We could not find studies that established the seasonal patterns in forage intake, dietary energy intake and nutritional status of wild woodland caribou populations (forest-dwelling or mountain ecotype). Without such information, it is difficult to identify potential interactions between food and reproductive success in woodland caribou that may affect population dynamics.

5.5 Synthesis and Implications

That nutrition can and does have important influences on performance of wild ungulates is well established with a compelling literature collected worldwide on a variety of ungulate species. For any given ecological setting, however, what is not clear is the extent of nutritional limitations, whether or not nutritional limitations are of adequate magnitude to appreciably influence demographics of the herd, the season(s) of influence, what aspects of vegetation across landscapes contribute to limitations, and what can be done to mitigate or alleviate these limitations via habitat management.

Despite the importance of nutrition, development of ecological theory that describes nutrition's role as a key link between habitat and herbivore populations has been slow to develop. To a large degree, the theoretical basis of nutrition's influences is integrated in density dependence theory, i.e., forage "regulates" populations systematically because per capita forage declines as herbivore populations increase and, eventually, herbivore populations achieve equilibrium with forage (Caughley 1976, 1979; Skogland 1991). To a large degree, this theory was built (e.g., see Caughley 1976, 1979; Klein 1968) on observations of several spectacular boom and bust "irruptions" of large ungulate populations following introductions particularly on islands without predators, or in areas where predation and hunting was eliminated (Rasmussen 1941; Leopold 1943; Klein 1968; Caughley 1970). Additional empirical work indicated that effects of density on populations often is not apparent until populations approach "ecological" carrying capacity (Fowler 1987). Does this mean that nutrition is mostly irrelevant except for ungulate populations that are near carrying capacity, and that nutrition is unimportant for herds that are held relatively constant via hunting and/or substantial predation?

The boom and bust cycles following "release" of herbivore populations occurred in relatively unusual situations, and population theory built on these occurrences may incompletely describe nutrition's influences. Cook (2002) and Cook et al. (2004) argued nutrition's influences often are subtle, multifaceted, and include "limiting" (Skogland 1991) effects on populations (i.e., processes that normally operate more or less independently of density). For example, where nutrition is marginally inadequate, it may affect by only a few percentage points *each* of a host of performance attributes (e.g., ovulation rates, embryonic/fetal survival rates, neonatal survival, juvenile winter survival, age at first breeding, adult winter survival, and susceptibility to predation). Yet, the cumulative nutrition effect across all might be a reduction in net productivity of the herd 20-30%, without affecting any individual attribute enough to be detectable in light of our ability (or inability) to measure these

precisely in natural settings. Effects of predation or hunting, in contrast, are obvious and relatively easy to measure. Limiting effects of nutrition probably vary temporally as a function of secondary succession patterns (Hett et al. 1978; Gill et al. 1996; Peek et al. 2001; Peek, Dennis, and Hershey 2002) and spatially over broad areas as a function of winter severity, precipitation, soils, and so forth (Verme 1977; Cook 2002).

There also is a widespread perception that nutritional limitations, when they occur, operate primarily in winter (Wallmo et al. 1977; Lyon 1980; Nelson and Leege 1982; Coughenour and Singer 1996; Unsworth et al. 1998). This clearly is inconsistent with a substantial empirical record as reviewed above. Of course, forage conditions normally are at their best in late spring through early to mid-summer, but females with a calf at heel, particularly if they are compensating from weight loss the previous winter, require abundant and very high quality forage over most of summer and early autumn. In some ecosystems, summer forage may satisfy these needs, but in others, it evidently does not (Cook 2002, p. 324). The debate of summer versus winter may be naïve and trivial in some respects, however, because forage conditions in winter and summer probably interactively affect herbivore populations, and because the relative influence of either probably varies from one setting to another, depending on winter severity, precipitation regimes, and other environmental factors. Certainly, the further north, the harsher and longer the winters, and the more likely it is that winters exert an overbearing influence on ungulate survival. Even so, the harsher and longer the winters, the more important it is that summer forage adequately provide for rapid growth of young and recovery from winter weight loss.

Much still is unknown about how nutrition influences ungulate populations, and thus there is substantial need for more work in this arena. However, unambiguously documenting the magnitude, extent, mode, and seasons of nutrition's influences on wild herds presents considerable challenges to wildlife biologists. It is not an objective of this document to review in detail field methods (see Schwartz and Hobbs 1985; Hobbs and Swift 1985; Harder and Kirkpatrick 1994; Haufler and Servello 1994; Cook 2002), but we highlight the following.

Documenting nutrition's influences has usually included two approaches: monitoring the animals themselves or monitoring the vegetation on which they depend. The former typically involves collecting data of performance attributes (e.g., pregnancy status, nutritional condition, and so on) as described in this review; however, the effectiveness of these data is mixed due to uncertainty as to

- (1) normal performance when nutrition is not limiting (i.e., need standards for comparison);
- (2) what performance attributes best provide insights of nutrition's influence;
- (3) how performance attributes measured in one season or year are affected by nutritional influences in previous seasons or years; and
- (4) how nutrition's influences are masked by other factors (Gerhart et al. 1997b).

Additionally, animal performance data alone usually will not provide precise information of what habitat attributes specifically are responsible for observed nutritional influences. Vegetation evaluations (e.g., Schwartz and Hobbs 1985), on the other hand, have potential to provide more insights of what habitat attributes affect animal performance via nutritional pathways. Standard evaluations of vegetation typically include estimates of forage biomass and, occasionally, estimates of forage quality, such as digestible energy, protein, or mineral content. Effectiveness of these data types for identifying nutrition's influence on populations suffers for several reasons:

- (1) nutritional requirements in units of concentration in forage may not be known with sufficient accuracy for reliable evaluations of forage adequacy;
- (2) forage quality levels particularly across temporally and spatially heterogeneous landscape may not be related to forage quality of diets because herbivores have considerable ability to select among habitats and plants within habitats to obtain nutritious food (Coughenour and Singer 1996; Hobbs 2003);
- (3) explicit relations between forage attributes (amount, distribution, and structure) and how much food animals can consume each day, relative to how much they need, is poorly understood; and
- (4) it is not clear how to reconcile the interplay of time periods of nutritional excess and nutritional deficiencies based only on forage quality and quantity data. For example, Cook (1989) calculated nutrition-based carrying capacity (Hobbs and Swift 1985) for bighorn sheep for early summer to be several orders of magnitude greater than the number of sheep actually present, but found that carrying capacity in late summer fell to zero, because no food was present that satisfied requirement. It is therefore difficult to define “carrying capacity” of this summer range.

Our review identifies a compelling body of information that identifies nutrition’s practical relevance to ungulates. Parker et al. (1999) noted that nutrient requirements, foraging and digestive efficiencies, and forage characteristics provide quantifiable cause-and-effect relations that influence animal body condition, growth and annual body mass dynamics, and ultimately, reproduction and survival. We concur with their conclusion that nutritional ecology offers a quantitative, general and predictive basis for scaling-up key relations between individual animals and their habitats to populations across landscapes. Unfortunately, the science needed to accurately measure, monitor, and effectively manage nutritional resources for the benefit of large ungulates has been slow to develop, and additional development of the nutritional science explicitly for free-ranging ungulates is in order (specific recommendations are presented near the end of this review).

6.0 DOES FORAGE AVAILABILITY LIMIT CARIBOU POPULATIONS?

In this paper, we define a limiting factor as anything that reduces the rate of population growth in caribou. Female reproductive success of many polygamous ungulates is limited by the ability of females to acquire adequate food resources for lactation and calf development (Clutton-Brock, Albon, and Guinness 1989). Limiting factors may be responsible for population regulation if they have a density-dependent effect on population growth rate (Messier 1991). In populations controlled by density-dependent factors (e.g., disease, competition, predation), growth rates are usually inversely proportional to population density. For example, if a population is dense and animals live close together, intraspecific competition for food may be heightened. Factors that depress reproductive success or increase mortality are limiting; however, only density-dependent factors are regulating.

Many ungulate populations are capable of over-exploiting forage resources and thus becoming limited by shortages in food supply (Skogland 1986). Food limitation has been reported for a variety of ungulates including white-tailed deer *Odocoileus virginianus* (Teer, Thomas, and Walker 1965), moose (Messier 1991), elk *Cervus elaphus* (Sauer and Boyce 1983), red deer *C. e. scoticus* (Clutton-Brock, Guinness, and Albon 1982), and wild reindeer *Rangifer tarandus* (Skogland 1986).

Identification of limiting factors that may regulate caribou populations requires an understanding of the processes involved (Ouellet, Ferron, and Sirois 1996), including knowledge of predation rates, range condition, and forage requirements. Predation is expected to exert a powerful influence on prey

populations over evolutionary time (Lima and Dill 1990). This may be particularly important for prey populations that incur high neonatal losses due to predation, such as caribou (Adams, Dale, and Mech 1995). However, even if a prey population is regulated by predation, range quality and competition for food may affect individual growth rate, nutritional condition, pregnancy rate, and survivorship (Ouellet, Ferron, and Sirois 1996). In addition, the level of primary production in a system may determine the number of trophic levels, community structure, and the influence of top-down factors (Oksanen et al. 1981; Gratton and Denno 2003).

6.1 Top-Down Forces

Top-down forces exhibit a strong influence on caribou trophic interactions and there is a general perception among caribou biologists that predation is the primary limiting factor for woodland caribou, particularly where caribou are sedentary and predators can feed on multiple ungulate prey species (Bergerud and Elliot 1986; Edmonds 1988; Rettie and Messier 1998; Hayes et al. 2003; see Table 6.1 for detailed description of studies). Predation was the dominant cause of adult woodland caribou mortality in most studies that we examined where large carnivores were present (Edmonds 1988; Rettie and Messier 1998; Schaefer et al. 1999; Kinley and Apps 2001; Sebbanne et al. 2002; McLoughlin et al. 2003; Wittmer et al. 2005). Data on causes of calf mortality were scarce in the literature but predation was implicated as an important cause of low recruitment and/or population decline (Crête and Desrosiers 1995; Rettie and Messier 1998; McLoughlin et al. 2003). Bergerud (1971b) found that natural mortality of adults was a minor factor in affecting population growth rate in Newfoundland, where wolves were absent; however, predation on calves by lynx and bears, as well as disease transmission (*Pasteurella multocida*) by lynx during failed predation attempts, were important causes of calf mortality for Newfoundland populations (Bergerud 1971b; Mahoney and Virgl 2003). Coyote predation on calves was suspected to be an important cause of low recruitment in the declining woodland caribou population on the Gaspé Peninsula (Crête and Desrosiers 1995). Lambert et al. (2006) reported that predation (black bear and wolf) appeared to be an important cause of calf mortality for a woodland caribou herd in Charlevoix, Quebec (boreal population). Neonatal mortality rate, based on marked fawns, was 57% (N=14) and 5 died from predation within days or weeks of birth. Adams, Dale, and Mech (1995) found that wolves accounted for 42% of deaths of radio-collared neonate caribou and were the most important cause of death during a five-year study in Denali National Park, Alaska.

Studies of caribou response to experimental reduction of wolves demonstrate the importance of predation to caribou demography. Bergerud and Elliot (1986) conducted an experimental manipulation of wolf abundance to measure the impact of predation on population dynamics of three woodland caribou herds in northern British Columbia (northern mountain population). Two populations inhabited areas where wolf densities ranged between 9-10 wolves/1 000 km² and exhibited population declines ($\lambda = 0.88, 0.89$). Wolves were reduced for another population from 10 to 1-4/km² and these caribou increased ($\lambda = 1.06$) during years when wolves were reduced. Percentage of calves at 5 months increased from 6% prior to wolf removal (1977) to 16-17% after removal (1978-80) and declined again to < 5% following wolf recovery (1982). Percentage of calves in the control populations ranged from 10-13% during the same years. Wolf densities were similar each year on all three ranges before wolf reduction on the treatment range (5.2-11.2 per 1 000 km²), but were 62-86% lower on the treatment range (0.8-3.8 per 1 000 km²) following wolf reductions.

Hayes et al. (2003) examined the effects of wolf reduction on one of three woodland caribou herd ranges in Yukon (northern mountain population) and found that wolf predation strongly limited recruitment of caribou, but adult survival did not improve when wolf numbers were reduced. The combination of reduced hunting and reduced predation by wolves was concluded to be the primary factor causing the increase in the treatment herd of caribou. There were no apparent trends in caribou herd population parameters and snow depth or snowmelt phenology. Winter forage quality was

assumed to be adequate based on the observation that caribou fecal samples in winter indicated that lichen, the preferred winter food, constituted 53–84% of the diet. These data were not sufficient to adequately assess winter nutrition in relation to caribou density and forage availability, nor did they address potential affects of summer nutrition on calf survival and other population processes. Crête and Desrosiers (1995) determined that autumn calf:cow ratio on the Gaspésie Peninsula declined from approximately 20-30 calves per 100 females (1984-1985) to only four (1987) after coyotes colonized the area. Predators were reduced in the park and surrounding areas between 1990 and 1992 and recruitment increased to 42 calves per 100 females in 1994 (Ouellet, Ferron, and Sirois 1996).

Table 6.1 Summary of Selected Studies That Described Limiting Factors of Woodland Caribou Populations

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
Mahoney and Virgl 2003 Newfound- land (Island)	Limiting factors inferred from causes of mortality: predation, accidents, malnutrition, unknown	present: black bears lynx	Undetermine d (potentially predation)	Pop. Status: stable Pop. Growth rate: $r_s = -0.01$ ± 0.06 Calf recruitment: Calf:cow ratio 0.24 ± 0.02 Percentage of calves 13 % Adult survival rate: 0.87 Mean pregnancy rate: 96% Cause of mortality: predation 33%, disease 20%, unknown causes 40%	Radio telemetry: N = 24 adult caribou (17 females: 7 males) and 46 calves. Population size and trend: radio telemetry, aerial survey and mark-re-capture. Pregnancy rates and recruitment (to 10 months in age): direct observations (e.g. calf-at-heel, distended udder) Survival/rate of increase: based on radio-collared animals Causes of mortality: examination of collared animal remains (e.g. nutritional condition) (N = 15 calves) Nutrient supply/demand was not measured. Lack of data on black bear density prohibited conclusive evidence of predator limitation. 60 % of calf mortalities were from unknown causes or infection – methodology did not permit evaluation of interactions among nutritional status and susceptibility to other causes of mortality (e.g., predation, disease).
Bergerud 1971a,b Newfound- land (Island)	Limiting factors inferred from causes of mortality: social interactions, senility, accidents, predation, disease, parasites, forage	present: black bears, lynx	Predation and disease: combination of lynx predation and <i>Pasteurella</i> <i>multocida</i> infection transmitted by lynx	Pop. Status: stable to increasing Pop. Growth rate: Interior herd $r = 0.03$ Avalon herd $r = 0.12$ Calf recruitment: Percentage of calves 13%, N = 12494	Population size and trend: aerial and ground survey (1957-67). Pregnancy rates and recruitment (to 6 months in age): direct observations (e.g. calf-at-heel, distended udder) Survival/rate of increase: based on aerial census and population trends, no error estimates available Causes of mortality: examination of animal remains (N =

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
	abundance on winter ranges			<p>Mean pregnancy rate: Females ≥ 2 years in age 84.5% Females ≥ 3 years in age 94%</p> <p>Mortality rate: Interior herd 5% Avalon herd 6%</p> <p>Cause of mortality (% of known mortalities): Adult-female: primarily aberrant birth 50%</p> <p>Adult-male: aggressive interactions during rut 71%</p> <p>Calf-female: primarily disease <i>Pasteurella multocida</i> 68%</p> <p>Calf-male: primarily disease <i>Pasteurella multocida</i> 78%</p>	<p>111, 12 adult females, 21 adult males, 40 female calves, 38 male calves.</p> <p>No data available on the nutritional status of populations.</p> <p>Forage abundance on winter range: assessed from vegetation surveys (N = 22) across herd winter ranges.</p>
Crête and Desrosiers 1995 Atlantic (Gaspésie)	Limiting factors inferred from population parameters, mortality factors, and evidence of disease	Present: black bear, lynx, coyote	Predation on calves	<p>Pop. Status: decline</p> <p>Parturition rate: Mont Albert 56% 1988 100% 1990 Mont Jacques-Cartier 80% 1988 86% 1990</p>	<p>Adult survival/rate of increase: based on radio-collared female caribou (N = 20 \geq 1 year in age) and aerial inventories in autumn (1987-1992).</p> <p>Parturition rate: observations of percentage of females with a calf at heel during calving time for adult females (radio-collared: 1990, N = 11 on Mont Albert and 7 on Mont Jacques-Cartier; and uncollared: 1988, N = 9 on Mont Albert and 10 on Mont Jacques-Cartier).</p>

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
Schaefer et al. 1999 Boreal	Limiting factors inferred from population parameters	Present: wolves and black bears	Predation and emigration to the migratory George River Herd	<p>Calf recruitment: Calf:cow ratio 0.20-0.30 1984/85 0.04 1987 0.42 1994</p> <p>Percentage of calves 17.6% 1953-1983 4.5% 1984-1989 13.4% 1990-1992</p> <p>Adult survival rate: 0.92-0.93</p> <p>Cause of mortality: Calves Coyotes 7 Black bears 3 Golden eagle 1</p> <p>Adults Avalanche 1 Falling off cliff 1 Unknown natural cause 1 Coyote 2 potential scavenging</p> <p>Diseases that might affect fecundity were not detected.</p> <p>Pop. Status: Early period: stable Late period: decline</p> <p>Pop. Growth rate: Later period: $r = -0.134$</p>	<p>Calf recruitment (in autumn): aerial surveys in autumn. Samples sizes for percentage of calves in the population during aerial inventories in autumn (1953-1983, N = 1573, prior to the arrival of coyotes; 1984-1989, N = 1652, following colonization by coyotes; 1990-1992, N = 372, following implementation of a recovery plan that included predator reduction)</p> <p>Causes of mortality: examination of collared animal remains (N = 11 calves). Five deaths could not be attributed to a cause either because of insufficient remains or lack of distinguishing signs. Post-kill examination of remains does not rule-out the possibility of scavenging by coyotes, rather than kill.</p> <p>Evidence of disease: examination of blood samples and vaginal swabs taken from females (N = 20) in November.</p> <p>Adult survival (> 1 year-old females): based on 49 radio-collared females during early period (1981-88) and 36 radio-collared females during the late period (1993-97).</p> <p>Calf recruitment: aerial surveys of collared animals from March-April during 8 years (1981, 1983, 1984, 1987,</p>

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
				<p>Calf recruitment: Significantly lower during late period than early period.</p> <p>Percentage of calves Early period 18.5 ± 1.2 Late period 8.9 ± 2.4</p> <p>Calf:cow ratio Early period 0.38 ± 0.05 Late period 0.17 ± 0.04</p> <p>Adult survival rate: Early period 0.80 ± 0.05 Late period 0.70 ± 0.05</p> <p>Parturition rate: Early period 74.2 ± 7.78 Late period 71.0 ± 6.46</p> <p>Causes of mortality: Early period (18 deaths): wolf 11, black bear 6, unknown predator 1 Late period (12 deaths): wolf 8, black bear 1, harvest 3</p> <p>Emigration: Early period none Late period 5 of 36 radio-collared females</p> <p>Total winter snowfall did not differ significantly</p>	<p>1994-97).</p> <p>Parturition: mean calves/100 females based on observation of a calf with radio-collared females during aerial surveys in mid-June during 9 years (1982-84, 1987, 1988, 1994-97).</p> <p>Rate of increase: survival-fecundity rate of increase (r)</p> <p>Causes of adult (> 1 year-old females) mortality: Examination of collared animal remains.</p> <p>Information on causes of calf mortality were unavailable</p> <p>The absence of nutritional factors in the population decline was attributed to the relative consistency of pregnancy and parturition rates.</p>

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
<p>Jolicoeur, Courtois, and Lefort 2005</p> <p>Sebbanne et al. 2002</p> <p>Boreal</p>	<p>Limiting factors inferred from causes of mortality: social interactions, senility, accidents, predation, disease, parasites</p>	<p>present: wolves, black bears</p>	<p>predation</p>	<p>between early and late periods</p> <p>Pop. Status: 1980s increase 1992-01 decline</p> <p>Pop. Growth rate: 1980s unavailable 1998-01 finite rate of increase = 0.82</p> <p>Calf recruitment: Calf:cow ratio 1980's = 0.26-0.79 1990's = 0.19-0.27 2000-01 = 0.36-0.77</p> <p>Percentage of calves 1980s 13-32 % 1990s 11-16 % 2000-01 20-29 %</p> <p>Adult survival rate: 1977-82 = 0.87 ± 0.09 – 0.95 ± 0.05 1998-01 = 0.69 ± 0.07</p> <p>Pregnancy rate: 1999 100%</p> <p>Mean birth rate: 1978-82 = 83%</p> <p>Cause of mortality: 1977-82:</p>	<p>Recruitment (to 11 months in age): annual estimates N = 46-126, 1979-01)</p> <p>Pregnancy rate: blood test (pregnancy-specific protein B) for 28 females from samples taken in January-March (1998-99, Sebbanne et al. 2002).</p> <p>Birth rates: annual estimates N = 6-10, 1978-1982 from direct observations (e.g. calf-at-heel) for adult females (> 2.5 years old)</p> <p>Adult survival/rate of increase: based on radio-collared animals (≥ 1 year in age), multi-year estimates of adult survival (1977-1982), adult female survival (1998-01).</p> <p>Causes of mortality: examination of collared animal remains (N = 7 mortalities 1977-82, N = 16 1999-01)</p> <p>Nutritional status was inferred from blood parameters and examination of femur marrow fat percentages.</p> <p>Evidence of disease was determined from blood samples and examination of fecal matter for parasites.</p>

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
Courtis 2003 Boreal	Limiting factors inferred from population parameters and availability of terrestrial lichen	present: wolves, black bears, human hunters	Predation and hunting	<p>predation 2 poaching 2 conflict during rut 1 capture-related 2 1999-01: predation 10 malnutrition 2 capture-related 2 fall from cliff 1 birth complication 1</p> <p>Pop. Status: Herd26 decline Herd12 stable Herd42 stable</p> <p>Pop. Growth rate: Herd26 $\lambda = 0.95$ Herd12 $\lambda = 0.99$ Herd42 $\lambda = 1.02$</p> <p>Calf recruitment: 1999 Calf:cow ratio Herd26 0.21 ± 0.03 Herd12 0.33 ± 0.05 Herd42 0.38 ± 0.06</p> <p>Percentage of calves Herd26 $11.9 \% \pm 1.9\%$ Herd12 $16.0 \% \pm 2.5\%$ Herd42 $20.2 \% \pm 3.8\%$</p> <p>2000 Calf:cow ratio</p>	<p>Adult female survival/finite rate of increase: based on mortality of radio-collared animals and aerial census of calf:cow ratios in March.</p> <p>Recruitment (to 10 months in age): aerial surveys of collared females in March 1999, 2000, 2001</p> <p>Causes of mortality: examination of collared animal remains (N = 23 mortalities of 68 radio-collared females)</p> <p>Although 61 % of mortalities were due to predation or hunting, cause of the remaining 39 % of mortalities was unknown and does not rule-out the potential importance of nutrition.</p>

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
Simkin 1965 Boreal	Limiting factors inferred from population parameters, spurious observations of cause of death (disease and wolf kill) as reported by hunters, and food carrying capacity	Present: wolves, black bears, lynx		<p>Herd26 0.50 Herd12 0.31 Herd42 0.50</p> <p>2001 Calf:cow ratio Herd26 0.65 Herd12 0.33 Herd42 0.35</p> <p>Adult survival rate: Herd26 0.87 ± 0.05 Herd12 0.80 ± 0.06 Herd42 0.81 ± 0.06</p> <p>Cause of mortality: predation 7 hunting 6 natural cause (unknown) 5 poaching 1 unknown cause 4</p>	<p>Calf recruitment (to 10-11 months in age): systematic aerial inventory in winter (1960 – 1964, 28 072 miles of transect for a total sampling area of 114 723 square miles (total no. caribou observed N = 1103 all aerial surveys, 45 Kapuskasing, 6 Geraldton). Calf:cow ratios and % calves for the Irregular Lake area of northwestern Ontario were from spring and summer ground surveys (May to September) and are not accurate reflections of parturition rate or recruitment (N = 88 caribou).</p> <p>Details were unavailable as to how lichen-based carrying capacities were estimated in relation to caribou intake</p>
				<p>Calf recruitment: Mean percentage of calves (all ecotypes) 16.7% Woodland caribou Kapuskasing 6.67% Geraldton 16.67%</p> <p>Northwestern Ontario-Irregular Lake Percentage of calves 35.2% Calf:cow ratio 0.86</p>	

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
	estimated from availability of terrestrial lichen				requirements. Inaccuracies in caribou density estimates for forested areas make estimation of food carrying capacity tenuous. Methodology does not permit conclusions as to limiting factors
Cringan 1957 Boreal	Forage abundance	absent	Availability of lichens and late seral forests	Selective use of lichens	Forage utilization: use relative to availability of shrubs (N = 495 plots) and lichens (sample size unknown). The critical importance of lichens is inferred from its heavy utilization by caribou, the slow growth potential of lichens, and their greater abundance in mature conifer forests. This evidence does not substantiate the critical importance of lichens. The importance of summer diet in caribou energetics and reproduction was not measured.
Rettie and Messier 1998 Boreal	Limiting factors inferred from population parameters and mortality factors	present: wolves, coyotes, black bears, lynx	Proximal: predation Ultimate: habitat alteration	Pop. Status: stable Pop. Growth rate: $r_s = -0.05 \pm 0.06$ Calf recruitment: Calf:cow ratio 0.28 Adult survival rate: 0.84 ± 0.05 Pregnancy rate: $94 \% \pm 3\%$ Birth rate: $86 \% \pm 7\%$ Cause of mortality: predation 6	Adult survival/rate of increase: based on radio-collared female caribou and aerial surveys in March (1993-1996), pooled data among five populations. Recruitment (to 10 months in age): pooled data for aerial surveys of collared females in March, 1994-1996 Pregnancy rate: serum progesterone levels of adult females (N = 51) sampled in March (1992-1995) Birth rate: aerial surveys of radio-collared females (N = 28 pregnant females) in May (14-25 May in 1992, 23-25 May in 1993 and 1994) and July and August (1993 and 1994). Causes of mortality: examination of collared animal remains (N = 8)

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
McLoughlin et al. 2003 Boreal	Limiting factors inferred from population parameters and mortality factors	present: wolves, bears	Proximal: predation Ultimate: habitat alteration	other causes 2 Pop. Status: stable in 2 ranges decline in 4 ranges Pop. Growth rate: 4 declining: $\lambda = 0.955-0.976$ 2 stable: $\lambda = 0.991-1.010$ Pregnancy rate: 90-100% Birth rate: 70-95% Calf recruitment: Calf:cow ratio 0.11-0.23 among all ranges Adult survival rate: 0.86-0.93 among all ranges Cause of mortality: predation 58 natural causes 5 hunting/poaching 9 suspected human cause 8 unknown 32 Status: decline Calf recruitment: Percentage of calves 12%	Concluded adult mortality was similar to that of increasing populations under natural mortality. Adult mortality may not be sufficient to explain the lack of increase in populations. Demography of populations inhabiting 6 ranges from 1993 to 2002 Adult survival/finite rate of increase: based on monthly aerial monitoring of radio-collared female caribou (1993-02) for 6 herd ranges. Pregnancy rate: serum samples from 5 population ranges (N = 93) Birth rate: observations of radio-collared females with calves (April-June). Calf recruitment: aerial surveys in March of radio-collared females, calves per 100 females. Causes of mortality: examination of collared animal remains (N = 112)
Fuller and Keith 1981 boreal	Not assessed	present: wolves low in abundance	Not determined	Calf recruitment: overall mean of monthly estimates from incidental observations during flights to locate radio-collared caribou during fall and winter (1976-1978) (N = 280 caribou in total). Calf mortality based on	

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
				<p>Percentage of yearlings among captured animals 14%</p> <p>Calf survival rates 42% mid May-mid June 67% July-February 25% estimated 1st-year annual survival</p> <p>Adult mortality: 15%</p>	<p>observations of calves with radio-collared mothers</p> <p>Calf survival: estimates are tenuous due to low sample sizes of collared animals and estimation for periods lacking empirical data.</p> <p>Low samples sizes of collared animals and data insufficiency prohibited accurate assessment of pregnancy or parturition rates.</p> <p>Adult mortality rate: percentage of adult radio-collared caribou that died, 1976-77 (N = 27).</p> <p>Causes of calf mortality were unknown.</p>
Kinley and Apps 2001 Southern Mountain	Limiting factors inferred from population parameters and mortality factors	present: coyotes, wolves, grizzly bears, black bears, cougars	Predation on adults and forest alteration and fragmentation	<p>Pop. Status: decline</p> <p>Pop. Growth rate: $\lambda = 0.62 - 0.88$</p> <p>Calf recruitment: Calf:cow ratio 0.05 ± 0.05</p> <p>Adult mortality: 0.24 ± 0.19</p> <p>Adult mortality was significantly greater for females than males, and for caribou in the southern zone than northern zone. The southern zone had significantly greater road density, proportion of disturbed habitats and fragmentation.</p>	<p>Adult survival/finite rate of increase: annual mean based on radio-collared caribou (N = 8-15) and aerial surveys in March or April (1994-1998, 2000).</p> <p>Calf recruitment (to 10-11 months in age): annual mean based on aerial surveys of collared caribou in March or April, 1994-1998, 2000</p> <p>Causes of adult mortality: examination of collared animal remains (N = 16)</p> <p>Reasons for low calf recruitment were unknown.</p>

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
Edmonds 1988 Boreal Southern Mountain	Limiting factors inferred from population parameters and mortality factors	present: coyotes, wolves, grizzly bears, black bears, cougars	predation	<p>Causes of mortality: Cougars 6 Bears 2 Wolverine 1 Vehicle 1 Shooting 1 Fall 1 Unknown 4</p> <p>Pop. Status: decline (both ecotypes)</p> <p>Calf recruitment: Southern Mountain Calf:cow ratio 0.27 Percentage of calves 15%</p> <p>Adult survival rate: 78% (both ecotypes)</p> <p>Cause of mortality: Wolf predation 6 Bears 2 Unknown carnivore 1 Coyotes (potential carrion) 1 Human kill 1 Vehicle collision 1</p>	<p>Population status: inferred from low population size estimates during study (counts during collared animal aerial surveys and late winter surveys of winter range: Mountain caribou ~ 183, woodland caribou ~ 50 -75)</p> <p>Population range areas were 11 000 km² (mountain caribou) and 4000 km² (woodland caribou)</p> <p>Recruitment (to 5 months in age): pooled data for aerial surveys of collared caribou (N = 2 subadult and 10 adult females, 1 calf, 9 subadult and 2 adult males) in October, 1981-1986</p> <p>Adult survival: based on radio-collared caribou (1981-1986)</p> <p>Causes of mortality: examination of collared animal remains (N = 12, mountain and boreal populations)</p>
Wittmer et al. 2005a, b Southern and	Limiting factors inferred from causes of mortality and spatial patterns	present: grizzly bear, black bear, wolverine, wolf, cougar	Proximate: Predation on adult caribou Ultimate:	<p>Pop. Status: decline</p> <p>Pop. Growth rate: finite rate of increase $\lambda =$ 0.92</p>	<p>Population size and trend: aerial census and radio telemetry (N = 386 adult caribou from 17 subpopulations: 338 females, 48 males).</p> <p>Pregnancy rate: serum progesterone levels from 134 adult</p>

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
Northern Mountain	of population dynamics		forest alteration, colonization of alternate prey, and predator management policies	<p>Calf recruitment: Percentage of calves 11.57 % ± 1.5 %</p> <p>Adult survival rate: 0.55 ± 0.10 – 0.96 ± 0.03</p> <p>Mean pregnancy rate: 92.1 % ± 2.24 %</p> <p>Cause of mortality: Human induced: 4%</p> <p>Natural mortality: 59%</p> <p>Of known causes N = 98: Predators 68%, accidents 21%, poor nutritional condition 11%</p> <p>Unknown cause: 37 %</p>	<p>females (> 2.5 years old) sampled in March (1984-1997)</p> <p>Recruitment (to 10 months in age): aerial census of calves in March</p> <p>Adult survival/rate of increase: based on radio-collared animals and aerial census, multi-year estimates of adult female survival for 10 subpopulations (1984-2004)</p> <p>Causes of mortality: examination of collared animal remains (N = 165 mortalities from 15 subpopulations, 1984-2004)</p> <p>No data available on the nutritional status of populations or causes of calf mortality.</p> <p>High pregnancy rates, low calf recruitment rates, and high adult mortality (primarily from predation) were concluded to support the predator limitation hypothesis; however nutrient supply/demand was not measured. The use of pregnancy rate to contrast the alternative hypotheses is problematic. As summer nutrition is an important determinant of pregnancy rate and winter nutrition may be more influential in parturition rates and calving dates (Skogland 1983, Couturier et al. 1990, Cameron et al. 1993), a herd may be nutritionally stressed in winter and still have high pregnancy rates. Non-lactating females are generally high in herds that have low rates of neonatal survival and consequently, pregnancy rates are usually high (Skogland 1991, Gerhart et al. 1997b).</p> <p>Experimental manipulation of wolf abundance to measure impact of predation on population dynamics.</p>
Bergerud and Elliot 1986	Limiting factors inferred from population	present: wolves, grizzly bears	predation	Status: decline Pop. Growth rate (1977-	

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
Northern mountain	parameters and manipulation of wolf densities			<p>1982): Spatsizi-Lawyers $\lambda = 0.88$ Level Mtn. $\lambda = 0.89$ Horseranch $\lambda = 1.06$</p> <p>Wolf densities were similar each year on all three ranges before wolf reduction on the Horseranch range (5.2-11.2 per 1000km², depending on year), but were 62 to 86% lower on the Horseranch range (0.8-3.8 per 1000km²) following wolf reductions.</p> <p>Parturition rate in unperturbed populations (Spatsizi-Lawyers and Level Mtn.): Mean calf:cow ratio 0.84 (N = 896)</p> <p>Calf recruitment: Horseranch Percentage of calves: 6% in 1977, prior to wolf removal; 16-17% (1978-80), after removal; < 5% (1982), following wolf recovery. Spatsizi-Lawyers and Level Mtn. Mean percentage of calves ranged from 10-13%</p>	<p>Removal of wolves: Wolves were reduced through intensive harvesting (1978-1981) on the Horseranch range to monitor the impact on calf survival and herd growth. Two other herd ranges were used as controls (Spatsizi-Lawyers and Level Mtn.) without wolf reductions.</p> <p>Census of caribou: aerial surveys on alpine breeding ranges in September and October</p> <p>Census of wolves: aerial surveys in January or March along travel corridors and water courses frequented by wolves.</p> <p>Caribou demographic parameters: aerial and ground surveys</p> <p>Parturition rates: evidence of distended udders during aerial and ground surveys in June</p> <p>Recruitment: aerial surveys in autumn</p> <p>Rate of increase/natural mortality: estimated from census data, finite rate of increase (λ)</p>
Hayes et al.	Limiting factors	present:	predation	Status:	Experimental manipulation of wolf abundance to

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
2003 Northern mountain	inferred from population parameters and manipulation of wolf densities	wolves, brown bears and black bears		<p>Aishihik (1990-1998) pre-treatment decline treatment stable to increasing Ibex (1990-98) increasing Chisana (1987-98) decline Wolf Lake (1987-98) increasing to stable</p> <p>Pop. Growth rate: Aishihik (1990-1998) pre-treatment λ unavailable treatment $\lambda = 0.98-1.15$ Ibex (1990-98) $\lambda = 1.14$ Chisana(1987-98) pre-treatment $\lambda = 0.93$ treatment $\lambda = 0.89$ Wolf Lake (1987-98) pre-treatment $\lambda = 1.11$ treatment $\lambda = 1.00$</p> <p>Pregnancy rate: Aishihik (1991-1996) pre-treatment 96-100% treatment 88-100% Ibex (1995) 100% Chisana(1993-1995)50-95% Wolf Lake (1993, 1995- 1996) 86-100%</p> <p>Calf recruitment: Calf:cow ratios Aishihik pre-treatment 0.15 ± 0.09 treatment 0.42 ± 0.04</p>	<p>measure impact of predation on population dynamics.</p> <p>Removal of wolves: Wolves were reduced through intensive harvesting (1993-1997) on the Aishihik range to monitor the impact on caribou calf survival and herd growth. Three other herd ranges were used as controls (Wolf Lake, Ibex, Chisana) without wolf reductions.</p> <p>Abundance of wolves: aerial surveys January-March 1992-1998 using radio telemetry and aerial snow-track methods.</p> <p>Abundance of caribou/rate of increase/rate of increase: total counts and stratified random block sampling during aerial surveys, finite rate of increase (λ)</p> <p>Pregnancy rate: Blood progesterone, samples collected between December 10 and April 3 from cows in each herd (N = 216 in total). Presence of calves or distended udders during surveys in May on the Chisana range.</p> <p>Adult survival: based on radio-collared animals (N = 81 Aishihik caribou (1991-92 pre-treatment, 1993-97 treatment), 59 Wolf Lake caribou (1993-1997), and 84 Chisana caribou (1989-1997)</p> <p>Calf recruitment: aerial surveys in October using radio-collared animals and sampling of 28-100 % of each herd.</p> <p>Forage quality: measured as the relative diet composition of important foods as estimated from fecal pellet samples (N = 20 per herd) collected in February or March.</p> <p>Snow accumulation: Environment Canada snow depth data and assumed thresholds of 55 cm as minimum snow</p>

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
				<p>Ibex pre-treatment 0.56 ± 0.07 treatment 0.44 ± 0.08 Chisana pre-treatment 0.04 ± 0.04 treatment 0.07 ± 0.04</p> <p>Adult survival: Aishihik pre-treatment 0.52-0.94 treatment 0.86-0.94 Chisana 0.65-0.94 Wolf Lake 0.74-0.98</p> <p>Forage quality (percentage of lichens in diet): Aishihik $80\% \pm 12\%$ Ibex $84\% \pm 4\%$ Chisana $53\% \pm 2\%$ Wolf Lake $70\% \pm 7\%$</p> <p>Snow accumulation: No relationship to population parameters Aishihik Reached or exceeded 55 cm in 8 of 12 winter when herd declined (1981-1993) and in 3 of 5 winters when the herd increased (1994-1998). Reached or exceeded 85 cm in Wolf Lake range in most years when herd increased (1987-1993)</p>	<p>depth and 85 cm as critical snow depth affecting caribou condition and survival in late winter.</p> <p>Snowmelt phenology: total number of growing degree days in May, based on temperatures from Environment Canada weather stations.</p>

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
Farnell and Gardner 2002 Northern mountain	Limiting factors inferred from population parameters	present: wolves (assumed to be low densities), brown bears, lynx, coyote, golden eagle	Interaction of predation, weather and poor winter forage quality	<p>Snowmelt phenology: No apparent relationship to recruitment and adult survival, but low sample size (N = 4 herds) may mask possible interactions among factors.</p> <p>Pop. Status: decline</p> <p>Annual rate of decline: 1989-92: -11% 1992-93: -31.5% 1993-01: -10.4%</p> <p>Pregnancy rate: Calf:cow ratios 90% Serum progesterone samples indicated low pregnancy rates in 1993 (25%, N=4) and 1994 (74%, N = 31) and higher rates in 1995 (100%, N = 19), 2000 (~90%, N = 25), and 2002 (96%, N = 24)</p> <p>Parturition rate: 41%</p> <p>Calf survival to June: 11% Calf recruitment: 7% Adult Survival Rate: General decline in adult survival from an average of</p>	<p>Pop. Status/rate of change: aerial inventories during periods of herd aggregation in Sept.-Oct. (1987-01).</p> <p>Mean annual pregnancy rates: serum progesterone levels and presence or absence of a calf, antler retention, or distended utter in late May (1993-97, 1999, 2000).</p> <p>Mean parturition rate: number of calves (estimated by calf:cow ratio) on 31 May (1993-00)</p> <p>Calf survival to June: number of calves (estimated by calf:cow ratio) in June (1993-96, 1999)</p> <p>Calf recruitment: based on calf:cow ratios in October (1993-00)</p> <p>Adult survival: multi-year averages based on radio-collared animals (N = 10-25, 1987-01)</p> <p>Prevalence of disease and parasites: frequency of disease agents base on serum antibodies (N = 129 samples), parasites in fecal samples collected in March (2000, 2001)</p> <p>Wolf densities; aerial snow tracking survey of entire range area in 2001.</p>

Study/ Caribou Ecotype	Factors Considered	Predators Present/ Absent	Limiting Factor(s)	Population Parameters	Methodology
				<p>83%, prior to the declining population trend in 1989, to 65% in 1990 and 67% in 2001.</p> <p>Disease: low prevalence Infectious bovine rhinotracheitis 1/129 <i>Leptospira interrogans</i> 3/129</p> <p>Low diversity, prevalence, and intensity of parasites, but samples were not taken in summer, when parasites levels in feces are expected to be greater.</p> <p>Snow depths were consistently below depths limiting caribou and averaged 49 cm</p> <p>Wolf densities: 5.6 wolves/1000 km², below the average wolf density reported for Alaska and Yukon study sites (9 wolves/1,000 km²) (Gasaway et al. 1992)</p>	<p>Authors conclude that low calf recruitment is due primarily to low survival to June and suggest predation is the primary limiting factor. Calf autumn body weights were above average for Alaskan caribou on varying planes of nutrition. Even so, pregnancy and parturition rates were low in some years, suggesting nutritional constraints.</p> <p>Winter diet, based on fecal analysis (N = 95, 1994, 1995, 2000, 2001) was consistently high in moss 51 % (mean percentage of plant fragments) and low in lichen 32 %.</p>

Bergerud (1980, 1985) suggested that many caribou populations in North America are regulated by wolf predation, that wolf predation can halt population growth of caribou at densities of approximately 0.4 caribou per km², and that caribou are not food stressed at this density. Bergerud and Elliot (1986) synthesized recruitment and mortality data for 22 caribou herds (migratory tundra and sedentary boreal populations) for which wolf density information was available and found that recruitment exhibited a significant negative correlation ($r = -0.833$) with wolf density, whereas mortality was positively correlated ($r = 0.852$). The authors concluded that caribou cannot maintain their numbers when wolves exceed > 6.5 per 1 000 km², as this threshold reflected the point along the wolf density gradient when adult mortality exceeded recruitment. In spite of the evidence of limitation, studies of woodland caribou have yet to demonstrate population regulation by wolves. Although increases in caribou numbers following experimental wolf reductions indicated limitation by predators, the limiting effect of wolves must increase when caribou density increases and decrease when caribou density declines to regulate populations (Chowns and Gates 2004).

Bergerud and Mercer (1989) reviewed historical information for 33 introductions of caribou in eastern North America between 1924 and 1985 and concluded that predation (natural and hunting) and disease from deer were the major factors in the decline of caribou following settlement. Outside of Newfoundland, six introductions failed when animals were released where white-tailed deer were common, two failed when wolves and/or white-tailed deer were present. In Newfoundland, where wolves and deer were absent and predators included lynx and black bear, five introductions failed and it was speculated that the animals joined nearby herds. Conversely, introductions of caribou were successful on islands of Lake Superior (Slate Islands and Michipicoten Island), where wolves and deer were absent and forests were predominately mixed species stands or early seral forests with relatively low abundance of lichens. The authors indicated that there was no evidence that introductions failed because of food limitation; however, no quantitative data were available on food availability, other than qualitative assessment of lichen availability, or causes of mortality. Bergerud and Mercer (1989) implicated predation as the reason for the failed introduction on Bowman Island, Lake Superior, due to the presence of wolves on adjacent islands; however, evidence suggested most of the radio-collared animals ($N = 5$) may have died on the ice between islands, and only one mortality was a confirmed wolf kill.

6.1.1 Rangifer Life History Strategies and Vulnerability to Predation

Various aspects of *Rangifer*'s life history strategy and its sedentary populations may augment the importance of predation as a limiting factor in forested environments. Migration in reindeer and caribou is an important evolutionary adaptation to spatial variation in food supply and/or predators (Skogland 1991). Ungulates that migrate are able to avoid regulation by predators and attain higher equilibrium numbers limited only by food limitation (Fryxell, Greever, and Sinclair 1988; Skogland 1991). In Denali National Park in Alaska, offspring from caribou that migrated to calving grounds experienced only half the wolf predation than calves born in other areas such as lowland spruce forests (Adams, Dale, and Mech 1995). Caribou migration occurs when wolf mobility is limited by denning and pup rearing (May to August). Heard and Williams (1992) found that the primary denning area of wolves represented only 25% of the range of migratory forest-tundra caribou in Northwest Territories. Migration to less productive areas (e.g., tundra or alpine areas) that lack alternative prey for wolves serves to keep predator densities low and may enhance calf survival (Table 6.2). In addition, wolf packs that follow migrating caribou herds on the tundra occupy much larger territories and occur at lower densities on tundra than in boreal forests where caribou are sedentary. Fuller and Murray (1998) synthesized population density information for 18 field studies of wolves across North America. Their findings demonstrated that pack territory size had a significant negative relationship with wolf density. Further, wolf density was positively correlated with ungulate biomass in stepwise regression models and wolf densities were greater in southern study sites where moose and deer were

present. Wolf densities and their effects on caribou thus may be elevated in systems where caribou are sedentary and alternate prey species are present.

Table 6.2 Density (no. of caribou/100 km²) of *Rangifer* Populations in Relation to Ecotype and Level of Predation

Category	Location	Density	Source
Major predators rare or absent	Norway	103-141	Reimers et al. 1983
	Newfoundland	105-350	Bergerud and Mercer 1989
	Barff, South Georgia	4100	Leader-Williams and Ricketts 1982
	Royal Bay, South Georgia	8600	Leader-Williams and Ricketts 1982
	St. Matthew Island	1915	Klein 1968
	West Greenland (Akia-Maniitsoq Herd)	400	Cuyler et al. 2002
Migratory (arctic, forest-tundra)	Hudson Bay Lowland, Ontario	14.1	Magoun et al. 2005
	Quebec/Labrador (George River Herd)	110	Messier et al. 1988
	Fox Peninsula, Baffin Island, Nunavut	30-620	Ferguson and Messier 2000
	Northwest Territories (Kaminuriak Herd)	> 20 000	Parker 1972
Mountain and forest-dwelling	Yukon (Wolf Lake Herd)	0.3-0.6	Hayes et al. 2003
	Yukon (Ibex Herd)	0.8	Hayes et al. 2003
	Yukon (Chisana Herd)	0.4-1.4	Hayes et al. 2003
	British Columbia (Wolverine Herd)	7	Wood 1998
	Saskatchewan	< 5	Rettie and Messier 1998
	Lake Nipigon, Ontario	0.6	Cumming and Beange 1987
	Wells Gray Park, British Columbia	5	Seip 1992
	James Bay Lowland, Ontario	0.6	Magoun et al. 2005
	Birch Mountains, Alberta	4	Fuller and Keith 1981
	North Shore of St. Lawrence River, Quebec	1.6	Courtois et al. 2003
	Quebec	1	Crête and Manseau 1996

The low reproductive potential of caribou may augment the effects of extraneous factors in limiting sedentary woodland caribou populations and limit reproductive response to changes in forage productivity where predators are present. For non-migratory ungulates, an important evolutionary strategy may include a high reproductive output and selective use of highly productive early successional forests (e.g., moose). Ungulates with high productivity will generally coexist with wolves at higher densities than ungulates with low productivity. Throughout their range in North America, moose and deer are able to attain much higher densities than caribou (Fuller and Murray

1998). Unlike moose (Franzmann and Schwartz 1985) and white-tailed deer (Verme 1965), twinning appears to be extremely rare in wild caribou populations in North America (Dauphiné 1976; Bergerud 1969; (McEwan 1971; McDonald and Martell 1981; Nowosad 1973). The reasons for low twinning in caribou are poorly understood and further research is required to evaluate the importance of nutrition, predation, and the effects of evolutionary history on maternal investment.

Woodland caribou may be more vulnerable to predation than other boreal ungulates due to their size and grouping behaviour in winter. Seip (1995) speculated that the aggregating behaviour of caribou in winter, even if caribou generally occur at low densities, may allow wolves to be more effective in locating caribou than more dispersed ungulates. Dale, Adams, and Bowyer (1995) found that wolves in Alaska preyed more heavily on caribou than moose and dall sheep, even though moose and sheep were more abundant. The authors speculated this preference might have been due to the lower risk of hunting caribou (Haugen 1987) and higher profitability in killing caribou once potential prey were found. In contrast to moose that were dispersed at low densities in winter and dall sheep that remained in mountainous escape terrain, caribou were typically found in groups and wolves often made multiple kills in single attacks.

6.2 Bottom-Up Forces

6.2.1 Evidence of Food Limitation in Rangifer

Food limitation has been most frequently documented in *Rangifer* where predation, hunting pressure, or dispersal are absent or constrained, such as introductions of caribou to islands (Klein 1968; Leader-Williams 1980). In these cases, depletion of winter foraging range is apparent and mortalities are associated with winter starvation and the cumulative effects of extreme winter weather at high population densities. Norwegian reindeer herds exhibited similar density-dependent effects manifested through winter food limitation and severe weather (Skogland 1985).

Competition for resources among large mammals generally occurs at densities close to ecological carrying capacity, thus restricting its regulatory impact to relatively high population densities (Fowler 1981). A comparison of caribou populations along a north-south gradient suggests that migratory forest-tundra woodland caribou attain high densities and are regulated by either competition for resources or the combined density-dependent effects of predation and competition for resources (Table 6.2) (Messier et al. 1988; Hearn et al. 1990; Crête and Huot 1993). Crête and Manseau (1996) found that densities of forest-tundra caribou on summer range (3 088 caribou/100 km²) in Quebec were almost three orders of magnitude greater than sedentary populations (1 caribou/100 km²) further south where wolves and moose were present. Forest-dwelling caribou typically occur at densities of 1-4 individuals per 100 km² (Rettie and Messier 1998; Seip 1991; Edmonds 1988; Fuller and Keith 1981) and it is unlikely that sedentary boreal caribou populations could exhibit regulatory effects of food limitation at such low densities. Caribou were successfully introduced to islands lacking predators on Newfoundland (boreal forest zone) and reached densities of 105-350 animals per 100 km² approximately 20 years after initial introductions (Bergerud and Mercer 1989). Fryxell, Greever, and Sinclair (1988) reported similar trends in the density of migratory and non-migratory wildebeest in the Serengeti as is apparent for caribou in North America. A non-migratory population of wildebeest was regulated by predation at a density of 15 animals per km², while a migratory population was regulated by food at a density of 476 animals per km².

Where caribou share range with predators, such as the majority of woodland caribou populations in North America, food limitation is frequently assumed to be of minor or secondary importance in explaining population trends (Bergerud 1974; Schaefer et al. 1999; Rettie and Messier 2000; Courtois 2003; Hayes et al. 2003; Jolicoeur, Courtois, and Lefort 2005; Wittmer, Sinclair, and McLellan 2005, Table 6.1). We could find only one unpublished study (Farnell and Gardner 2002) that implicated an interaction among predation, weather and poor winter forage quality in the decline of a woodland

caribou population (Chisana herd, Yukon, northern mountain population); however, the actual mechanism of decline could not be determined. Population estimates indicated that this declining herd had relatively low pregnancy rates in some years, low parturition rates, and winter diet was dominated by moss, suggesting poor nutritional conditions. This population was the only one we reviewed that exhibited pregnancy rates below the 82% threshold suggested by Bergerud (1980). Hayes et al. (2003) reported pregnancy rates of 25% in 1993 and 78% in 1994. Density-dependent limitation was discounted because the density of the herd prior to its decline (136 caribou/1000 km²) was within the low end of ranges reported for naturally regulated (without wolf control) herds in Alaska (100-500 caribou/ 1 000 km²) and within the normal ranges of densities for Yukon woodland caribou (30-183 caribou/1 000 km²) (R. Farnell, unpublished data, cited in Farnell and Gardner 2002). Boertje, Valkenburg, and McNay (1996) suggested that direct and indirect effects of adverse weather increased vulnerability to predation and influenced population size in Interior Alaska caribou herds during the 1990s.

6.2.2 Methodological Limitations in the Evaluation of Forage Limitation

Collection of the information necessary to evaluate top-down and bottom-up effects (e.g., nutrition, mortality factors, predator/prey densities) on a far ranging species like caribou is a daunting and costly task. As a result, researchers have relied on inferred relationships based on population parameters. In general, low pregnancy or parturition rates, delayed calving dates, low weights or nutritional condition scores are indicative of poor nutrition or vulnerability to disease. Predator limitation is often inferred from high pregnancy or parturition rates, good nutritional condition and low recruitment, or high adult mortality. We found that declining woodland caribou populations were generally characterized by low recruitment (~11-14% calves, calf:cow ratio < 0.23) and marginal to high adult survival (> 70%). Recruitment was relatively high in stable populations (~16-20% calves, calf:cow ratio 0.30–0.38) and pregnancy and parturition rates were similar, regardless of population trend. Predation was the dominant cause of mortality in most studies, regardless of population trend, and generally represented > 40% of known causes of mortality. Malnutrition was documented in only a few studies (Bergerud 1971b; Sebbanne et al. 2002; Jolicoeur, Courtois, and Lefort 2005; Wittmer et al. 2005) and was considered a minor mortality factor.

We suggest that the use of population parameters and mortality factors to assess limiting factors may mask seasonal nutritional deficiencies. Almost all studies of woodland caribou populations that we examined inferred the absence of nutrient limitation from high pregnancy rates, high parturition rates, and/or date of calving (Table 6.1). Although such trends perhaps suggest adequate winter nutrition, they do not necessarily indicate adequate summer nutrition. Gerhart et al. (1997b) demonstrated that using pregnancy rates or parturition rates of random samples of a herd may underestimate the importance of nutrition and recommended using samples of lactating females. Due to the interactions among nutrition, lactation, and probability of pregnancy (see Section 5.1.1), non-lactating females are generally high in herds that have low rates of neonatal survival and consequently, pregnancy rates may be high (Gerhart et al. 1997b; Skogland 1991). In settings where predation on juveniles is very high, particularly if predation is high in summer, then pregnancy rates may be “artificially” elevated because a relatively high proportion of cows would escape much of the nutritional demands of raising a calf (i.e., their fat levels will be elevated). Rettie and Messier (1998) reported higher pregnancy rates among females without a calf (0.97, N = 33) than females with a calf (0.85, N = 13) in Saskatchewan, suggesting the potential for nutritional effects on woodland caribou populations. Cook et al. (2004) found that even if summer nutrition level was good enough such that all, or nearly all, lactating cows became pregnant, there were still nutritional deficiencies in terms of calf growth, yearling growth, yearling breeding probability, and fat accretion in adult cows, all of which significantly increase susceptibility to winter starvation in harsh winters.

The identifiable causes of mortality in relation to recruitment and survival data may suggest the relative importance of one or the other limiting factor, but do not take into account possible interactions that affect vulnerability to mortality. Physical condition has been shown to predispose animals to predation (Pimlott, Shannon, and Kolenosky 1969; Keith et al. 1984) and an increased susceptibility to predation, due to poor nutrition, would not be apparent from mortality information from collared animals. Similar to studies of boreal woodland caribou, Hearn et al. (1990) reported that predation was the most common cause of death for the George River Herd (forest-tundra population) between 1983 and 1987, yet this herd is believed to be regulated by summer nutrition (Crête and Huot 1993). The similarity in documented mortality factors for herds with different relative importance of limiting factors highlights the need to evaluate multiple explanatory factors in assessing population limitation.

In addition, estimates of mortality factors, based on collared animal remains, may be biased towards more obvious proximal cues. The relative importance of different mortality factors is often based on the sample of identifiable causes, yet unknown causes may occupy a high percentage of mortalities. Evidence of predation (e.g., disarticulation, crushed bones, puncture wounds) is likely more easily discernible than nutritional deficiency in examination of animal remains and may result in the biased clumping of nutrition-related mortality into the category of “unknown cause”. Whitten et al. (1992) concluded that calf mortality could be underestimated using only radio-collared calf data due to the high incidence of mortality within 48 hours of birth, before calves can generally be collared. In a study of early calf survival in the Porcupine caribou herd, Whitten et al. (1992) found that predation was an important cause of death in radio-collared calves greater than 48 hours old; however, most mortality (59-74%) of calves born to radio-collared females occurred within 48 hours of birth. Many of these deaths were attributed to stillbirths, defects, or low birth weights.

Studies that attempted to quantify the availability of food to caribou generally provided coarse estimates of food availability or limited their assessment to winter food (lichen). Bergerud (1971b) assessed the abundance of forage on the winter ranges of woodland caribou in Newfoundland and concluded there was no absolute shortage of food. The percent cover of ground lichens, bryophytes, deciduous shrubs and forbs, evergreen shrubs, and conifers were measured in 22 locations in the winter ranges of caribou across the island. Terrestrial lichen quantities were reported to exceed values documented for other caribou ranges in northern Saskatchewan, Northwest Territories, Ontario, and the Gaspé Peninsula, Quebec. Terrestrial lichen production was estimated to be approximately 150 to 350 pounds per acre (170–397 Kg/ha). Courtois (2003) suggested that interspecific competition for food was unimportant in population regulation of three woodland caribou populations in central Quebec (boreal population) due to the near 100% pregnancy rate of adult females equipped with radio collars (N = 68) and the estimation that the biomass of terrestrial lichens could support 3–4 times the actual caribou density in each population. Estimation of food carrying capacity was based on the assumption that caribou consume approximately 5 kg of lichen per day between October and March and 3.5 kg/d in September and April (1 135 kg/year). Terrestrial and arboreal lichen biomass was measured using stratified random sampling of 100 km² sampling areas (N = 16) in the 42 539 km² study area. No quantitative data on the nutritional status of caribou were available for these studies and experimental work for other ungulates suggests that coarse estimates of forage availability would fail to detect subtle effects of forage quality on reproductive parameters in wild ungulate populations.

We suggest that using lichen abundance to assess nutritional status and food limitation is inadequate and Boertje (1990) recommended a more complete evaluation of diet quality, diet composition, activity, and energy requirement in assessing forage limitation for a particular caribou population. The importance of summer nutrition for weight gain prior to the winter period of weight loss, and the importance of dietary protein and minerals for lactation and successful reproduction, suggests that seasonally available vascular plants may be equally as important or more important than lichens for reproduction in females. Caribou on lichen-poor diets in arctic Alaska that substituted *Vaccinium* spp.

for lichen exhibited high calf production and survival (Boertje, Davis, and Valkenburg 1985). In a captive study of pregnant female reindeer, Rognmo et al. (1983) found that nutrient consumption of animals fed lichens *ad libitum* between February and May was approximately $387 \text{ kJ} * \text{kg}^{-0.75}$, assuming a 70 kg animal (or 2 240 kcal of metabolizable energy), well below the estimate of $617 \text{ kJ} * \text{kg}^{-0.75}$ ($147 \text{ kcal} * \text{kg}^{-0.75}$) per day (ME) (Table 5.2) estimated by Boertje (1985a). Female reindeer fed this diet produced calves with lower birth weights and calf mortality during the first three weeks was higher than for calves born to females maintained on an improved nutrition diet. Jacobson and Skjenneberg (1975) found that adult female milk yield and calf growth rate were lower for captive reindeer fed a lichen-only diet (N = 4) than reindeer fed a nutrient-rich diet (N = 6). Statistical comparisons were not made, due to low sample size; however, milk yield was 42–68% lower and mean daily weight gain of calves 30–54% lower for animals fed a lichen-only diet.

We suggest caution in dismissing the potential importance of nutrition, as a lack of evidence is not conclusive that food does not limit caribou populations or interact with other mortality and recruitment factors. The necessary quantitative data on predator densities, caribou densities, forage availability, and dietary energy intake is often absent from population studies due to logistic and financial constraints.

6.2.3 Empirical Evidence of Multiple Limiting Factors

Research conducted on caribou in Denali National Park, Alaska, suggests the importance of climate and nutrition to caribou populations that exhibit low recruitment due to predation (Adams, Dale, and Mech 1995; Adams, Singer, and Dale 1995; Adams 2005). Although Denali caribou occurred at relatively low densities (20-30 individuals/100 km²), adult females were large bodied, and productivity was high (Adams and Dale 1998a), climatic variation associated with severe winters affected calf production and survival. Increased winter severity before conception, combined with shorter growing seasons, reduced reproductive performance (Adams and Dale 1998a, 1998b). Severe winter conditions during gestation decreased birth mass (Adams 2005), postnatal growth and development, and calf survival from birth to autumn (Adams, Dale, and Mech 1995; Adams, Singer, and Dale 1995). Adams and Dale (1998a) speculated that high neonatal mortality during the first few weeks of life, while negatively influencing population growth, might contribute to the improved nutritional condition of reproductive females due to the lack of costs associated with lactation. Under such circumstances, assessing nutritional constraints of a population, based on nutritional condition of adult females or pregnancy rates, would mask important environmental effects on populations. These findings suggest that even if predation was determined to be the primary limiting factor for a caribou population, changes that increase the productivity of an ungulate population or reduce other mortality factors could affect caribou population dynamics.

Similar to caribou in Denali National Park, Bergerud and Elliot (1986) found that wolf predation was an important cause of low calf recruitment for woodland caribou populations in British Columbia (northern mountain population); however, the authors also reported that calf recruitment to five months was lower during years of average or late snowmelt than during years of early snow ablation. The authors attributed this to a reduction in snow-free substrates that may camouflage calves from predators, as recruitment did not vary on the Horseranch range (1978-1980) when wolves were reduced. However, the impact of delayed snowmelt on forage availability could also implicate an interaction between nutrition and vulnerability to predation when interpreting these data.

6.3 Relevance of Scale

A growing number of studies have demonstrated that habitat selection varies according to scale (Johnson 1980; Boyce et al. 2003; Fortin et al. 2003; Brown 2005), and Rettie and Messier (2000) suggested that limiting factors with greater abilities to limit survival should be influential at coarser spatial scales. In terms of general life history characteristics, large-scale movements of caribou reduce

predation risk for many caribou populations. As noted by Rettie and Messier (2000), the importance of predation at coarse spatial scales is evident from the observation that caribou achieve maximum densities only when they are able to avoid wolves at the scale of population range occupancy. Caribou achieve high densities in the absence of predators or where animals migrate to minimize the effects of predation (Crête and Manseau 1996; Magoun et al. 2005). For such populations, food supply is the functional limiting factor (Adamczewski et al. 1988; Messier et al. 1988; Bergerud, Ferguson, and Butler 1990; Crête, Huot, and Gauthier 1990). However, the importance of nutrition is apparent from the annual reproductive cycle of caribou and narrow calving period between mid-May and mid-June. The timing of parturition by caribou is closely synchronized to plant phenology, regardless of predation pressure (Post et al. 2003). The progression of calving seasons for a predator-free population in West Greenland and a depredated population in Alaska was synchronized with the emergence of forage plants in spring and 50% of births occurred when approximately 60–70% of forage plants were emergent.

6.3.1 Seasonal Range Selection and Movements

Studies of seasonal habitat selection by caribou suggest that both predation and food supply may influence caribou spatial behaviour. Caribou inhabiting mountainous regions occupy high elevation areas in winter with advantageous foraging conditions for arboreal lichens and lower predation risk (Servheen and Lyon 1989; Ouellet, Ferron, and Sirois 1996; Johnson, Parker, and Heard 2001). In areas of high snow accumulation, caribou may depend on arboreal lichens as a sole source of food. As winter progresses, snow accumulation at low elevations may prevent cratering for low-growing vegetation; however, the accumulation and compaction of snow at higher elevations provides a supportive base for caribou to access lichens on standing or fallen trees.

Seasonal habitat selection by mountain caribou in spring may reflect a trade-off between the need to gain access to newly emerging green vegetation at lower elevations and predation risk. Caribou in the Columbia and Central Selkirk Mountains were found at high elevations in late winter and summer/fall, and at lower elevations in spring (Apps et al. 2001; Hamilton, Wilson, and Smith 2000). Hamilton, Wilson, and Smith (2000) found that caribou were associated with sites with higher solar radiation in spring and early summer. Site productivity was an important explanatory variable in describing spring habitat selection of caribou in the Columbia Mountains, but was not important in summer (Apps et al. 2001). These data suggest that caribou descended to lower elevations to access newly emerging vegetation, but returned to higher elevations once green vegetation emerged at those elevations. Although Apps et al. (2001) found that caribou in the Columbia Mountains selected lower elevations with higher site productivity in spring, they also preferred more rugged areas with steep slopes. The preference for steep, rugged terrain by mountain goats is generally explained as an evolutionary response to predation risk and direct observations indicate that goats will often move into such terrain when approached by large mammalian predators (Fox and Streveler 1986).

Predation on calves is an important cause of low recruitment in many caribou populations (Bergerud 1971b) and female caribou may select calving areas with reduced predation risk. Conversely, forage is relatively abundant at this time of year, compared to the winter period of plant senescence and snow accumulation. During spring, female woodland caribou may disperse at low densities and calve on islands, remote shorelines, alpine or wetland habitats with good escape cover or naturally low densities of predators (Bergerud 1985; Brown et al. 1986; Bergerud and Page 1987). Barten, Bowyer, and Jenkins (2001) found that during peak parturition, female caribou (barren-ground) with young (N = 26) used high elevation sites with fewer predators and lower abundance of forage compared to females without young (N = 30). Forage quality and availability were determined using field vegetation sampling, collection of fecal pellets, and laboratory analysis of forage plant nitrogen content, and nitrogen and neutral detergent fibre of fecal matter. Dry matter digestibility of plant samples was determined using a captive fistulated reindeer. Diet composition and quality were similar

among parturient and non-parturient females; however, the authors speculated that increasing population density could increase intraspecific competition and thus nutritional costs of using sites with less forage and fewer predators. Bergerud, Ferguson, and Butler (1990) found that woodland caribou near Lake Nipigon, Ontario selected islands during spring and summer where there were large ratios of shoreline to area and predators were absent. There was less green forage on the islands than on the winter range and many of the small islands were overgrazed. Findings by Ouellet, Ferron, and Sirois (1996) supported the hypothesis that cow-calf groups remained at high elevations to avoid predation by coyotes and black bears. During spring, rather than following elevation-related changes in emergence of new plant growth to maximize nutrient intake, cow-calf groups remained in alpine habitats at high elevations.

For sedentary populations of caribou that inhabit lowland conifer forests, mosaics of wetland and pine-lichen or black spruce forests are important in spring and summer (Rettie and Messier 2000; Lantin 2003; Johnson et al. 2004; Brown 2005). These habitat mosaics may facilitate foraging, as well as predator avoidance, due to the low selective value of wetlands to wolves in relation to low biomass of moose (Cumming, Beange, and Lavoie 1996). The spring and summer diet of caribou is abundant in species associated with peatlands (e.g., horsetails, sedges, graminoids, and buckbean) and Helle (1980) suggested that spruce-peatland mosaics provided important nutrients for lactation in reindeer.

It is difficult to ascertain from most habitat selection studies whether caribou response is more greatly influenced by forage availability or predation risk. A limitation in many habitat-based studies of woodland caribou pertains to the use of remote satellite telemetry to assess caribou-habitat relationships and the influence of limiting factors. Given that the energetic costs of movement and access to different habitats is lower for proximal than distant habitats, foraging theory (Stephens and Krebs 1986) would suggest that caribou habitat use is more likely to vary at fine than coarse scales (Belovsky 1991). The resolution provided by remotely sensed telemetry data and digital land cover data (e.g., Landsat classified imagery) may not be sufficient to detect important fine-scale responses of caribou to variation in forage availability or quality. Most telemetry-based habitat selection studies do not permit determination of whether caribou were selecting habitats due to their reduced predation risk or greater availability of forage. Moreover, the consequences of the observed behavioural decisions of caribou to reproductive fitness are often unknown.

6.3.2 Daily Area and Site Selection

Food resources may have increased importance at the scale of daily area and foraging site selection by caribou. Johnson et al. (2002) found that winter movements of caribou (southern mountain) within homogenous habitat patches had lower cost of movement, were associated with cover types where foraging probably occurred, and were closer to areas of higher predation risk than interpatch movements. Caribou winter-foraging site selection is closely related to the biomass of arboreal or terrestrial lichens (Mosnier et al. 2003; Johnson, Parker, and Heard 2001; Terry, McLellan, and Watts 2000; Wilson 2000; Rominger, Robbins, and Evans 1996). Unlike most available studies, Johnson, Parker, and Heard (2001) and Johnson et al. (2002) used quantitative data to explicitly compare the relative importance of multiple factors (e.g., predation risk, forage, energetic costs) to caribou spatial behaviour at different scales.

Although a number of studies have documented the significance of lichen abundance in woodland caribou feeding site selection in winter, few studies have described foraging strategies in summer. This is likely due to the emphasis on lichens and mature forest as critical habitat features for caribou in relation to forest habitat alteration. Also, logistic constraints make locating and measuring winter feeding sites (i.e., craters, foraging trails in snow) easier than summer feeding sites, when animals are dispersed over large forested areas. We do not dispute that lichen in caribou diet and mature forest are

important aspects of caribou biology with management implications, but this research emphasis could potentially underestimate the importance of summer nutrition in relation to caribou behaviour and reproductive success. A lack of empirical data does not constitute evidence that summer-fall forage is not important.

6.3.3 Diet Selection and Activity Budgets

At the scale of diet selection and daily activity budgets, available empirical data are insufficient to determine if caribou maximize energy intake or time available for predator avoidance/vigilance (e.g., by minimizing time spent feeding). If caribou time spent feeding reflected time minimization, diet should generally reflect forage availability and maximal intake of biomass per unit time. If caribou attempt to maximize nutrient intake, their diet should reflect some optimal trade-off among nutrient content of available species and the relative abundance and search/handling time required for each forage item. Data on woodland caribou activity budgets in relation to forage intake, predator vigilance and subsequent effects on fitness are inadequate to draw clear conclusions. Observed seasonal patterns in dietary intake are not inconsistent with nutrient maximization or time minimization. In spring and summer, caribou feed on nutrient-rich newly emerging vegetation as it becomes available (Bergerud 1972). In autumn and winter, with the disappearance of forage high in protein, there may be a more uniform distribution of nutrients in plants. Caribou that feed on lichen mats or arboreal lichens, allowing a high number of bites per minute and ingested quantity per bite, may ingest more nutrients than an animal selectively searching. Johnson, Parker, and Heard (2001) found that mountain caribou in British Columbia did not select forage species with the greatest nutrient content. Caribou maximized net gain by increasing the intake of lichen species that were more abundant and readily available. Although caribou diet selection in mountainous regions is likely dictated by accessibility, selection of arboreal lichens is not inconsistent with energy maximization or time minimization. Caribou likely have reduced energetic costs and time constraints in feeding on arboreal lichens as opposed to cratering through snow in winter to access ground level forage. Also, *Bryoria* spp. (14.7 kJ g^{-1}) have a relatively high digestible energy content compared to ground species of lichens (*Cladina mitis* 8.2 kJ g^{-1} , *Cladonia* spp. 7.6 kJ g^{-1}) (Johnson, Parker, and Heard 2001).

6.4 Interactions among Limiting Factors and Effects on Forage

Although predation is believed to be the main factor limiting caribou populations, the interaction of factors may provide greater insight to the ultimate cause of regional declines in caribou. For example, weather, through alteration of forage quality or availability, affects condition of caribou, which in turn affects calf mortality and vulnerability to predation. Many studies of mountain and boreal caribou suggest that predation is the proximal cause of caribou declines, but habitat alteration and subsequent changes to predator-prey relationships are implicated as the ultimate cause of population limitation (Edmonds 1988; Rettie and Messier 1998; Kinley and Apps 2001; McLoughlin et al. 2003; Wittmer et al. 2005). Caribou may alleviate predation risk through habitat selection (Seip 1992; James 1999; McLoughlin, Dunford, and Boutin 2005) that, in turn, may affect forage availability. Decisions made by caribou clearly involve trade-offs among competing needs to avoid predation, as well as maximize forage intake and nutrient supply. Factors that negatively affect an animal's ability to obtain adequate food resources, avoid predation, and reproduce may be cumulative in their effects on individual fitness. Such interactions may have subtle but substantial effects on population dynamics.

Diseases and parasites are endemic to caribou and a normal occurrence in most populations; however, potential interactions with other limiting factors are not well understood. Although parasitism may be the actual agent of death in many wild ungulates it is often associated with debilitation of the animal's natural immunological defences from other causes, such as poor nutritional state. Klein (1968) speculated that lung worm *Dictyocaulus* spp. might have contributed to the reduction of a food-

limited reindeer population on St. Matthew Island; however, infestations were not acute and did not reach epizootic proportions prior to a caribou die-off. Changes in climate or habitat availability that may increase white-tailed deer populations could increase the importance of *P. tenuis* on caribou range distribution. The failure of caribou reintroduction attempts in Ontario was attributed to the nematode (Bergerud and Mercer 1989; Cumming 1992) and Racey (2005) suggested that deer range expansions and contractions in northwestern Ontario corresponded to variation in winter severity and warming trends over a 70-year period.

Precipitation in the form of accumulating snow, icing, and freezing rains may affect caribou behaviour, reproduction, and survival. Deep or crusted snow increases the energetic cost of movement (Fancy and White 1987) and foraging at a time when the energetic costs of pregnancy are high (Adamczewski, Hudson, and Gates 1993). Poor winter nutrition can result in low calf birth weights and later parturition dates (Gates, Adamczewski, and Mulders 1986; Cameron et al. 1993) and weak calves may be more likely to die from predators, pneumonia, and other causes (Thomas and Gray 2002). Adult mortality may also increase as snow conditions increase susceptibility of individuals to predation (Gauthier and Theberge 1986). Disturbances that increase canopy openness are expected to have greater accumulation and crusting of snow in late winter, increasing energetic costs and potentially causing range abandonment (Schaefer and Pruitt 1991).

The following sections provide a review of the effects of different factors on forage availability and quality and population dynamics.

6.4.1 Climate

Climatic conditions greatly affect growth and nutritional quality in plants and severe weather may augment the limiting effects of other factors affecting herbivore populations. Weladji et al. (2002) reviewed the importance of climatic variation to northern ungulate populations and warned against generalizing across northern systems and species, due to the complexity of interactions affecting population dynamics.

Climatic variation in air temperature, precipitation and, sunlight exposure may alter the quantity and quality of forage available to caribou (Chapin and Shaver 1985; Chapin et al. 1995). Yearly variation in snow cover, snow depth, and timing of snowmelt affect plant emergence and length of the growing season and therefore forage quality (Bø and Hjeljord 1991; Post and Klein 1999; Finstad et al. 2000b). Finstad et al. (2000a) found that annual variations in summer weather influenced growing degree days and therefore forage availability and digestibility on the Seward Peninsula, Alaska. Although cloud cover and shade may decrease production of plant biomass in some assemblages, decreased light may improve forage quality of plant species adapted to canopy shade (Weladji et al. 2002). High temperatures may lower plant digestibility due to increased lignification of cell walls and cloudy wet summers are reported to improve ranges for some ungulates (Bø and Hjeljord 1991; Lenart et al. 2002). Lenart et al. (2002) examined the effects of weather on summer forage of woodland caribou (Chisana herd, northern mountain population) by experimentally manipulating light, air temperature, and precipitation in 30 treatment plots (1.8 by 3.6 m) on subarctic tundra habitat. Treatments simulated summer conditions reflecting a warm dry summer, a warm wet summer, a cloudy dry summer, and a cloudy wet summer. Reduced light, representative of cloudy summers, resulted in higher nitrogen concentrations in all plant growth forms and reduced biomass in forbs during the second half of the growing season (July and August). Water treatment increased total plant biomass during midseason or late spring and also increased late season biomass in control plots, but had no effect on biomass in shaded plots. Percent digestibility was lower in shade plots near the end of the season for graminoids, forbs, and prostrate willows.

As previously discussed, forage conditions on summer or winter range can have direct effects on nutritional condition in caribou, thus implicating the potential role of climatic variation in caribou

population dynamics. Finstad et al. (2000b) used reproductive data collected for reindeer on the Seward Peninsula between 1987 and 1997 and modeled relationships between climate and forage quality to evaluate the effects of climate on reindeer reproductive performance. The proportion of yearlings lactating in June and July was positively related to the number of growing degree days the previous May and June and negatively related to both the growing degree days in the previous July and snow depth the winter prior to birth. Low snow depths were speculated to improve female condition at time of birth, thereby affecting calf birth weight and survival, while warm springs and cool summers were thought to improve forage quality. The authors concluded that snow depth, spring temperature, and summer temperature were the primary factors affecting yearly variation in age of first reproduction in reindeer of the Seward Peninsula.

Extreme weather conditions in winter may have the greatest climate-related influence on caribou populations. Snow accumulation greatly affects lichen availability (Rominger and Oldemeyer 1990) and greater snow depths may prohibit foraging on terrestrial lichens. Conversely, sufficient snow accumulation and compaction may be required to access arboreal lichens (Rominger, Robbins, and Evans 1996), particularly if lichens have been heavily grazed on the lower portions of trees. Tucker et al. (1991) examined the winter spatial behaviour of a coastal population of woodland caribou in Newfoundland and found that caribou avoided inland areas where snow accumulation was greater. The authors speculated that the extreme snow and icing conditions created by the maritime climate restricted caribou winter range and could potentially limit maximal population size. Evaluations of foraging conditions were not available to test a density-dependent relationship between weather and forage availability. Caribou populations could be limited by weather under maritime climates, if icing were to substantially reduce availability of food.

Negative relationships have been reported between the reproductive performance or survival in *Rangifer* and severe weather conditions or delayed snowmelt (Skogland 1985; Fancy and Whitten 1991; Ferguson and Mahoney 1991; Adams and Dale 1998a; Finstad et al. 2000b; Dau 2005). The reproductive performance of female Alaskan caribou was affected by winter snowfall and natality declined in relation to greater snowfall in the winter prior to the autumn breeding season (Adams and Dale 1998a). Ferguson and Mahoney (1991) suggested that weather may have affected productivity of a woodland caribou herd inhabiting the coast of southwestern Newfoundland. Measures of productivity (1966-1990) were based on the number of calves seen by hunters in fall, calves and yearlings in annual harvests, and fall and spring survey estimates of pregnancy rates, and percentages of calves and yearlings in the herd. Colder winter temperatures were associated with fewer calves the next fall and pregnancy rates and yearlings/100 females in the spring were negatively correlated with snow on ground the previous winter. Predator densities or predation rates on caribou were not considered and the effect of hunting effort or success was not incorporated into productivity estimates. Edmonds and Smith (1991) found that calf recruitment in mountain caribou of Alberta was lower in years following relatively high snowfall in April and May of the previous spring. Klein (1968) attributed the die-off of introduced reindeer on St. Matthew Island to overgrazing of lichen on winter range and severe snow accumulation. Natural predators of caribou were absent from the island and the herd increased from 29 animals in 1944 to 6 000 in 1963. The population underwent a crash die-off to 50 animals within a single year. Animals showed signs of severe malnutrition in the year prior to the die-off and lichens had been completely eliminated as a significant component of the winter diet. Winter foraging on the island was restricted to windswept areas with reduced snow depth and the die-off occurred during a winter of extreme snow accumulation, when almost all animals died of starvation. Aanes, Sæther, and Øritsland (2000) found that climatic effects on population parameters were strongest at high population densities for an introduced population of Svalbard reindeer.

Weladji et al. (2002) concluded that climatic variation may have important indirect effects on caribou in arctic and subarctic environments through changes in insect harassment. Regional patterns in

temperature, humidity, and wind velocity all affect insect abundance and harassment intensity. Total foraging time is an important determinant of fattening in *Rangifer* and insect harassment during summer could affect caribou nutritional condition and reproductive performance through decreases in foraging time and increased energy expenditure (Fancy 1986; Walsh et al. 1992). Without empirical data on the effects of insect harassment to activity and energy budgets in caribou inhabiting boreal forest, inferences regarding climate-insect related effects on woodland caribou populations are tenuous.

6.4.2 Natural Disturbances

Although caribou are adapted to a landscape that includes fire, Cumming (1996) noted that the disturbance patterns produced by fire are not necessarily favourable to caribou in the short term. Within annual ranges, caribou generally avoid young seral stage forests and select mature stands (Dunford 2003, Brown 2005). In the short term, fire may consume forage items used by caribou or limit accessibility to foraging areas. Metsaranta, Mallory, and Cross (2003) speculated that the accumulation of deadfall after fire might limit use of upland sites by caribou due to travel impediments. Regression models based on areas used by caribou and areas disturbed by fire indicated a negative relationship between habitat suitability and density of deadfall. Although early seral stage forests may be abundant in forage species used by many ungulates, predator densities may also increase in response to increased usage by other ungulates (e.g., moose). As a result, greater predation risk may reduce the profitability of foraging in early seral stage communities.

We did not find evidence in available literature of population-level effects (i.e., population limitation or density-dependent regulation) to woodland caribou caused by an interaction between natural disturbances and nutrition, largely due to the absence of evidence of forage limitation in woodland caribou populations. However, some discussion of changes in forage species availability in relation to natural disturbances and forest succession may provide insight into potential seasonal constraints.

The generalist feeding habits of caribou in summer suggest that disturbances to summer range should not negatively impact nutrition. Early seral forests that follow fire or industrial disturbances are generally abundant in rapidly growing vascular plants, including grasses, forbs and deciduous shrubs. In addition, a large portion of a forest's biomass is held within the canopy of mature forests, while most biomass in young regenerating forests is near ground level and therefore more accessible as forage. Winter forage availability may be more greatly affected by natural disturbances than summer forage. During winter, caribou diet is dominated by lichens, associated with mature boreal forest (Klein 1982; Brown, Rettie, and Mallory 2006). Fire is expected to destroy all terrestrial lichens, which require long periods of recovery following disturbance (Thomas, Barry, and Alaie 1996; Arseneault et al. 1997). Thomas, Barry, and Alaie (1996) examined successional changes in important forage lichens used by barren-ground caribou on their winter range in boreal forest and found that total lichen biomass in sample sites (N = 197) increased with age of forest to 100-150 years. Peaks in biomass following fire varied with lichen species and ranged from 40-60 years post-fire for *Cladonia* spp. to greater than 150 years for *Cladina rangiferina*. Winter habitat studies suggest that caribou avoid recent fires (up to 60 years) (Schaefer and Pruitt 1991; Thomas, Barry, and Alaie 1996; Joly et al. 2003). Although early successional forage present in burns may be attractive to caribou in spring or early winter, Joly et al. (2003) found that Alaskan caribou (N = 89-93) that occupied black spruce forests in winter used burned areas much less than expected. Range abandonment of recently burned wintering areas by woodland caribou in Manitoba was attributed to a reduction in lichen (*Cladina* spp.) abundance, increased thickness and hardness of snow in relation to canopy openness, and increased accumulation of deadfalls (Schaefer and Pruitt 1991).

Although fire may be detrimental to the short-term availability of lichens, it may be necessary to ensure long-term forage productivity by removing competitive growth of feather mosses in mature

stands (Klein 1982; Schaefer and Pruitt 1991; Goward 2000). Bergerud (1971a) suggested that fire may benefit caribou forage availability in the long term by reducing closed-canopy forest and permitting lichen and shrub strata to develop. Late seral stages of conifer forest following fire exhibit high structural diversity (Harper et al. 2002) that may be important in providing caribou with foraging patch diversity in an otherwise low productivity landscape. Harper et al. (2003) found that after about 100 years following fire in black spruce boreal forest there is a greater abundance of deadwood in various stages of decay, more epiphytic lichens on trees, and more ericaceous shrub species in the understory, created largely through gap replacement dynamics. Caribou preference for boreal conifer forests is generally assumed to be a predator avoidance strategy; however, the structural and compositional diversity of late seral stage forests may be important in caribou foraging and further research is required to elucidate the importance of patch complexity in caribou range occupancy and foraging behaviour.

Natural disturbances may have more important effects on caribou predator-prey relationships than foraging dynamics. Edwards (1954) speculated that fire was responsible for the decline of woodland caribou (southern mountain population) in Wells Gray Park, British Columbia. Evidence was qualitative and based on observations of long-term patterns in fire and caribou abundance between approximately 1920 and 1950. Edwards attributed the increase in mule deer, moose, and cougars and decline of caribou to changes in preferred habits of these species; however, more recent empirical evidence has demonstrated the importance of cougar predation in early seral forests to caribou declines (Kinley and Apps 2001; Wittmer et al. 2005).

Important differences exist between natural disturbances and human-related industrial disturbances that may have meaningful implications for caribou. Whereas succession of lichens after fire will depend on cover type, soil type, and fire intensity, succession of lichens after forest harvesting will depend on surface treatment and restocking methods, in addition to substrate and canopy characteristics. Fire almost always consumes the ground cover of vegetation, including terrestrial lichens; however, ground lichen may survive and continue to grow after forest harvesting (Schaefer and Pruitt 1991; Webb 1998). Although harvesting will remove all arboreal lichens on harvested trees, low intensity ground fires may leave arboreal lichen communities intact. Availability of browse species preferred by moose may be greater after harvesting than after fire due to increased hardwood regeneration. Local fire history, forest management activity and the proximity of alternative, lichen-rich stands should be considered in the long-term management of caribou habitat.

6.4.3 Human Disturbances

Disturbance has the potential to change the availability of food items for caribou. Forest harvesting can cause changes in site productivity, hydrology and light regime; however, risk of a reduction in summer forage availability for caribou seems low due to their generalist feeding habits. The potential for soil damage is greater in summer than winter, when the ground is frozen and snow-covered, and greater on upland sites than lowland areas with a thick, protective fibric layer (MacDonell and Groot, unpublished report; Groot 1987). On peatlands, susceptibility to disturbance increases from *Ledum* to *Alnus*/herb-poor to *Alnus*/herb-rich site types (Groot 1987). Although Groot (1998) observed reductions in elevation and aerobic zone thickness and increases in water level at disturbed sites, damage was local to the disturbed machine tracks. The hydrological effects of site disturbance were deemed minor compared to the effects of forest canopy removal. Groot (1998) examined the physical effects of equipment disturbance during forest harvesting on peatlands of the boreal forest region and concluded that site disturbance was unlikely to reduce forest productivity. The decomposition of plant debris formerly held in the canopy may actually improve soil productivity following tree harvesting. Coxson and Marsh (2001) suspected that harvesting residue piled or mixed in soil during summer harvesting promoted vascular plant growth on harvested sites. Proceviat (2003) examined changes in caribou forage plant availability along a chronosequence (1-150 years post-harvest) of boreal forest

stands that had undergone careful harvesting techniques (partial cutting methods designed to minimize damage to standing trees). Although relative abundances of individual forage species varied along the chronosequence, summer forage abundance was similar in both early and late successional forests. Groot (1996) found no evidence of reduced tree seedling growth on peatlands disturbed by forestry activity, and observed fairly rapid colonization of disturbed surfaces by *Sphagnum*, sedges, and grasses. Spring preference for burns and brush habitat by mountain caribou in the Spatsizi Plateau Wilderness Area, British Columbia (Boonstra and Sinclair 1984) is consistent with other mountain caribou populations that descend to lower elevations in spring to access newly emerging vegetation. Industrial disturbances are not expected to negatively affect summer nutrition in caribou by reducing forage availability and quality.

During winter, caribou rely heavily on a single food source and winter nutrition could be affected by industrial disturbances that remove mature conifer forests abundant in lichens. Forest management is expected to reduce the short-term availability of lichens for caribou but not their long-term availability. Clearcut harvesting will remove most arboreal lichens and may lengthen the lichen rotation cycle by changing microclimate and substrate (Stevenson 1979; Lesica, McCune, and Cooper 1991; McCune 1993; Goward 1994; Essen, Renhorn, and Peterson 1996). Extreme temperatures and dry conditions on harvested sites may facilitate lichen die-off and slow colonization (Eriksson 1975). Miège et al. (2001a, 2001b) found that greater canopy removal during forest harvesting resulted in lower abundance, diversity and richness of terrestrial lichen as measured 2.5 years post-harvest on mountain caribou winter range in British Columbia. Reductions in slash build-up may be critical to the maintenance of forage lichen abundance (Webb 1998; Miège et al. 2001a). Miège et al. (2001a) found that plots with more than 50% slash cover had 85% less forage lichen than plots with no slash loading. Harris (1996) examined post-harvest regeneration of reindeer lichens (*Cladina* spp.) (N = 51 sample sites) in the boreal forest of northwestern Ontario and found that residual *Cladina* spp. fragments were abundant after harvesting and may facilitate colonization. Relatively high precipitation was suspected to have buffered the negative effects of greater solar radiation and enhanced terrestrial lichen survival and growth on harvested sites. Canopy closure during succession may also limit lichen recovery and Harris (1996) found that lichens were abundant on sites before canopy closure (1 year post-harvest), while nearby sites on similar soils had less lichen after canopy closure (25 years post-harvest).

Reductions in lichen abundance and diversity on harvested sites could reduce caribou forage intake rates or force animals to move to alternate wintering areas (Cumming and Beange 1987). Rominger et al. (2000) conducted feeding trials with three tame woodland caribou (southern mountain population) and found that the dry-matter intake rate and crude protein intake rate were significantly lower in clearcut than in old-growth portions of pens. In the Clay Belt of northeastern Ontario, Wilson (2000) found that winter feeding sites used by woodland caribou had an average biomass of arboreal lichen of 55 kg/ha. Proceviat (2003) found that stands aged 1 to 8 years post-harvest in the same area had arboreal lichen biomass values less than 15 kg/ha; however, mean biomass of arboreal lichens remained greater than 60 kg/ha after 30 years post-harvest. Due to the preference of many woodland caribou populations for mature conifer forests, harvesting that targets late seral stands could potentially affect caribou winter nutrition.

Apart from nutrition, long-term disturbance may also affect caribou energy balance in winter through changes in activity patterns. Bradshaw, Boutin, and Hebert (1998) demonstrated a potential energetic cost to woodland caribou in Alberta (boreal population) from direct disturbances caused by petroleum exploration. Published information on the behavioural responses of woodland caribou to single disturbance events, winter mass loss of caribou, and the energetic costs of movement (McEwan 1970; Dauphiné 1976; Boertje 1985a; Bradshaw 1994) was used to predict the potential energetic costs and mass loss of caribou in relation to observed levels of petroleum exploration activity in northeastern Alberta. Caribou were assumed to lose 10-15% of their autumn mass in winter and the number of

disturbance events required to cause > 15 and > 20% mass loss was estimated to be 20–34 and 41–137, respectively. There were five occasions from 1988 to 1993 when the encounter rate (number of potential encounters per square kilometre) in a particular region and winter exceeded a level expected to result in caribou losing more than the estimated mean 15% autumn mass. There were four occasions when the encounter rate exceeded the lower limit expected to cause > 20% mass loss. Duchesne, Côté, and Barrette (2000) found that the presence of ecotourists caused woodland caribou in Quebec (boreal population) to increase time spent vigilant and standing compared to their behaviour during days without visits. Increased vigilance and standing came primarily at the expense of time spent resting and foraging and caribou reduced time spent foraging as the number of observers increased. Potential effects on caribou condition were not measured; however, range abandonment was not observed and ecotourism was deemed a relatively benign disturbance.

6.4.4 Predation

There is a general consensus that predation acts to reduce the importance of forage as a limiting factor in woodland caribou by holding populations at densities lower than carrying capacities defined by absolute food abundance (Ahti and Hepburn 1967; Bergerud 1974; Thomas and Gray 2002). Even so, predation may influence many aspects of animal decision-making, such as where to feed and what to eat. The best habitat for foraging may not be the best habitat for avoiding predation and animals must balance trade-offs among competing needs so as to improve overall fitness. More time doing one activity means less time to engage in another activity, potentially increasing predation risk or limiting forage intake.

Clear distinctions between nutrient limitation and predator limitation are not easy to assess. Poor food supply may require longer foraging time for gut fill and increase predation risk. An herbivore that is not food limited may still incur greater fitness from increased food availability if there is more time for animals to engage in the non-feeding activities. If exposure to predators does not increase with foraging, then there would be no benefit in minimizing time spent feeding, and the animals' foraging behaviour would reflect nutrient maximization, even when predators limit fitness (Belovsky 1991). To further complicate the matter, habitat selection by caribou at large scales (e.g., for mature conifer forest with relatively poor nutrient availability) may reduce predation risk but may allow or require caribou to spend more time engaged in foraging activity to meet nutritional needs. Caribou reduce predation risk by avoiding areas with higher densities of predators and alternate prey or by spacing out at low densities and giving birth at sites with low predation risk (Bergerud and Page 1987; Seip 1992). Behavioural responses of caribou to predation risk may therefore reduce foraging efficiency and increase competition for food, as caribou forage more frequently in less profitable habitats.

Female woodland caribou that used island and shoreline habitats in Ontario during calving had lower predation risk at the cost of reduced forage availability and quality (Ferguson, Bergerud, and Ferguson 1988; Bergerud, Ferguson, and Butler 1990). Examination of body characteristics of caribou indicated that males that inhabited Pic Island, Lake Superior, had smaller antlers and shorter mean total body length than other woodland caribou in North America. Although densities ranged from 2–7 caribou per km², suggesting that food did not limit population growth, starvation of several animals was evident in one winter when lichen was depleted (Ferguson, Bergerud, and Ferguson 1988). Ferguson, Bergerud, and Ferguson (1988) found that woodland caribou inhabiting areas with predators adjacent to Lake Superior minimized feeding time as an antipredator strategy by selecting forage items with large bite size. On Pic Island, where predators were absent, caribou did not select forage items with larger bite size but spent longer periods foraging to maximize forage intake. The authors suspected this strategy enabled caribou inhabiting an island without predators to compensate for the reduced phytomass and plant diversity. Such data are not definitive and are hindered by a lack of control over site differences that may influence feeding time, regardless of predation pressure.

Poor nutrition may increase susceptibility of animals to predation. In a study of wolf predation on multiple ungulates in Denali National Park, Alaska, Mech et al. (1995) suggested that nutritional condition predisposed ungulate prey to wolf predation. Deep snow may directly affect ungulate prey condition and mobility and thus increase vulnerability to predation by wolves (Nelson and Mech 1986). The mean percent femur marrow fat content ($47 \pm 5\%$, $N = 44$) of caribou during six winters was lower than the 70% value cited by Dauphiné (1971) as a lower limit in body weight. Mech et al. (1995) found that the proportion of wolf kills that were adult female caribou in Denali was greatest during late winter, when females typically have low energy budgets and high reproductive costs associated with late gestation. Adams, Dale, and Mech (1995) found an indirect effect of snow depth during gestation on neonatal predation risk. The birth weight of caribou calves was negatively related to winter snowfall. The mortality rate for neonates was strongly inversely correlated with average birth weight, but neonatal losses were not correlated with spring wolf density or mean calving elevation.

7.0 MANAGEMENT IMPLICATIONS

Resource managers must balance competing land use objectives such as wildlife conservation and industrial development of all forms (e.g. forest management, oil and gas exploration, hydro and transportation infrastructure) while increasing our understanding of natural disturbance dynamics. A better understanding of the relationships among forest management, caribou foraging ecology, and population dynamics is needed to ensure management activities are effective. Human activities may be cumulative with natural disturbance and succession in changing the availability of suitable caribou habitat. The cumulative effects of harvesting, road development, and natural disturbances may cause regenerating forests to remain inaccessible to caribou, especially at the outer limits of continuous caribou range, where opportunities for dispersal may be limited. Provision of a continuous supply of suitable habitat at large spatial scales is expected to improve opportunities for maintaining woodland caribou range occupancy (Brown et al. 2007).

Management strategies to sustain caribou should recognize the ecological complexity of this species and its adaptations to environmental heterogeneity (Klein 1991). Caribou exhibit considerable phenotypic plasticity, as evidenced by the diverse diet and habitat use of different populations throughout the global range of *Rangifer*. Climate extremes, food, predation, insects, parasites, disease, and interspecific competition have all been implicated as factors limiting caribou populations. Population-specific differences in the constraints to caribou survival (e.g., predator densities, habitat availability) call for local solutions to local problems.

7.1 Summary of General Principles

- 1. Behavioural decisions made by woodland caribou and the constraints on their survival are affected by multiple factors and at multiple spatial scales. Strategies employed to maintain or improve caribou foraging opportunities should not be considered in isolation of other important limiting factors.**

The relative importance of nutrition will vary among populations and seasons. In areas where caribou are limited by predation and quantitative estimates of seasonal dietary quality indicate that forage supplies are sufficient, management to enhance the abundance of vascular forage may be counterproductive to caribou needs.

- 2. Adaptive management, based on the best available information, should be employed to address existing conservation concerns for caribou.**

Management strategies that incorporate strong management level-hypotheses should be tested with rigorous experimental designs and use adequate replication and data collection. The information gained from such research should be used to inform management decisions and policy development.

3. Harvested stands that are abundant in forbs and other vascular forage items may provide foraging habitat for caribou in spring and summer, but also have potentially negative effects for predator-prey relationships.

Early seral stages of forests following stand harvesting are not expected to negatively impact the availability of summer forage for caribou; however, their value may be reduced or outweighed by the negative effects of increased predators and alternate prey over longer time periods.

4. Industrial or recreational activities that cause repeated and direct disturbance of caribou during late winter should be minimized through appropriate management actions.

Caribou enter a negative energy balance during winter and use stored body fat reserves to supplement winter food resources. Behavioural adaptations to minimize heat loss and energy expenditure may include reduced movement and selection of habitats with improved foraging opportunities and thermal cover. Human disturbances that force caribou to move to less favourable wintering areas or increase their energy expenditures should be minimized through timing or access restrictions.

7.2 Stand-Level Recommendations

1. Avoid excessive accumulation of slash (i.e., downed woody debris) on harvested sites.

Some slash, in the form of well decomposed woody peat, may provide a favourable microclimate and substrate for *Cladina* spp. (Eriksson 1975); however, extensive slash accumulation can impede caribou movements and reduce forage abundance or accessibility (Miège et al. 2001a). Slash should be piled in a manner that does not create a barrier to caribou movement or damage existing terrestrial lichens (Miège et al. 2001a).

2. Where harvest machinery is expected to severely damage terrestrial lichen, winter harvest operations should be considered as a means to minimize site disturbance.

Timing operations to commence immediately after freeze-up, with most or all work completed in the earlier part of the winter season, may reduce site disturbance to forage. Managers should evaluate the importance of existing large lichen mats as caribou foraging areas and consider avoiding operations in areas where damage is expected to reduce caribou forage intake. Risk is greater on shallow soils and very dry sites and lower on organic sites with a thick fibric layer.

3. Where arboreal lichen is important winter forage, residual tree retention strategies should include trees that support large amounts of lichen species.

Management strategies that ensure the continued accessibility of lichen biomass on standing trees (i.e., sufficiently low on stem), as well as lichen available on windthrow and litterfall (Terry, McLellan, and Watts 2000) could help to retain foraging opportunities in harvested areas. Stand retention strategies should favour trees with high biomass of arboreal lichen and high windthrow recruitment.

4. Continue to experiment with careful cut and partial harvesting techniques that include strategies to maintain caribou forage.

Compared to clearcutting, partial harvest systems could maintain habitat value with minimal loss of forage species (Miège et al. 2001b). However, the long-term effects of different retention strategies

and repeated site entries to lichen abundance and caribou behaviour are unclear and require long-term monitoring studies.

Tree thinning that increases light availability and promotes growth of lichens or other vascular forage species could improve caribou foraging opportunities; however, the extended disturbance to these sites could have negative effects on the abundance of alternate ungulate prey and thus caribou range occupancy.

7.3 Landscape-Level Recommendations

1. Woodland caribou have evolved on a landscape that includes fire, and management strategies based on natural disturbance dynamics are expected to maintain caribou foraging habitat.

Managers should take an ecosystem approach to caribou conservation and strive to reproduce the pattern and structure of vegetation similar to that created by natural fires within the limits of silvicultural limitations. Such natural disturbance paradigms for management have been shown to be useful, but are not without limitations (NCASI 2006). Nonetheless, fire and gap dynamics have played a significant role in the creation of structural and compositional diversity in late seral stage black spruce boreal forests and may be important in the creation of summer foraging habitat when caribou diet is diverse. Where caribou range overlaps with predators and alternate prey, management strategies should provide a sustainable mosaic of caribou habitat that was traditionally maintained by fire.

2. Forest management strategies for woodland caribou could benefit from the incorporation of dietary quality assessment at the appropriate spatial scale(s).

Within larger forest patches, and as appropriate for each vegetation community and caribou population, stand retention strategies should aim to supply an abundance and diversity of summer forage items. A mix of open and closed canopy stands may improve foraging opportunities for caribou in summer. During early summer, open canopied stands with high light exposure may provide abundant forbs and deciduous shrub leaves. During the latter part of summer, when dry conditions reduce plant quality, closed canopies may provide more succulent forage than would be available in open sites (Servheen and Lyon 1989). Harvesting methods that retain thermal cover may aid in delaying phenological development in vegetation (Servheen and Lyon 1989).

Stands rich in terrestrial lichens, particularly drier upland sites, should be favoured for retention as caribou winter foraging habitat throughout woodland caribou range. Where succession of pine- or spruce-lichen stands to a moss-dominated understory is expected to reduce caribou winter forage, natural or artificial disturbance may be necessary to ensure long-term productivity of winter forage (Schaefer and Pruitt 1991; Sulyma and Coxson 2001).

Given that closed canopy forests produce very little forage, and the oft used method of estimating canopy cover using spherical densiometers is badly biased, it would help to quantify the range of canopy cover under which reasonably dense and nutritious understory forage might be anticipated.

3. Harvesting strategies should provide habitat that permit caribou to forage in response to changing snow conditions and in relation to important winter forage items.

Areas of excessively deep snow should be considered low-value winter foraging habitat for caribou, except where sufficient snowfall is required to access arboreal lichen. Excessive snow accumulation can inhibit caribou movements, increase energy expenditure, and reduce foraging efficiency in winter. A number of researchers have suggested that the threshold depth for cratering by caribou in winter is 50-80 cm (Stardom 1975; LaPerriere and Lent 1977; Darby and Pruitt 1984).

Conversely, where arboreal lichens are a critical food source in winter, low intake may occur during winters with low snowfall that provides less lift to access lichens in trees (Rominger, Robbins, and Evans 1996). In this case, topography that provides sufficient snow accumulation on the ground and snow clearance from tree canopies should be considered when delineating winter foraging habitat. Sites with a combination of high wind and solar radiation may facilitate formation of a hard snow pack. An increased understanding of the influence of forest type, stand density, and composition variation on snow redistribution by wind and sublimation in relation to topography would be useful.

Vascular shrub species may be important alternate forage items during autumn and winter in relation to changing snow conditions. Areas with minimal snow depth may improve access to green forage and should be considered when maintaining early winter foraging habitat.

8.0 KNOWLEDGE GAPS AND RESEARCH NEEDS

Given the vulnerability of woodland caribou to disturbance and evidence of large-scale range recession (Schaefer 2003), management actions based on inaccurate or incomplete information on caribou foraging and habitat ecology could hinder conservation efforts, despite good intentions. Given that woodland caribou prefer late successional forest, the long time frame required to restore caribou habitat during forest management (Brown et al. 2007) could result in poor management decisions having long-term, possibly irreversible effects on caribou range occupancy.

A key assumption of many boreal woodland caribou studies, although rarely tested, was that population densities were below food-based carrying capacities. Our review of nutritional effects in ungulates suggests that coarse estimates of forage availability and inferences drawn from population parameters may underestimate nutritional effects in woodland caribou. In the absence of reliable estimates of the nutritional requirements of woodland caribou, our review has relied heavily on nutritional information for barren-ground caribou and reindeer. The applicability of this information to woodland caribou is uncertain and requires further investigation. Variations in the duration of the growing season and plant productivity in different environments mean that sedentary woodland caribou inhabiting boreal forest may exhibit different annual cycles in growth and nutritional requirements. Dietary and energetic constraints on woodland caribou should be examined in relation to demographic parameters that vary independently of predation (Boertje 1990). Identification of nutrient limitation in a woodland caribou population would require information on the diet quality, diet composition, activity, and energy requirements of study animals from the population of interest, as well as comparative data on dry matter intake and nutrient intake by a well nourished herd.

There has been little synthesis of the relative roles of different ecological factors in affecting population change in woodland caribou. A fundamental problem with using population parameters to infer the importance of limiting factors is that dependent variables (e.g., recruitment rate or pregnancy rates) are used to explain ecological interactions without proper quantification of the assumed causative factors (i.e., independent variables). As a result, it becomes difficult to assess the relative explanatory power or potential interactions of top-down and bottom-up forces in relation to trends in population change. There is a need for a more inclusive approach to testing the causes of caribou population declines. Studies that demonstrate correlational trends between potential threats (e.g., industrial disturbance) and caribou behaviour or population response have limited value in understanding the mechanism of decline. Further, experimental studies of caribou population responses to wolf reduction clearly demonstrate that wolf predation can limit caribou, but observing an increase in caribou when predators are removed is a rather predictable outcome and does not demonstrate the lack of importance of other factors in affecting populations. Although some studies have identified multiple factors that influence the dynamics of caribou populations, few studies explicitly attempt to document where and when each is important and how they vary and interact.

How temporal variation in top-down and bottom-up factors affect caribou population dynamics is poorly understood and requires further investigation.

8.1 Application of Trophic Interaction Models

Studies that are focused on trophic interactions, as opposed to individual species conservation, emphasize that top-down and bottom-up forces act simultaneously on populations and suggest that dichotomies between the two forms of regulation are largely artificial (Oksanen et al. 1981; Leibold 1989; Hunter and Price 1992; Menge 1992). Current theories on trophic interactions suggest that the number of trophic levels in food chains determines plant standing crop, but plant productivity constrains the number of trophic levels, thus ultimately constraining the top-down forces that may regulate standing crops (Power 1992). Under such a model, top-down forces may dominate trophic dynamics, but the bottom-up attributes of the system are ultimately responsible for food web structure (Fretwell 1987). Such models necessarily simplify the natural world; competitive interactions, anti-predator adaptations, and variation in foraging efficiency of ungulates or hunting efficiency in predators may alter the relative importance of top-down and bottom-up forces. Hunter and Price (1992) recognized the role of environmental heterogeneity in their development of a trophic interaction model to explain the role of top-down and bottom-up forces in terrestrial systems. From the broad perspective of ecosystem organization, variation in plant quantity and quality are expected to determine spatial and temporal patterns in herbivore populations, as well as their initial carrying capacities. Heterogeneity among herbivores, in turn, determines the distribution and abundances of predators in the system. Species at any level of the trophic web can dominate population dynamics.

Serious methodological issues hinder our ability to test such models for natural systems involving caribou. Power (1992) questioned our ability to measure the appropriate independent and dependent variables in trophic models. For example, the level of primary forage productivity and biomass of caribou and moose is difficult to determine in remote areas of boreal forest. Also, the spatial scale of home range occupancy of consumers may differ and be greater than the scale of heterogeneity in primary plant productivity (Power 1992). This may be a problem for woodland caribou that occupy large home ranges (e.g., thousands of square kilometres) and inhabit relatively homogeneous black spruce boreal forest (Brown 2005). Conversely, the home range of moose is two orders of magnitude smaller and generally less than 50 km² (Doerr 1983; Cederlund and Sand 1994). Finally, dynamic feedbacks, such as omnivory, adaptive anti-predator behaviour (e.g., migration), and forest succession may make the outcome of trophic interactions time-dependent (Power 1992).

As noted by Hunter and Price (1992), cataloguing the outcome of single-factor studies and assessing the relative importance of predators, climate, or forage, based on the number of manuscripts in support of each, tells us little about how nature works. An understanding of the mechanisms driving caribou population change can only be gained by employing study designs that simultaneously address multiple parameters across multiple trophic levels. Existing evidence suggests the importance of alternate prey in caribou-wolf interactions and future empirical investigations should include evaluation of the role of environmental heterogeneity at each trophic level, in terms of density and diversity of forage plants, ungulates, and predators.

8.2 Summary of Research Needs

1. A better understanding of woodland caribou foraging ecology and nutrition is required to properly evaluate its effect on population parameters.

For *Rangifer* spp., there are strong indications that nutrition, growth, productivity, and survival are linked; however, our knowledge of these relationships is incomplete and additional information is needed to guide management. Research should be used to determine seasonal patterns in diet composition and quality, nutrition and energy balance, and the consequences to fitness that result

from habitat selection at larger spatial scales. There is a need to identify thresholds in nutritional condition and range quality and their relationships to reproductive parameters in woodland caribou.

2. Multifactorial hypothesis testing is needed to better understand interactions among limiting factors that may affect caribou populations.

Research aimed at deciphering the mechanism of caribou declines should include appropriate methodologies to isolate the relative importance of habitat quality, predation, weather, and other factors that may affect caribou populations. Research should address the extent to which low calf recruitment is due to low pregnancy rates, low parturition rates or high calf mortality, as well as interactions among factors that may affect vulnerability to predation. Variables that should be considered include nutrition, range quality, weather, densities of predators and alternate prey, and predation rates on different prey. Captive studies could be combined with field studies so as to isolate and test the effects of nutrition on caribou nutritional condition and reproduction. Variables that should be considered include physical condition, pregnancy rate, parturition rate, age of first reproduction, calving dates, calf mass at birth, and survival.

3. The effects of herbicides on summer and winter forage availability require further study.

The effects of herbicides on caribou forage availability are complicated by seasonal changes in diet and hypothesized changes to predator-prey relationships in early seral forests. On the one hand, herbicides may have a positive effect on terrestrial lichens if competing vegetation is reduced; however, this would include a reduction in availability of vascular plants eaten by caribou during the summer growing season. Due to the abundance of moose browse in early seral forests following harvest, application of herbicides could minimize browsing opportunities for moose and thus minimize potential changes to caribou predator-prey dynamics. Ultimately, this could have greater importance to caribou population declines than changes in forage availability, but such subtle interactions are untested. Examination of the potential benefits and costs of herbicide use to caribou foraging strategies and population dynamics could improve management initiatives.

4. Fine-scale studies of foraging behaviour by caribou in summer are needed to gain a more complete picture of the temporal patterns in caribou response to variation in forage availability.

Most foraging behaviour studies of woodland caribou have been limited to winter due to the importance of lichen in caribou diet. Empirical data is sparse for both summer and winter concerning the relative abundance of different forage species necessary for caribou to forage at a feeding site. Optimal foraging theory should be explored as a tool to evaluate behavioural decisions made by caribou in relation to limiting factors.

5. The hypothesized link between habitat alteration and caribou mortality should be addressed using appropriate experimental design and hypothesis testing, integrated with forest management planning that carefully monitors short- and long-term treatment effects.

Testing of the link between habitat alteration and caribou declines should include careful monitoring of changes in population parameters of caribou, predators, and alternate prey. Evaluation of the effects of forest management on caribou nutrition will require more than just measuring changes in plant distribution and productivity in relation to habitat alteration and forest succession. Industrial disturbances could alter the spatial and temporal availability of forage species and influence foraging energetics by affecting caribou movement rates and energy balance (Terry, McLellan, and Watts 2000); however, empirical data pertaining to forestry disturbance are currently lacking to test this hypothesis.

9.0 CONCLUSIONS

Current evidence suggests that caribou respond to variation in forage availability at relatively fine scales, such as movement within seasonal ranges or daily areas of selection. Seasonal range selection that improves foraging opportunities is apparent for mountain caribou that subsist on an arboreal lichen diet in winter and select habitats with improved foraging opportunities in relation to snow conditions and topography. Forest management is not expected to negatively affect the availability of summer forage for woodland caribou. The greatest potential for forest management to impact woodland caribou populations may lie in its effect on vegetation assemblages and consequently, predator-prey dynamics.

Our review of available literature supports the conclusion that predation has been an important factor affecting the population dynamics of woodland caribou and that predation has had a substantial influence on the evolutionary strategy of woodland caribou. Preference by caribou for mature conifer forest is widely acknowledged and conversion of mature conifer forests to early seral stages are strongly implicated in caribou declines. Although the availability of vascular forage is not expected to be lower in early seral forest, changes in plant assemblages are associated with changes in the distribution and densities of ungulates and their predators. In spite of relatively high availability of vascular plants in early seral forest, caribou largely avoid or underutilize these habitats. Woodland caribou densities are substantially lower where sedentary populations share range with high densities of predators and alternate prey, compared to migratory populations where alternate prey are reduced or absent. Evidence of regulation by food limitation is lacking in sedentary woodland caribou populations in the boreal forest; however, the effects of food limitation on population parameters and the mechanism by which food may limit individual fitness has not been adequately addressed in available literature.

Constraints on caribou fitness may vary along a continuum in time and space and improved understanding of the interactions among factors is needed in developing management strategies that address the diverse needs of wildlife. Evidence of predator limitation should not imply that food availability is not important to caribou populations. Even if predator densities or predator-induced mortality rates are high for a caribou population, assessing the importance of food cannot be accomplished without careful examination of caribou foraging behaviour and nutrient budgets. Although predation can hold caribou populations at low densities, Boertje (1990) suggested that caribou nutrition limitation can be expected to occur over a wide range of caribou densities, due to the range of factors that can influence nutrition (e.g., behaviour, climate, and vegetation). The simultaneous importance of food and predators has been clearly demonstrated for other predator-prey systems under controlled experimental conditions (Gratton and Denno 2003). Deciphering the relative roles of top-down and bottom-up forces could affect how management activities should proceed and similar models should be developed for forest-dwelling woodland caribou populations. Even for populations that are held below carrying capacities defined by food, the absolute availability of food may be less constraining to fitness than the quality of forage on selected ranges. For example, caribou selection of mature conifer forest reduces predation risk but may limit the availability of forage items to abundant but less nutritious species (e.g., lichens versus vascular plants).

While we accept the commonly held view that predation has a major effect on woodland caribou behaviour and population change, the importance of bottom-up forces to herbivores should not be underestimated. Empirical studies of other *Rangifer* spp. indicate that nutrition, growth, productivity, and survival are closely linked. Hunter and Price (1992) offered a compelling comment regarding the importance of bottom-up forces in food webs: "...the removal of higher trophic levels leaves lower levels intact (if perhaps greatly modified), whereas the removal of primary producers leaves no system at all."

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