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ECOLOGICAL INTERACTIONS AMONG CARIBOU, MOOSE, AND WOLVES: LITERATURE REVIEW

TECHNICAL BULLETIN NO. 893
DECEMBER 2004

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PRESIDENT'S NOTE

Most populations of forest-dwelling (or woodland) caribou and reindeer (*Rangifer tarandus caribou*) in Canada and elsewhere are declining. Excessive predation, largely by wolves (*Canis lupus*), and hunting are widely believed to be the direct or proximate causes. The declines are complex because forest harvesting, especially clearcutting of older-aged boreal forests, is hypothesized to be indirectly responsible by exacerbating the effects of hunting and predation. Inasmuch as forestry practices have been implicated in the widespread caribou population declines and because the woodland caribou was designated as nationally threatened in Canada in May 2002 under the Federal Species at Risk Act, woodland caribou are of prime importance to the forest products industry in Canada.

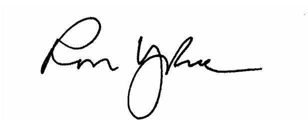
The most widely described hypothesis for forest harvesting indirectly exacerbating predation and hunting effects on caribou holds that extensive clearcut forestry operations result in large areas with deciduous vegetation for 5-15 years. Such browse allows populations of moose (*Alces alces)* to increase. Subsequently, the greater abundance of moose is thought to lead to increased populations of wolves, which in turn then exert greater pressure on the caribou, which are more vulnerable to wolves than are moose. In addition, the understory vegetation promotes growth of black bear (*Ursus americana)*, which prey upon newborn caribou calves. Concomitantly, the forestry operations provide greater access to woodland caribou by hunters.

NCASI-Canada commissioned a scientific review of the literature regarding the central hypothesis that increases in one species (moose) will increase the predator population (wolf) and increase predation on associated prey species (caribou). Potential solutions for mitigation and recovery, particularly in forest management practices, are also examined. The goal is to inform forest managers and decision makers who endeavour to maintain viable populations of woodland caribou while simultaneously deriving economic values from forests.

The review points out that woodland caribou have disappeared in much of the southernmost parts of their range across Canada, including all of the Maritime Provinces. They no longer occur in the New England or the Great Lakes states, while a small herd persists in the Selkirk Mountains of Idaho and Washington. They occupy large home ranges, undertake extensive seasonal movements, and generally avoid areas with little forest. They particularly exploit mature and over-mature conifer stands with irregular structure. Such stands are less suited to other hooved mammals (ungulates), or to wolves and black bears. Some woodland caribou live in muskeg, fens, and bogs in northern Alberta, Saskatchewan, and part of Quebec and the Labrador Peninsula. Such areas are of little importance to commercial forestry. In winter, terrestrial lichens (both ground and arboreal varieties) provide important forage in many areas, often in century-old forests.

Strategies for protecting and/or restoring populations while allowing forest harvesting historically involved a land allocation process in which crucial habitats for calving, breeding, and wintering were identified and protected. In addition, important travel routes were located and forests there were maintained as intact travel corridors. More recently, an ecosystem-oriented approach has been advocated that includes three primary aspects: a) large forest blocks are protected; b) timber harvesting is concentrated in extensive management blocks where irregular forest structures, age classes, composition, and spatial distribution would be maintained via silvicultural practices that emulate patterns created by natural disturbances inherent to each region; and c) zones for intensified forestry are identified to increase timber productivity to compensate for losses due to protected areas. The latter component has apparently not yet been realized in many areas.

Such conservation strategies comprise large-scale land management experiments that offer unique opportunities to learn while managing—adaptive management. In such experiments, forest managers, scientists, the public, and others collaborate to monitor responses (such as populations of caribou, wolves, and moose) to implementation of various plausible land and resource management alternatives, including reduction in hunting. Because these opportunities exist, the technical review describes important aspects of woodland caribou ecology, with particular emphasis on interactions among caribou, forestry, and predator-prey dynamics. This review identifies important information gaps that might be filled via adaptive management experiments or other focused research.



Ronald A. Yeske

December 2004

MOT DU PRÉSIDENT

La plupart des populations de caribous et de rennes des bois (*Rangifer tarandus caribou*) dépendant de la forêt sont en déclin au Canada et ailleurs. De façon générale, on croit que la chasse et la prédation excessive, principalement par les loups (*Canis lupus*), sont les causes directes ou immédiates de cette situation. Cette décroissance est complexe car on suppose que la récolte forestière, surtout la coupe à blanc des forêts plus anciennes de la région boréale, n'a qu'une influence indirecte et ne fait qu'empirer les effets de la chasse et de la prédation. Le caribou des bois revêt une grande importance pour l'industrie canadienne des produits forestiers dans la mesure où les pratiques forestières sont associées à la diminution généralisée des populations de caribou. De plus, le Canada l'a désigné « espèce nationale menacée » en mai 2002 en vertu de la *Loi sur les espèces en péril*.

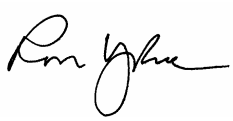
L'hypothèse la plus répandue sur l'accélération indirecte par la récolte forestière des effets de la chasse et de la prédation sur le caribou est que l'exploitation de la forêt par une coupe à blanc intensive produit de très grandes zones de végétation de feuillus pendant une période de 5 à 15 ans. De tels brouts augmentent les populations d'orignaux (*Alces alces*). On pense qu'une plus grande abondance d'orignaux mène ensuite à une hausse des populations de loups qui, à leur tour, exercent une pression accrue sur le caribou, espèce plus vulnérable aux loups que ne l'est l'orignal. De plus, la végétation de sous-bois augmente le nombre d'ours noirs (*Ursus americana)* qui eux s'attaquent aux nouveaux-nés des caribous. En même temps, les activités forestières assurent aux chasseurs un plus grand accès au caribou.

NCASI-Canada a commandé une revue scientifique de la littérature sur la principale hypothèse qui veut qu'une augmentation de la population d'une espèce (orignal) accroisse celle d'un prédateur (loup) et intensifie la prédation sur les espèces proies associées (caribou). Les auteurs ont examiné les solutions possibles d'atténuation du problème et de renouvellement de la population, en particulier dans le cadre des pratiques d'aménagement forestier. L'objectif de la présente étude est d'informer les gestionnaires forestiers et les décisionnaires qui font tout pour maintenir des populations viables de caribous des bois tout en profitant de la valeur économique des forêts.

La présente étude révèle que le caribou des bois a disparu d'une grande partie de son territoire le plus méridional au Canada, entre autres toutes les provinces maritimes. On ne le trouve plus en Nouvelle-Angleterre ou dans les États de la région des Grands Lacs, mais une petite harde subsiste dans les monts Selkirk de l'Idaho et de l'État de Washington. Il occupe de vastes domaines vitaux, se déplace sur de grandes distances au fil des saisons et, de manière générale, évite les secteurs où il y a peu de forêts. Il profite particulièrement des peuplements de conifères matures et anciens qui ont une structure irrégulière. Ces derniers conviennent moins bien aux autres mammifères pourvus de sabots (ongulés), aux loups et aux ours noirs. On retrouve certains caribous des bois dans des muskeg, de même que dans des tourbières minérotrophes ou ombrotrophes du nord de l'Alberta, en Saskatchewan ainsi que dans une partie du Québec et de la péninsule du Labrador. En matière d'exploitation forestière commerciale, ces territoires sont peu intéressants. En hiver, les lichens terrestres (variétés au sol et arboricoles) procurent une quantité importante de fourrage dans de nombreux endroits, souvent dans des forêts centenaires.

Les stratégies de protection et de restauration des populations ont traditionnellement fait appel à un processus d'affectation des terres où l'on identifiait et protégeait des habitats essentiels pour la reproduction, la mise bas et l'hivernation tout en permettant la récolte forestière. En plus, on repérait les principales routes de déplacement et on préservait la forêt autour afin qu'elle serve de couloir de déplacement. Plus récemment, on recommandait l'utilisation d'une approche orientée sur les écosystèmes qui reposait sur les trois aspects primaires suivants : a) la protection de vastes blocs de forêts, b) la concentration de la récolte de bois dans d'importants blocs d'aménagement avec conservation des structures irrégulières de la forêt, des classes d'âge, de la composition et de la distribution spatiale au moyen de pratiques de sylviculture qui simulent le résultat des perturbations naturelles propres à chaque région; et c) l'identification de zones dédiées à l'exploitation forestière intensive afin d'accroître la productivité pour compenser les pertes engendrées par les aires protégées. Cette dernière composante ne semble pas s'être concrétisée dans bon nombre d'endroits.

De telles stratégies de conservation constituent des expériences d'aménagement des terres à grande échelle procurant des occasions uniques d'apprendre tout en gérant (gestion adaptative). Au cours de ces expériences, les gestionnaires forestiers, les scientifiques, le public et d'autres collaborent au suivi des réponses, comme celles des caribous, des loups et des orignaux, à la mise en œuvre de diverses solutions crédibles de gestion des ressources et des terres, incluant une réduction en matière de chasse. La présente revue technique décrit les aspects importants de l'écologie du caribou des bois avec une attention particulière sur les interactions entre le caribou, la foresterie et la dynamique « prédateur-proie » étant donné qu'il existe des solutions. Elle met en évidence les principales informations qui manquent et qui peuvent être comblées au moyen d'expériences de gestion adaptative ou d'autres études ciblées.



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Décembre 2004

ECOLOGICAL INTERACTIONS AMONG CARIBOU, MOOSE, AND WOLVES: LITERATURE REVIEW

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ABSTRACT

Woodland caribou populations are declining in many areas of Canada and there is concern that the decline may be associated with timber harvesting. Caribou, moose, and wolves share a long evolutionary history and their relationships may become altered by large-scale landscape disturbance. This technical bulletin presents a review of scientific literature pertaining to the hypothesis that increases in moose and wolf populations after timber harvesting have adverse effects on caribou. Specifically, large-scale habitat changes that have allowed moose populations to increase and thereby sustain higher wolf numbers presumably have resulted in excessive predation on caribou, apparently resulting in caribou population declines.

Differentiation of caribou by ecotype rather than phenotype has advantages for conservation purposes. The "forest-dwelling" ecotype of woodland caribou often move across extensive areas at low densities, and populations have been difficult to define and monitor. Woodland caribou and moose often partition habitats on the landscape, such that caribou tend to graze mostly lichens and occupy nutrient-poor forest types, while moose browse vascular plant species such as willows, which are associated with more productive environments. The relatively high reproductive potential of moose enables their populations to respond rapidly to a superabundance of forage produced after forest fires or logging. Carrying capacities for caribou increase more slowly and are likely to decline suddenly after such disturbances.

Some caribou populations experience the effects of multiple predators such as grizzly bears, black bears, cougars, coyotes, wolverines, lynx, eagles, and humans. The predation rate is determined by the predator's functional and numerical responses to changes in prey density. Some of the most viable caribou populations are those that employ anti-predator strategies which reduce encounter rates with wolves at calving time. These include migrating away from wolf denning habitat, seeking refuge on islands, bogs, and shorelines, and parturient females dispersing away from caribou concentrations.

Food selection by wolves is influenced by profitability relative to energetic costs of travel, especially in snow, and dangers in attacking large prey. If primary prey become less abundant, it may be more profitable for wolves to switch to another prey species. Critical thresholds in predator and prey densities affect population dynamics. In some areas, woodland caribou populations are too low to sustain wolves without alternate prey such as moose. Caribou appear in decline or may be eliminated in areas where wolves exceed critical densities. On the other hand, caribou populations have been known to change by several orders of magnitude, especially where herds are migratory and alternate prey for wolves are low in numbers or lacking. Several factors such as age, nutritional state, season, disease, parasites, and genetic load are capable of affecting caribou vulnerability to predation. The very young and the very old are usually the most heavily preyed upon.

Recent changes in ungulate and carnivore distributions may be influenced by climate change and human activities. Measures implemented to conserve woodland caribou populations include hunting restrictions, reintroductions, predator control, parks and protected areas, and national and provincial recovery strategies.

Caribou habitat and commercial forest overlap in some regions and the effects of forestry on caribou vary according to the ecological setting. Roads and seismic-exploration trails may allow greater penetration of wolves into areas occupied by caribou, and vehicular traffic may displace caribou into closer proximity to moose and wolves. The design of forest harvest pattern may significantly affect predator-prey relationships. A mosaic of small cutovers across extensive areas or cutting upland sites in close proximity to fen/bog habitat may be undesirable for caribou management. Silvicultural activities that are compatible with lichen retention and discourage moose browse production are expected to be the most beneficial for caribou. Although fire control may conserve caribou habitat in the short term, fire is an integral part of the boreal forest and this animal is adapted to a fire environment. Further research and management needs have been recommended.

KEYWORDS

Alces alces, boreal forests, *Canis lupus*, clearcutting, moose, predator-prey dynamics, *Rangifer tarandus caribou*, silviculture, timber harvesting, wolves, woodland caribou

RELATED NCASI PUBLICATIONS

Technical Bulletin No. 562. (February 1989). *Mountain goat/forest management relationships: A review.*

LES INTERACTIONS ÉCOLOGIQUES ENTRE LE CARIBOU, L'ORIGNAL ET LE LOUP : UNE REVUE DE LA LITTÉRATURE

BULLETIN TECHNIQUE NO. 893
DÉCEMBRE 2004

RÉSUMÉ

Dans bien des endroits au Canada, on note que les populations de caribous des bois diminuent et on craint que ce déclin soit relié à la récolte du bois. Le caribou, l'orignal et le loup partagent une longue histoire évolutive et verront peut-être leurs rapports modifiés par des perturbations à grande échelle du paysage. Le présent bulletin technique est une revue de la littérature scientifique axée sur l'hypothèse qui veut qu'une augmentation dans les populations d'orignaux et de loups après une récolte du bois a des conséquences négatives sur le caribou. Plus précisément, on croit que la hausse des populations d'orignaux observée dans les habitats ayant subi des modifications à grande échelle permet d'assurer la survie d'un plus grand nombre de loups entraînant vraisemblablement une prédation excessive sur les populations de caribous, menant possiblement ces derniers à leur déclin.

En matière de conservation, la différentiation des caribous par écotype plutôt que par phénotype présente des avantages. Les caribous des bois de l'écotype qui dépend des forêts se déplacent souvent sur de grandes distances et en petit nombre. Il est donc difficile de caractériser et de suivre leurs populations. Les caribous des bois et les orignaux se partagent souvent les habitats. Les caribous ont tendance à brouter les lichens et à occuper les forêts pauvres en nutriments tandis que les orignaux se nourrissent de plantes vasculaires (par ex. le saule) associées à des environnements plus productifs. Le potentiel de reproduction relativement élevé de l'orignal lui permet de répondre rapidement à une surabondance de forage qui suit un feu de forêt ou la récolte du bois. La capacité de charge du caribou augmente plus lentement et est susceptible de décroître rapidement après de telles perturbations.

Certaines populations de caribous subissent les effets de la présence de multiples prédateurs comme les grizzlys, les ours noirs, les couguars, les coyotes, les carcajous, les lynx, les aigles et les humains. La réponse numérique et fonctionnelle d'un prédateur aux changements de densité de ses proies détermine le taux de prédation. Les populations de caribous les plus viables sont celles qui font appel à des stratégies anti-prédatrices qui permettent de réduire le taux de rencontre avec les loups au moment de la mise bas, entre autres celles qui consistent à s'éloigner de la tanière des loups, à chercher refuge sur des îles, dans des tourbières ou sur un rivage, ou à s'écarter du troupeau dans le cas des femelles parturientes.

Le choix de la nourriture des loups est conditionné par le rendement en fonction des coûts énergétiques de déplacement, notamment dans la neige, et les dangers de s'attaquer à de larges proies. Si la proie principale devient moins abondante, il peut être plus avantageux pour les loups de s'attaquer à une autre espèce. Des seuils critiques dans la densité des prédateurs et des proies influencent la dynamique des populations. Sans la présence d'une autre espèce comme l'orignal, les populations de caribous des bois sont trop faibles à certains endroits pour assurer la subsistance des loups. Elles semblent diminuer ou peuvent disparaître dans les endroits où le nombre de loups dépasse les seuils de densités critiques. Par contre, on sait que les populations de caribous peuvent changer de plusieurs ordres de grandeur, surtout dans le cas où les hardes sont migratrices et la quantité de proies de substitution pour les loups est basse ou nulle. Plusieurs facteurs peuvent agir sur la vulnérabilité du caribou à la prédation, notamment son âge, son état nutritionnel, les saisons, les maladies, les parasites et son fardeau génétique. Les proies favorites sont habituellement les très jeunes caribous et les très vieux.

Les changements climatiques et les activités humaines ont peut-être provoqué les récentes variations dans les distributions des ongulés et des carnivores. Les mesures mises en œuvre pour conserver les populations de caribou comprennent des restrictions en matière de chasse, la réintroduction de l'espèce, le contrôle des prédateurs, la création de parcs et d'aires protégées, de même que l'implantation de stratégies de renouvellement par le gouvernement fédéral et les provinces.

L'habitat du caribou et la forêt commerciale se chevauchent dans certaines régions, mais l'impact des activités forestières varie en fonction du contexte écologique. Les routes et les sentiers de prospection sismique peuvent favoriser une plus grande pénétration des loups dans les zones occupées par les caribous, et le trafic des véhicules peut déplacer les caribous à proximité des orignaux et des loups. La conception de la répartition des coupes forestières peut influencer la relation « prédateur-proie » de façon significative. En matière de gestion du caribou, il peut ne pas être souhaitable de faire appel à une mosaïque de petites aires de coupe sur de grandes surfaces ou de d'effectuer une coupe en hautes terres près d'une tourbière. Les activités de sylviculture compatibles avec la rétention du lichen et défavorables à la production de brout pour l'orignal sont les plus susceptibles d'être bénéfiques au caribou. La maîtrise des incendies de forêt permet de conserver l'habitat du caribou à court terme. Cependant, les incendies font partie intégrante de la forêt boréale, et le caribou s'est adapté à leur existence dans son environnement. La présente étude identifie les besoins en matière de gestion et de recherches futures.

MOTS CLÉS

Alces alces, *Canis lupus*, caribou des bois, coupe à blanc, dynamique prédateur-proie, forêts boréales, loups, orignal, *Rangifer tarandus caribou*, récolte du bois, sylviculture

AUTRES PUBLICATIONS DE NCASI DANS CE DOMAINE

Bulletin technique No. 562. (février 1989). *Mountain goat/forest management relationships: A review.*

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ECOLOGICAL INTERACTIONS AMONG CARIBOU, MOOSE, AND WOLVES: LITERATURE REVIEW

1.0 INTRODUCTION

Populations of woodland/forest caribou and reindeer (*Rangifer tarandus*) are declining and threatened throughout the circumpolar region, possibly because of the interaction of human disturbance and predation. In contrast, insular and montane populations are relatively stable, and barren-ground populations are capable of synchronous growth to high numbers and may experience cyclic changes (Mallory and Hillis 1996).

The "forest-dwelling" woodland caribou was designated as nationally *Threatened* by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in May 2002 under the Federal Species at Risk Act. Most, if not all, Canadian jurisdictions where woodland caribou remain have declining populations. Caribou have disappeared in much of the southernmost parts of their range across Canada, including all of the Maritime Provinces. In the continental United States, they no longer occur in the New England or the Great Lakes states, while a small herd persists in the Selkirk Mountains of Idaho and Washington (Thomas and Gray 2002).

Large-scale human activities in caribou range have been in the form of agricultural land clearing, mineral extraction, hydroelectric development, transportation infrastructure, oil and gas exploration, and timber harvesting. Schaefer (2003) expressed the concern that half of the historic range of woodland caribou in Ontario was lost from 1880 to 1990, and the southern limits of current caribou range strongly coincide with the northern front of forest harvesting. In mountains of British Columbia, lower elevations were the first to be impacted by development, and logging now extends to higher elevations and caribou winter range (Stevenson 1991). Similar concerns are also evident in other parts of Canada including the Yukon (Farnell et al. 1998), Alberta (Smith et al. 2000), Saskatchewan, (Rettie and Messier 1998), Manitoba (Hirai 1998), Quebec (Courtois 2003), and Newfoundland (Chubbs et al. 1993).

Wolves (*Canis lupus*) are obligate predators of ungulates (Mech 1970), and caribou are a source of food for wolves wherever they co-occur. Predation has been identified by numerous researchers as a major factor contributing to declines or holding caribou herds at low densities in North America (e.g., Schaefer et al. 1999, Crête and Desrosiers 1995; Rettie and Messier 1998; Edmonds 1988; James 1999; Seip 1992; Bergerud and Elliot 1986; Bergerud and Elliot 1998; Farnell and McDonald 1988; Hayes et al. 2003; Walters et al. 1981; Gasaway et al. 1983; Boertje et al. 1996).

Forest resource managers increasingly need reliable information about the effects of their management activities on a variety of resources. For example, even though much is known about the direct effects of forestry activities on wildlife, there may be indirect effects as well. Often, indirect effects are subtle and more difficult to measure because of ecological complexity. The purpose of this report is to review the literature regarding the central hypothesis that increases in one species (moose *Alces alces*) will increase the predator population (wolf) and increase predation on associated prey species (caribou). Potential solutions for mitigation and recovery, particularly in forest management practices, are also examined. The goal is to inform decision makers who endeavour to maintain viable populations of wildlife while simultaneously deriving economic values from forests.

2.0 CLASSIFICATION OF CARIBOU

All caribou and reindeer are considered to be the same species, *Rangifer tarandus.* They are circumpolar in distribution, inhabiting tundra, boreal forest, and mountains of Eurasia and North America. Although five subspecies have been described for North America, including the extinct Queen Charlotte Islands population (Banfield 1961), taxonomy at this level was based on morphological differences and may undergo revision based on more genotypic criteria (Thomas and Gray 2002). At present, all caribou that reside primarily in the western cordillera and the boreal forest of Canada (including all caribou herds east of Manitoba) are combined together as a woodland subspecies *R. t. caribou.* Mallory and Hillis (1996) stated that demographic characteristics of caribou could not be explained by subspecific classification.

Differentiation by ecotype, rather than by genotype, has generally been accepted as most appropriate for conservation purposes. Ecotypes are classes of populations that have adapted their habits and behaviour to different environments. Previous ecotype designation was expanded by Thomas (1995) to include forest, alpine, or tundra ecosystems used in summer and winter, migratory behaviour, and importance of terrestrial lichen, arboreal lichen, or graminoids as winter forage.

COSEWIC differentiates “forest-dwelling” from “forest-tundra” woodland caribou ecotypes. COSEWIC forest-dwelling populations consist of Northern Mountain, Southern Mountain, and Boreal which correspond to National Ecological Areas, while the Newfoundland population is considered isolated and distinct (Thomas and Gray 2002).

A mitochondrial DNA study by Dueck (1998) determined that all caribou originated from distinct northern and southern common ancestries (clades). These had been separated into glacial refugia during the last ice age, and only partially corresponded to existing taxonomic classifications. All reindeer, barren-ground caribou of Canada and Alaska, woodland caribou in the Yukon, and some woodland caribou in British Columbia emerged from the northern refugium. Most animals of northern Labrador, and the Ungava region of Quebec and the remaining woodland caribou belong to the southern clade. After glacial retreat, the two groups dispersed across Canada and their distributions overlapped, allowing many populations to contain genetic material from both clades. All forest-tundra ecotypes appear to be mixed haplotypes.

As a species, caribou possess a rich genetic foundation and appear to be able to develop convergent behaviour and phenotypes. The George River population of northern Quebec and Labrador is mostly southern haplotype, but its migratory and social behaviour is similar to populations of barren-ground caribou which are mostly northern haplotype (Thomas and Gray 2002). Herds in Alaska have been combined together into the barren-ground subspecies (*R. t. granti*) and they are all closely related genetically (Valkenburg et al. 2002). However, herds of the interior and southern regions of the state display many behavioural traits common to woodland caribou.

Despite the various attempts to differentiate caribou varieties, Roed and Whitten (1985) have shown that there is high genetic identity among caribou and reindeer, and all have descended from a common ancestral type in relatively recent evolutionary time. The absence of strong divergence in basic life history traits among mountain, barren-ground, and woodland caribou should allow generalization of knowledge gained from intensively studied ecotypes to the ecology of predator-prey relationships in less studied caribou populations.

3.0 CARIBOU POPULATIONS

Because woodland caribou often move across extensive areas in scattered groups at low densities, populations have been difficult to define. To promote woodland caribou conservation, the World Wildlife Fund produced a draft national map showing a "best estimate" of range occupancy and status, and highlighted significant gaps (Peterson et al. 2000). With improved data, Thomas and Gray (2002) mapped current and historical range of forest-dwelling woodland caribou, and area of occupation of local populations. Despite these efforts, accurately mapping caribou distribution has many challenges. Many ranges are poorly defined or undefined, the distributions of some ecotypes overlap, several populations appear to be intermediate or undescribed ecotypes, delineation of populations that extend across political boundaries is not always coordinated, information among jurisdictions varies in precision, and areas of low caribou density may be difficult to distinguish from gaps in occupation.

Historic distribution in Canada can probably be best described as a series of *metapopulations*. This term was described by Levins (1968) as "a population of local populations which are established by colonists, survive for a while, send out migrants, and eventually disappear." Expansion and contraction of a population may be going on in different localities at the same time (Andrewartha and Birch 1954), and the chance of local extinctions is reduced if there is adequate dispersal within the metapopulation. Although some local populations are currently grouped into metapopulations based on assumptions of gene flow, not enough is understood about movements among most groups to classify and map metapopulations (Thomas and Gray 2002). In Alberta, Saskatchewan, Quebec and other provinces, metapopulations may have become fragmented into fairly discreet populations (e.g., Stuart-Smith et al. 1997; Rettie and Messier 1998; Ouellet et al. 1996).

4.0 HABITAT PARTITIONING BETWEEN CARIBOU AND MOOSE

Woodland caribou and moose often share the landscape, but occupy different ecological niches. Caribou may also have a similar relationship with other ungulates such as deer (*Odocoileus* sp.), elk (*Cervus elaphus*), and bison (*Bison bison*). Moose select early successional mixedwoods characterised by fertile soils, wide plant diversity, and high productivity. In contrast, woodland caribou habitat is often described as late successional, conifer dominated, low productivity regimes.

A number of adaptations have permitted caribou to exploit a nutrient-poor niche on the landscape where other ungulates are unable (Thomas and Gray 2002). Although they consume a wide variety of plants, caribou have a very close relationship with the occurrence of lichen. According to Kelsall (1968), caribou are physiologically adapted to cope with low protein forage. Lichens, which form the bulk of the winter diet, are high in digestible carbohydrates for energy value, but poor in protein and minerals for growth or maintenance value. In a study of digestibility of summer forages used by George River caribou of northern Quebec and Labrador, Cote (1998) suggested that preference for lichen may be related to its abundance in the habitat. Green forage such as sedges (*Carex* spp.), grasses, horsetail (*Equisetum* spp.), leaves of willow (*Salix* spp.), and dwarf birch (*Betula* spp.) are high in protein and selected during the spring growing season. Also high in protein are fungi which are consumed when abundant in autumn. Kelsall (1968) summarized feeding trials showing that although caribou fed an unlimited supply of tall lichens lost weight, they can subsist on lichens for long periods.

It is difficult to determine how much habitat partitioning is a result of caribou actively selecting habitat away from moose and wolves, or is a result of wolves culling caribou that make wrong choices in home range selection. In times when moose and wolves were less abundant, Cumming et al. (1994) suggested that caribou were able to occupy more diverse habitats such as denser conifer forest with less ground lichen, or mixed woods with arboreal lichens similar to the predator-free Slate

Islands in Lake Superior. Ground lichens are rare on these islands and the forest is second growth following logging and forest fires, yet they are able to support the highest density of caribou in North America (Bergerud 1980). According to Ricklefs (1979), island invaders (especially birds) often exhibit ecological release resulting in their populations increasing greatly and spreading throughout a variety of habitats, including many which are not inhabited by the parent population on the mainland. Thomas (1995) stated that caribou populations in island habitats have less of the other stress factors that most populations experience.

Caribou from the Slates were released onto other islands in Lake Superior and results supported the concept suggested by Cumming et al. (1994) about habitat diversity and former caribou distribution. Bergerud and Mercer (1989) described Michipocoten Island as having deciduous forest, abundant sedges and evergreen shrubs, scarce lichens, and no predators. Eight caribou released there in 1982 increased to 26 animals after six calving seasons. On Bowman Island, characterised by more boreal forest elements and extensive terrestrial lichen cover, wolves were present and the six caribou that were reintroduced in 1985 dwindled to one by the next year. This indicates that caribou may not need to depend on climax lichen stands for survival unless they need to remove themselves from other ungulates and wolves.

5.0 WOLF-CARIBOU SYSTEMS

The longer a predator and its prey share a common evolutionary history, the more diminished the detrimental effects of the interaction tend to be. However, advanced co-evolved systems may be impacted by significant ecological changes (Ricklefs 1979). Wolves and caribou have been co-evolving together for 50-100 thousand years, and Davis and Valkenburg (1991) proposed that in Alaska this single predator-prey relationship probably predates wolf-caribou-moose systems. Distributions of wolves and caribou are very closely associated in Canada, and it is assumed that they have achieved an approximate “equilibrium” in catch-escape encounters (Thomas 1995). This relationship may become “unbalanced” where major changes such as extensive wildfires, windstorms, insect outbreaks, or human landscape disturbance alters habitat sufficient to allow intrusions of alternate prey such as moose.

When wolves and caribou both were present on the island of Newfoundland during earlier centuries, their populations probably underwent oscillations, but did persist. Coronation Island in southeastern Alaska is an example where wolves did not coexist with their ungulate prey because the area (73.3 km^2) was insufficient to sustain both (Klein 1995). Black-tailed deer (*O. hemionus sitkensis*) lived in a predator-free environment until two pairs of wolves were introduced in 1960. The wolf population peaked at 13 after four years, and then declined to a single individual in 1968. Before their extinction on the island, wolves caused a pronounced reduction of deer numbers which were able to persist only in a few areas of rough terrain and dense habitat. After wolves declined to a few individuals and fed more opportunistically (e.g., rodents, invertebrates, other wolves), they still did not allow the deer to increase even as forage recovered significantly from heavy herbivory.

6.0 REPRODUCTIVE POTENTIAL OF PREY

Messier (1994) stated that impacts of predation should consider reproductive potential of the prey. The intrinsic reproductive potential of moose is higher than caribou; twins are common in moose and rare in caribou (Thomas and Gray 2002). After forest retrogression to early seral stages following fire or logging, improved habitat quality may greatly increase the fecundity of moose (Franzmann and Schwartz 1985).

Geist (1974) theorized why there may be an evolutionary advantage for multiple births in moose and deer, and single births in caribou. The three main ecological variables affecting reproductive variables in ungulates are effective temperature at birth, predation pressure, and periodic superabundance of food. In mature boreal forest, moose forage may be of relatively low quality. Resources would be particularly difficult for a pregnant moose to procure in late winter, which is the same time that the foetus is undergoing rapid development. Under these conditions, it would be advantageous for a female moose to produce the smallest possible single calf that is not at risk of hypothermia, and that can keep up with its mother shortly after birth to avoid predation.

After a forest fire, a superabundance of food becomes available and initially the moose population may be far below carrying capacity. A female moose can maximize its response with either a much larger calf, or multiple births. A larger than normal calf may cause dystocia (calf stuck in the birth canal), or abandonment if the mother experiences severe pain. Females that ovulate two eggs when the carrying capacity undergoes a rapid rise are able to produce two normal sized calves, without birth complications. There would be natural selection for females that conceive twins when nutritional state is high.

Conversely, forest fire causes a sudden scarcity of the main forage for caribou. Because lichen returns slowly as the forest matures, theoretically, caribou may always be at carrying capacity. With little possibility of rapid increase in carrying capacity, selection for twins similar to moose is not expected.

In white-tailed deer, there is selection for multiple births of relatively small sized fawns. Geist (1974) suggested that this may be influenced by hiding behaviour of newborns in dense cover to escape detection by predators. Because caribou occupy fairly open habitat, a calf must be large and developed enough to outrun predators. This requires high parental investment into a single offspring to maximize growth rate.

Although fecundity may be intrinsically lower for caribou, many forest-dwelling populations do not appear to be limited by food resources, and parturition rates are typically quite high for the species. (e.g., Edmonds and Smith 1991; Seip 1992; Rettie and Messier 1998; Courtois 2003).

7.0 ALTERNATE PREY

Two species are considered to be in competition when the presence of one leads to a reduced population of the other. They may be in “direct competition” for resources or exhibit “apparent competition” if they share a common predator (Holt 1977). With a single prey type, a predator’s numbers are limited by only one feedback pathway. According to the theory, apparent competition may occur if the entry of an *alternate* prey species increases the density of the predator by expanding its resource base, leading to heavier predation on the original prey species which equilibrates at a lower density. The most vulnerable competitor would be the species least able to withstand predation. The survival of the most vulnerable species could actually be independent of its own carrying capacity, yet indirectly and critically dependent upon the carrying capacity of the less preferred prey. Holt (1977) stated that apparent competition has been inferred for some predator-prey relationships, but should always be verified by field experiments.

Direct competition between caribou and moose for food or other habitat components is assumed to be weak, but they may share wolves as their main predator. Based on research in Ontario, Simkin (1965) was the first to hypothesize that caribou could decline from apparent competition with moose, mediated by wolf predation.

Bergerud and Elliot (1986) described a similar phenomenon in British Columbia where moose increased in abundance and distribution after 1900, providing an increased prey biomass supporting higher wolf densities. This in turn led to higher predation on caribou and may have resulted in local extinctions. If caribou are its only prey type, a wolf population would be limited by caribou numbers. As moose become available as a second prey species, wolf densities could theoretically increase.

Seip (1992) conducted a five year study of woodland caribou populations and their interrelationships with moose and wolves in the Quesnel Lake area and Wells Gray Provincial Park of southeastern British Columbia. His results supported the following hypotheses:

- Wolf predation was the major cause of the declining caribou populations in southeastern British Columbia
- Wolf populations were sustained primarily by moose
- Wolf predation on caribou was greater in areas where caribou lived in close proximity to moose.

Alternate prey may include other ecotypes of caribou. The Red Wine Mountains caribou population of central Labrador declined approximately 75% from the 1980s to the 1990s as the migratory George River herd grew and expanded its range (Schaefer et al. 2001). Subpopulations of the Red Wine Mountains herd having the greatest range overlap with the George River herd experienced the highest mortality. Schaefer et al. (2001) concluded that refugia from other ungulates, including other caribou, were important for persistence of some caribou populations.

The negative effect of moose and wolf dynamics on caribou is further compounded by the interaction of other species. In addition to moose, other ungulates including deer, muskox (*Ovibos moschatus*), and bison, and incidental prey such as beaver (*Castor canadensis*) and hare (*Lepus americanus*) may be able to buffer declines in wolf populations when caribou are scarce.

8.0 PROFITABILITY OF PREY

8.1 Prey Selection

When there is a choice between two ungulate prey species ranging in size from sheep (*Ovis* sp.), deer, caribou, elk, and moose to bison, many researchers have observed that wolves tend to select the smallest species (e.g., Murie 1944; Mech and Frenzel 1971; Carbyn 1983; Bjorge and Gunson 1989; and Larter et al. 1994). However, if predators hunt according to profitability theory (Royama 1980), then size of prey would only be part of the selection process.

Kunkel et al. (2004), described profitability as the ratio of net energy gain to handling time, which is the total amount of time required to search for, chase, kill, eat, and digest the prey. According to Mech (1992), the time necessary for wolves to search for a vulnerable prey animal exceeds any other factor affecting kill rate.

During their 1986-1996 study in northwestern Montana and southeastern British Columbia, Kunkel et al. (2004) observed that wolves selected to travel where deer were concentrated into wintering areas and predictable to find. Although wolves killed more deer which were the most available, they selected elk and moose within these areas. Because elk provide three times more food biomass than deer, it was not unexpected that they should be selected if they were equally vulnerable. At the finest scale (encounters along travel routes) elk were selected, but not at the coarser scale (selection of travel routes). Because elk and moose were more dispersed than deer, it seemed to be unprofitable for wolves to hunt these species territory-wide because of the greater search distances required. After wolves choose their hunting areas, Kunkel et al. (2004) suggested that predation is more opportunistic. Although they may test every potential prey animal that is encountered, wolves may be more persistent at testing elk and moose because such prey are more profitable.

In Banff National Park, Huggard (1993) concluded that wolves selected elk and deer because they were encountered more often than bighorn sheep (*Ovis canadensis*) and mountain goat (*Oreamnos americanus*). He stated that because foraging theory suggests that all ungulate species should be equally profitable to wolves upon encounter, elements affecting encounter rates are critical in determining prey selectivity. Where predators decide to travel is an important factor in what species they encounter and finally consume (Scheel 1993).

In the Wabakimi Lake area of northwestern Ontario, wolves specialised on moose, even though caribou were easier to kill and less dangerous (Cumming et al. 1994). The researchers suggested that it may have been a more optimal foraging strategy for wolves to select moose which were more numerous and provided three times more biomass per animal than caribou. To reach caribou in winter, wolves had to travel greater distances and expend more energy in snow that often exceeded 50 cm.

A study in two west-central Alberta caribou ranges, where 31 radio-collared wolves from eight packs were monitored, showed that these wolves did not use the landscape randomly (Kuzyk 2002). Habitats with young vegetation and waterways associated with an abundance of moose were selected. In contrast, caribou in this region preferred forest 120-160 years of age (Szkorupa 2002), avoiding cutblocks (Smith et al. 2000) and perennial streams (Oberg 2001). Kuzyk (2002) determined that moose were the primary prey, followed by deer and elk. Although wolves have been implicated as the proximate cause for caribou decline in this area (Edmonds 1988), no evidence of predation on caribou was uncovered during the two years of this study. Wolves appeared to travel less when hunting for moose than when preying on deer or elk and stay at moose carcasses longer than at others. Also, wolves traveled 4.2 times less when they were near ungulate kill sites. Accordingly, Kuzyk (2002) reasoned that an abundance of moose in this system could reduce encounter rates between caribou and wolves. The density of wolves averaged 11/1000 km^2 and caribou would benefit only if wolf numbers remained low enough to be food satiated with moose.

In the study by Ballard et al. (1987), in south-central Alaska, moose were the year-round food base of wolves and caribou were available mainly in winter. Of 439 kills examined, 70% were moose and 21% were caribou. Out of the 30 wolf packs studied, the three packs occupying the poorest moose habitat had the largest territories, and were responsible for over half of the caribou kills.

In east-central Yukon, 21 wolf packs were followed for five winters from 1990 to 1994 when moose and caribou were increasing (Hayes et al. 2000). Wolves were recovering from a reduction program and reached a density of 10.4/1000 km^2 by 1994 (Hayes and Harestad 2000). Moose comprised 89% and caribou >10% of the 326 ungulate carcasses identified. Even when large numbers of migratory caribou were available (temporarily) in winter, packs continued to kill more moose than caribou. This was attributed to abundant calf and yearling moose that were more profitable than caribou for wolves to hunt.

8.2 Prey Switching

If the primary ungulate prey species becomes less abundant, its profitability may decline to a level below that of another species. Consequently, wolves may shift to a more profitable species, but continue to exert a high level of predation on the primary prey. According to Scheel (1993), prey switching is highly dependent on prey profitability.

In the Western Arctic caribou range of northwestern Alaska, Ballard et al. (1997) radio-collared 86 wolves from 19 packs and monitored their activities from 1987 to 1992. Wolf densities increased from 2.7/1000 km^2 to 4.4/1000 km^2 from 1987 to 1990, then dropped to 1.5/1000 km^2 the next year after a rabies outbreak. Moose have been established in the region since the 1950s. Caribou were the main prey when they were available, but at densities below 0.2 caribou/km^2, wolves switched to moose. When caribou migrated from pack territories, wolves switched to moose for about four months of each year.

The Gates of the Arctic National Park and Preserve of northern Alaska is a multi-prey ecosystem where research was carried out on wolf predation (Dale et al. 1995). Although caribou were the primary prey during the three 30-day study periods in March 1989, March 1990 and November 1990, their abundance and distribution were quite variable. Within pack territories, caribou density ranged from 0.06-2.34/km^2, whereas moose density ranged from 0.08-0.24/km^2. Wolves maintained high kill rates on caribou at low densities, and as caribou densities increased, kill rates decelerated rapidly. During these three periods of observation, wolves were not observed to switch to more abundant moose when caribou were scarce. Although moose provided wolves with a greater biomass of food per individual, Dale et al. (1995) stated that herds of caribou may have been more profitable because wolves were often able to make multiple kills during single attacks. Other explanations for wolves not switching were that adult moose occurred at low density, and their excellent condition may have reduced their vulnerability to wolves. Age structure of a moose population has an important effect on condition and vulnerability to wolf predation (Allen 1979).

When Gasaway et al. (1983) examined the interrelationships of wolves, prey, and humans in the interior of Alaska from the 1950s to the 1970s, they were unable to find evidence of major shifts in prey consumption because most caribou and moose populations tended to decline synchronously.

Relative profitability of prey species and prey switching may vary between local populations or varieties of wolves. The eastern Canadian subspecies, *C. l. lycaon,* has been described by Wilson et al. (2000) as a small deer-eating wolf that, unlike other gray wolves, readily hybridizes with coyotes (*Canis latrans*). Eastern wolves were considered to be among the smallest in North America even before any documented arrival of coyotes in the early 1900s (Goldman 1944). In Algonquin Park Ontario, 57 radio-collared wolves monitored during 1987-1992 preyed heavily on white-tailed deer (*O. virginianus*) even when they were rare (Forbes and Theberge 1996). Whenever the wolves switched to alternate prey, it was usually to beaver. Although they were scavengers of moose carcasses, these wolves were considered to be inefficient predators of moose. In southern Quebec, Potvin et al. (1988) observed that wolves persisted on killing deer in winter, even when they had almost disappeared and moose were available.

9.0 MULTIPLE PREDATORS

Ungulate populations that experience high levels of mortality from multiple sources are less able to sustain wolf predation and will be regulated at lower densities than populations without those additional limiting factors (Seip 1995). Except in a few cases listed below, wolves are the main predator of caribou. Grizzly bears (*Ursus arctos*), black bears (*U. americanus*), coyotes, cougars (*Felis concolor*), wolverines (*Gulo gulo)*, lynx (*Lynx lynx*), eagles (*Aquila* sp.) and humans may exert *additive* mortality on caribou where they share the environment with wolves. In reference to caribou populations in the Cordilleran Mountains that are subject to predation by all of these species, Thomas and Gray (2002) stated that the additive effects of mortality from many predators must severely limit those populations. The proportion of caribou mortality attributed to these different predators has rarely been determined. Messier (1994) suggested that wolves are able to regulate moose at low densities only when bears are present as an additional mortality factor.

The effect is termed *compensatory* if vulnerable surplus individuals are killed that would otherwise die of other causes such as disease, starvation, or other predators. Predator densities are often restricted by interactions with each other. Skogland (1991) described long term studies of ungulates (moose, red deer (*Cervus elaphus*), sika deer (*Cervus nippon*) and roe deer (*Capreolus capreolus*)) and large predators (brown bear (*Ursus arctos*), wolf, lynx, and wolverine) in boreal and temperate regions of Russia. When wolves (the main predator) were removed, ungulate survival in boreal regions increased only half as much as in temperate regions. This may have been partly due to a more diverse predator community in the boreal zone that is able to compensate, or fill the niche left vacant after the wolves were gone. Compensatory mortality of caribou after reduction of the main predator has not been well documented.

9.1 Grizzly Bears

As facultative carnivores, abundance of ungulate prey would not be expected to have significant effects on bear populations. Because bear predation on moose calves appears to be independent of moose density (Schwartz and Franzmann 1991; Ballard 1992), declines in ungulate populations could be prolonged by bears. Vegetation is a large dietary component and these omnivores can be opportunistic when animal matter is available. Animal food sources may be particularly important in early spring when protein requirements are high and vegetation has not yet began new growth.

Gau et al. (2002) concluded that barren-ground grizzly bears in the Northwest Territories are quite carnivorous and prey effectively on caribou to the extent that the viability of local bear populations may depend on caribou. At Denali National Park in Alaska, Adams et al. (1995a) found that the main cause of neonatal caribou mortality was grizzly bear, followed by wolves which were only 15% as abundant as the bears. Also in Alaska, grizzlies were a leading cause of calf mortality in the Delta herd (Valkenburg et al. 2002), the Fortymile caribou herd (Boertje and Gardner 2000), and the Porcupine herd (Young and McCabe 1997).

9.2 Black Bears

Although black bears are known to prey on caribou, reliable documentation is lacking (Ballard 1994). Because black bears and caribou in Saskatchewan were found to more closely share the same range and food resources at calving time, Rettie and Messier (1998) suggested that predation by black bears may have an impact on calves during their first few weeks of life. Black bears have been documented as significant predators of caribou on the island of Newfoundland (Mahoney and Schaefer 2002; Mahoney and Virgl 2003).

9.3 Cougar

Cougars are a major mortality factor for mountain caribou in the Selkirk Mountains of Idaho and southern British Columbia (Zager et al. 1996).

9.4 Coyote

Although coyotes were common on the Chisana caribou calving area in Alaska after a snowshoe hare decline, Valkenburg et al. (2002) considered them unlikely to ever kill as many calves as wolves or bears. In eastern North America, coyotes are larger than in the west, presumably because of adaptation to larger prey consisting of white-tailed deer (Thurber and Peterson 1991; Lariviere and Crête 1993). Coyotes are considered a major source of caribou calf mortality in Gaspesie Park in southeastern Quebec (Crête and Desrosiers 1995; Mosnier et al. 2003). Coyotes have dispersed across the island of Newfoundland since 1985 where they kill calf and adult caribou (Mahoney and Schaefer 2002).

9.5 Wolverine

Examination of wolverine stomachs by Mulders (2002) in the Northwest Territories showed that caribou was the primary food item. Low caribou populations east of Hudson’s Bay that occurred in the past may be why wolverines almost disappeared from Quebec and Labrador. The two species’ ranges show a high degree of overlap which suggests that wolverines may be somewhat dependent on caribou as a scavenger and, to some extent, a predator.

9.6 Lynx

Bergerud (1983) described a predator-prey scenario on the island of Newfoundland. Lynx were rare until the introduction of snowshoe hares in the 1860s. With this new food source, lynx populations were able to greatly expand. After the snowshoe hare populations experienced declines, lynx switched to caribou calves as prey. Calves were usually successfully defended by their dams, but died of septicaemia from wounds inflicted primarily on their necks. Even after wolves disappeared from the island, caribou populations risked extinction because of lynx predation on neonates. High prices for lynx fur coincided with the recovery of caribou (Bergerud 1971). In Alaska, lynx are predators of caribou calves (Valkenburg et al. 2002), and contributed to high mortality in the Fortymile herd during the winter of 2000-2001 (Boertje and Gardner 2001).

9.7 Eagles

On the Porcupine caribou calving grounds of Yukon and Alaska, golden eagles (*Aquila chrysaetos*) accounted for about 60% of the total calf predation during 1983-1985. Grizzly bears followed at 24% and wolves ranked third at 16% (Whitten et al. 1992). Golden eagles are also predators of caribou calves in Gaspesie Park (Crête and Desrosiers 1995).

9.8 Human

As hunting is generally considered additive to other limiting factors, any reduction in hunting mortality is assumed to be beneficial to a caribou population that is not food limited. There is widespread concern about new roads providing increased accessibility for poachers and subsistence users. In British Columbia and Ontario, over-hunting probably caused population declines in many areas during the 1900s (Seip and Cichowski 1996; Racey and Armstrong 2000). In some populations, poaching could equal recruitment (Johnson 1985). Of 31 caribou deaths accounted for from 1979 to 1984 in west-central Alberta, 17 were illegal kills and three were taken by aboriginal people (Edmonds 1988). In northeastern Alberta, humans accounted for 19% of documented caribou mortality between 1991 and 1995 (Stuart-Smith et al. 1997).

10.0 PREDATOR RESPONSE TO PREY

10.1 Functional Response

As prey density increases, the consumption rate of prey by the predator increases in this response, and then plateaus at satiation. Holling (1965) described three main types of functional responses (Figure 10.1). Type I is a linear increase in consumption that occurs only in species whose handling time of prey is minimal.

In type II, killing rate increases asymptotically because handling time requires increasing amounts of the predator's time and eventually limits the consumption rate. When wolves are in a single prey system, a type II response is expected because they must exploit that prey regardless of density (Messier 1995). Dale et al. (1994) observed a type II functional response in the Gates of the Arctic National Park, Alaska, where wolves predominantly killed caribou.

A type III response produces a sigmoid curve where the initial reaction of a predator to increased prey density at low prey levels is relatively weak. This response may be most apparent in multi-prey systems where predators switch between spatially separated prey species (Messier 1995). Adjustment of wolves to caribou or moose availability may take some time (Holleman and Stephenson 1981). Although caribou are easier to kill, wolves may select moose if they are easier to locate and more profitable. Bergerud (1983) has hypothesized that caribou reduced to low densities may be able to persist, but whenever they increase to some level, wolves switch back from moose and reduce them again.

10.2 Numerical Response

As prey density increases, the population density of the predator does likewise in response. Higher populations or higher vulnerability of prey can have a positive effect on reproduction, survival, and immigration of the predator. If large hunting territories are no longer required for sustenance, more emigration or splintering of wolf packs can occur. In addition to the functional responses defined by Holling (type I linear response, type II asymptotic response, and type III sigmoid response), Messier (1995) described a type 0 numerical response for cases in which predator numbers do not vary according to prey density. This may apply to multi-prey systems where a prey species such as caribou may only be available seasonally and has little effect on wolf numbers sustained by moose. After summarising wolf-moose studies, Messier (1994) described a type II numerical response that showed a sharp increase at low prey density and reached a plateau at 58.7 wolves/1000 km^2, implying a limit imposed by territorial behaviour.

10.3 Other Responses

Developmental and efficiency responses are longer term changes in interactions (Murdoch 1973). They may be apparent in some predator species (e.g., Murdoch 1971), but they have yet to be demonstrated in wolves. If the size of the predator changes, a developmental response has occurred. An individual predator may grow larger if more food becomes available. Also, there may be gradual evolutionary selection for larger individuals if a population switches to a larger prey species; then the size relationship is optimized through natural selection.

In the short term, as a prey species becomes more important in its diet, a predator may learn from cumulative experience how to capture the prey more effectively. This change in hunting skill of the predator is an efficiency response.

10.4 Total Response

The total predator response has been described as the product of the functional and numerical response (Solomon 1949). When divided by prey numbers, it yields an estimate of predation rate.

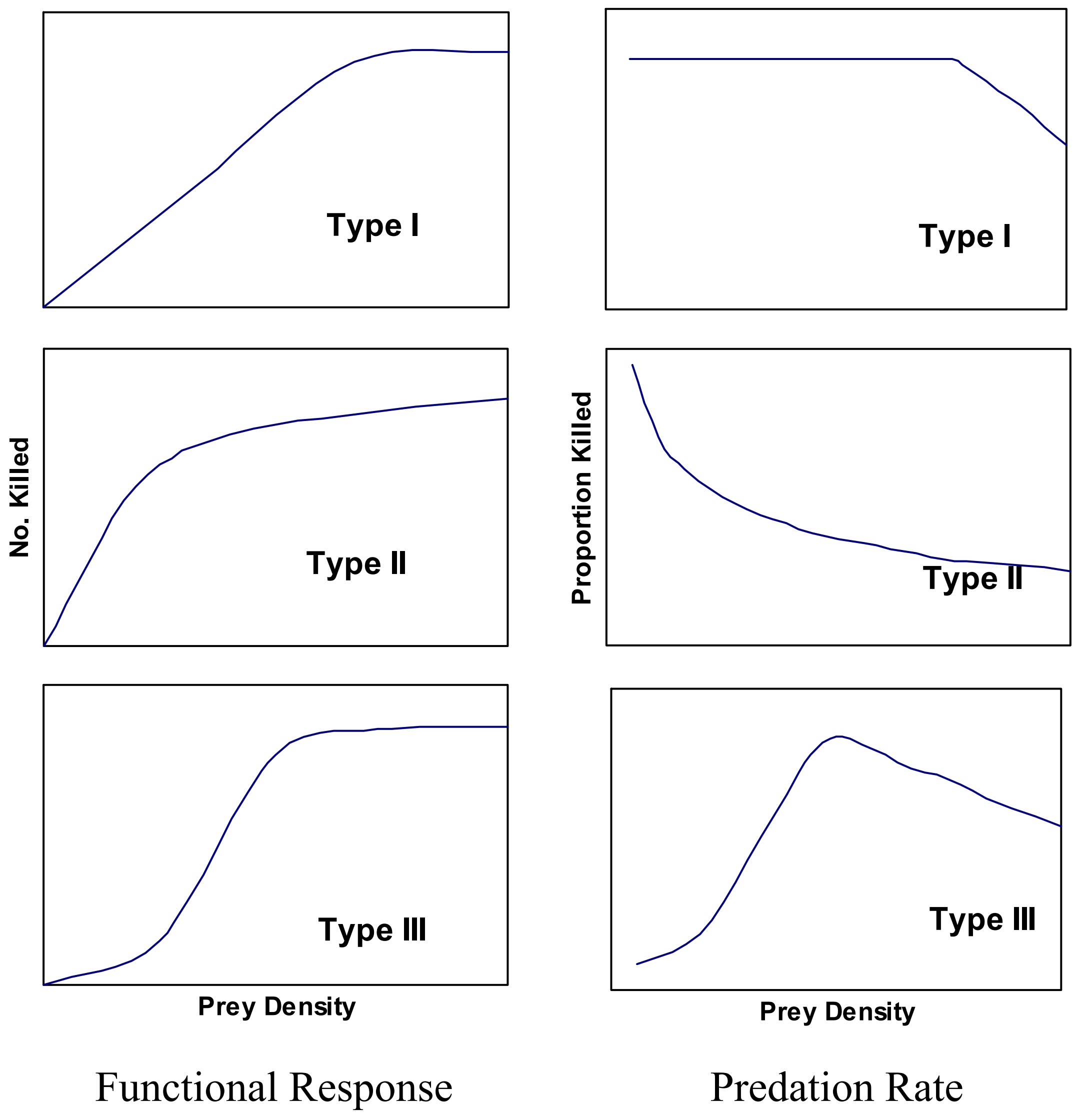

Figure 10.1 Three Types of Relationships between Functional Response and Prey Density, and Predation Rates in Absence of Numerical Response

11.0 ANTI-PREDATOR RESPONSES OF CARIBOU

Prey animals reduce their profitability by adopting anti-predator strategies. Strategies used by prey are a combination of physical and behavioural attributes. According to Reed (1999), adaptive behaviour is often ignored by researchers, but it can be critical for species' survival and predicting extinction patterns.

If a predator is effective and a prey population is exploited at a high rate, natural selection on the prey will tend to improve its escape mechanisms more rapidly. The most important effects of a new anti-predator tactic are the consequences on the prey that do not adopt it (Ricklefs 1979).

Several anti-predator behaviours used by caribou have been observed, and some are described below.

11.1 Flight

Prey that select relatively open habitat usually rely on unimpeded swiftness for escape (Ricklefs 1979). Burkholder (1959) and Thomas (1995) stated that caribou depend primarily on their ability to run, and Crisler (1956) observed apparently healthy caribou outrunning wolves. Because caribou lack effective group defence, fleeing is the principal mechanism to avoid predation (Lent 1974). Caribou may avoid young dense vegetation that impedes flight and reduces their ability to visually detect predators (Schaefer and Pruitt 1991). A sufficient lead time is essential for a reasonable probability of escape, and caribou may flee across predator barriers such as steep uphill terrain or into lakes and rivers (Bergerud and Page 1987; Thomas 1995).

Kelsall (1968) described a form of caribou escape behaviour as bounding off beaten trails into deep snow where wolves refused to pursue them. High speed chases through soft snow are energy cost prohibitive for canids (Crête and Lariviere 2003). To compare snow coping abilities among various wildlife species, Telfer and Kelsall (1984) developed a morphological index by combining foot loading and chest height. Ratings showed that caribou are better adapted to locomotion in deep soft snow than any other North American ungulate or large predator.

11.2 Calf Hiding

Although calves of barren-ground caribou are able to travel within a day or two of birth, Chubbs (1993) observed evidence that calves of woodland caribou may hide like deer fawns. This may be a local adaptation unique to some herds in Newfoundland where predation by lynx and black bears is significant.

11.3 Birth Synchrony

A glut of births may reduce predation on vulnerable newborns by rapidly satiating or confusing predators (Bergerud 1974; Dauphine and McClure 1974; Young and McCabe 1997). However, when comparing an Alaskan caribou population with a predator-free west Greenland population, Post et al. (2003) observed that timing of calving by caribou was synchronous with new growth of forage in spring, regardless of predation pressure.

11.4 Defence

Caribou cows are the only female cervid with antlers. In Alaska, they defend calves from coyotes, golden eagles and wolverines (Valkenburg et al. 2002). Caribou have been reported to use their antlers for defence when brought to bay by wolves (Miller 1975).

11.5 Migration

For large herbivores, migration appears to be an effective strategy to escape predation (Fryxell et al. 1988; Fryxell and Sinclair 1988; Mahoney and Schaefer 2002). Other advantages include gaining additional food resources, relief from thermal stress, avoiding insect harassment, and reducing contact with disease and parasite vectors. Migrant caribou usually outnumber sedentary counterparts by a wide margin (Fryxell et al. 1998; Thomas 1995). Of all tested ungulates, caribou were determined to be the most energetically efficient walkers (Fancy and White 1987).

Long distance migration of the George River herd of northern Quebec and Labrador reduced accessibility to wolves during the 4-5 months when raising pups restricted their movements (Messier et al. 1988). As this herd expanded, other sedentary populations in the region declined (Brown et al. 1986).

The Bluenose, Bathurst, Beverly, and Qamanirjuaq caribou herds migrate from the boreal forest of Manitoba, Saskatchewan, Alberta, and the Northwest Territories, to calving grounds in the tundra of Nunavut which is almost totally devoid of moose. These areas appeared to provide some refuge as Heard and Williams (1992) observed tundra wolf preference for denning near the treeline. Of 209 wolf dens located, 60% were within 50 km of the treeline, occupying an area that represented only 25% of the caribou calving grounds. Kuyt (1972) stated that the main calving area selected by the Beverly herd may be 200 miles beyond denning areas preferred by wolves.

When selecting den sites, tundra wolves are habitat specialists preferring esker-like formations that vary in relative abundance (Walton et al. 2001). In their study, radio-collared wolves followed caribou between winter and summer ranges, but not usually into the calving grounds. Parker (1972) reported that non-pregnant female barren-ground caribou were less likely to migrate to calving grounds.

According to Fancy and Whitten (1991), female caribou from the Porcupine herd selected calving areas north of the mountain foothills in northeastern Alaska and in the northern Yukon, primarily to reduce predation exposure. Highest calf mortality occurred in years when snowmelt was relatively late and calving occurred closer to the foothills where wolves and bears were abundant. Hayes and Russell (2000) modelled annual wolf predation on adult Porcupine caribou and projected a kill of about 7600 adult caribou/year, regardless of herd size. Fall and winter accounted for 84% of the kill, whereas migration to range with fewer wolves effectively released this population from predation during spring and summer.

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 et al. 1995a). Also, during a study from 1987 to 1991 when wolf numbers doubled in the park, the caribou population still increased by 30% (Mech et al. 1995). The caribou appeared to offset increased predation by adjusting their distribution to areas within the calving grounds where wolves were scarce.

Ballard et al. (1987) collared 151 wolves from 30 packs in south-central Alaska, and determined that calving caribou were usually unavailable to wolves. They remained within their territories and did not follow migrating caribou into calving areas.

In Spatsizi Provincial Park, northern British Columbia, Bergerud et al. (1984) observed that caribou sought high elevation slopes for calving that were away from moose, and partially out of the range of wolves and bears. A survey of caribou forage preferences, timing of changes in plant phenology, phytomass, and nutrient concentrations showed that at the time of calving these high elevation areas had quite limited food resources. In this region, parturient females appeared to sacrifice food abundance and nutrition to provide safety for neonates, and did not descend from high elevation refugia until calves were at least two weeks old.

Mountain caribou studied in west-central Alberta by Edmonds and Smith (1991) calved mostly in areas of low vegetation cover that were barely beginning to green up. Because vegetation at lower elevation winter range was more abundant and advanced in spring growth, they concluded that dispersal to higher elevation calving sites was a predator avoidance tactic carried out at the expense of the cow's nutritional needs. Edmonds and Smith (1991) also indicated that selection of slopes where snow cover quickly disappeared could have allowed lactating cows access to nutritious forage soon after calving. In contrast to Mentasta or Spatsizi caribou, the Alberta mountain caribou ascended to higher elevations after calving.

Barten et al. (2001) monitored 39 radio-collared females of the Mentasta caribou herd in Alaska in 1994 and 40 in 1995 to test hypotheses regarding forage acquisition and predation risk. Results indicated that parturient cows calved at elevations higher than the usual range of bears and wolves, and being above most approach routes of predators was an advantage in detecting and avoiding predators. In contrast, non-maternal females remained at the same general elevation as bears and wolves. Also, if females lost their offspring, they rejoined non-maternal females and predators at lower elevations. Not until calves became quite mobile did they and their mothers descend into the zone of predators. Because maternal females occupied range with less forage than did females without young, they appeared to trade off food abundance for neonate security. Caribou were highly selective during feeding and sacrificing nutrition could not be demonstrated.

Seip (1992) stated that many caribou populations that disappeared in British Columbia since the early 1900s were non-migratory. He also suggested that wolves might eliminate the Quesnel Lake herd because wolf numbers were sustained at high densities by moose. In contrast, the neighbouring Wells Gray herd which migrated to mountainous summer ranges separated from moose and wolves was increasing. However, after the mid 1980s caribou recruitment in the Quesnel Lake area increased, adult mortality decreased, and the population stabilized (Seip and Cichowski 1996). Although wolves are as abundant as before, the killing rate on caribou has subsided. An explanation they proposed was that the remaining caribou were descendents of individuals which traditionally used secure calving sites that went undetected by wolves. Although other factors such as changes in weather conditions and forage quality between study years may affect population growth and vulnerability to predation, they suggested that the effectiveness of predator avoidance is the dominant factor.

11.6 Island, Shoreline, and Bog Refuge

In Ontario, caribou have been observed calving on islands on Lake Nipigon (Cumming and Beange 1987) and in the Irregular Lake area (Simkin 1965). Also, Ferguson et al. (1988) studied a small caribou herd that resided mostly year round on Pic Island in Lake Superior that survived long after caribou on the adjacent mainland disappeared. Wolves seldom visited the island and forage was determined to be more abundant and diverse on the mainland. They concluded that caribou persisted on the island because it was a refuge from predation, despite lower food resources.

Near Pukaskwa National Park, Ontario, a small herd persisted along shoreline habitat on Lake Superior. It was spatially separated from wolves and moose that occurred mainly inland (Bergerud 1985). The lake provided escape and offshore islands were used as safe calving areas.

Refuges for calving have also been identified in other regions. At Reed Lake (Manitoba), caribou often calved on islands or mainland shorelines (Shoesmith and Storey 1977). Some caribou cows calved on islands in southeastern Manitoba (Darby and Pruitt 1984), and in southeastern British Columbia (Seip and Cichowski 1996). In Quebec and Labrador, Brown et al. (1986) found that most caribou calved on islands and in string bogs.

11.7 Aggregation

Turner and Pitcher (1986) described the *attack abatement avoidance effect* whereby a predator is less likely to find a single group of prey than one of many single and scattered, and the *dilution effect* whereby a particular individual is less likely to be killed when many others are present. A population would benefit if a predator is able to monitor the condition of herd members and remove the least fit. As group size increases (especially in sparsely forested or open terrain), individuals do not need to keep as vigilant for predators and are able to devote more time to feeding (Grier 1984). Another advantage of herding may be intimidation of a small predator. Cumming (1975) considered group size to be an anti-predator strategy for woodland caribou. Other benefits for caribou moving in herds include mutual cooperation in trail breaking and cratering in snow (Helle 1984).

Large group formation also has disadvantages. According to Miller et al. (1985), it increases the possibility of surplus killing by wolves (more prey are killed than consumed). In addition, there is the likelihood of greater escape interference from other herd members when under attack (Crisler 1956; Miller 1975). The optimal group size probably varies according to environmental conditions. Paradoxically, both large and small herd sizes reduce wolf predation (Thomas 1995).

11.8 Dispersion

While migratory caribou form large aggregations for "spacing away" from predators at calving time, Bergerud and Page (1987) described less mobile woodland caribou that disperse from each other at calving time as "spacing out" from predators. During an eight year study in northern British Columbia, they observed that cows sought adequate snow-free space for calving, which allowed their brown coloured young to be cryptic. Recruitment declined when dispersal into snow-free areas was restricted and resulted in higher vulnerability to predation.

In a calving study in west-central Alberta, Edmonds and Smith (1991) concluded that in years when snow cover lingered late into spring, caribou cows were less dispersed and calf survival was lower. They stated that reduced calf survival may have been due to increased predation, and was less likely caused by inclement weather.

As part of a predator-prey study in northeastern Alberta by James (1999), 109 caribou, 37 moose, and 20 wolves from seven packs were radio-collared. Use of fen/bog complexes and well drained upland habitats was monitored from 1993 to 1997 from radio telemetry and aerial grid surveys. Results supported the following three predictions of a spatial separation hypothesis:

- Caribou and moose selected different habitat types, while moose and wolves selected the same upland habitat type.
- Wolf predation on caribou was higher near habitats selected by moose.
- Scat analysis showed that relative predation on caribou was less than their relative frequency in the environment.

Although habitat partitioning may have reduced predation on caribou, the fen/bog complexes did not provide a total refuge from wolves.

Female caribou that calve in the forest of northeastern Alberta tended to be more widely dispersed alone, or in small groups, than at other times of the year (Fuller and Keith 1981). This may reduce conspicuousness to predators and lessen encounters with wolves that have territories. Similar maternal behaviour was observed by Edmonds (1988) in west-central Alberta, Rettie and Messier (1998) in central Saskatchewan, Brown et al. (2000) in Manitoba, and Brown et al. (1986) in Quebec and Labrador.

Cumming et al. (1994) described habitat partitioning by moose and caribou in a 6500 km^2 study area near Wabakimi Lake, northwestern Ontario. Autocorrelation of winter track locations from 1980-84 showed that wolf tracks were most often associated with moose tracks, and the two ungulates appeared to disassociate from each other. The mean distance between wolves and caribou (15.6 km) was more than five times the mean distance between wolves and moose (4.8 km), and Cumming (1975) found that predation rates on caribou varied according to distance from wolves. Caribou in the area remained far below carrying capacity and Cumming et al. (1994) did not suggest that caribou were excluded from predation.

Coyotes have been in southeastern Quebec only since the late 1970s, and they have become a major source of caribou mortality (Crête and Desrosiers 1995). In 1978, before coyotes arrived, only 15% of parturient females dispersed into the Gaspe uplands (Mosnier et al. 2003). By 2002, this rose to 70% and calf survival has improved, indicating that a rapid adaptive process is underway.

12.0 CRITICAL THRESHOLD DENSITIES

Turner and Gardner (1991) described critical thresholds as small changes in the spatial patterning of resources that are able to produce dramatic ecological responses. There are critical thresholds in predator and prey densities that affect population dynamics.

To maintain adequate nutrition, Hayes and Russell (2000) calculated that each adult wolf needs the equivalent of about 29 adult caribou per year. Kuyt (1972) estimated that a wolf would eat 23 caribou annually if they consisted of five calves, two yearlings, and 16 adults. Wolves vary in average size across the continent. For example, wolves from northern Alberta wolves may be 40-45% heavier than those from the Great Lakes region (Fuller and Keith 1980). Because of such differences, consumption rates are often expressed as kg prey/kg wolf/day as a more meaningful way to evaluate predation. According to Kuyt (1972), Kolenosky (1972), and Mech (1977), a minimum consumption rate of 0.06 kg/kg wolf/day may be required to maintain winter body rate in wolves. Average consumption rates may range much higher and be affected by variables such as pack size (Schmidt and Mech 1997) and prey density (Keith 1983).

As obligate predators of ungulates, wolves require certain minimum ungulate densities for their populations to be viable. In a four year study of 14 packs at different moose densities in southwestern Quebec, Messier (1984) approximated 0.2 moose/km^2 as the threshold below which wolf packs cannot persist without alternate prey. At densities less than 0.23 moose/km^2, wolves may not fully colonize an area because of severe food limitations and become “detached” from other packs (Messier and Crête 1985). In the study by Cumming et al. (1994) in northwestern Ontario, moose density was estimated to be only 0.15/km^2 and adding caribou to the prey biomass still indicated food limitations for wolves. Densities estimated at 0.006 wolves/km^2 were considered to be low enough for the packs to be detached.

Thomas and Gray (2002) stated that forest-dwelling caribou populations, occurring at densities as low as 0.01-0.2/km^2, cannot sustain wolves. In the absence of alternate prey, a pack of five would require a population of at least 1000 caribou to remain viable. Depending on how their discreteness is defined, few forest-dwelling caribou populations are likely to number as many as 1000.

The migratory caribou in northwestern Alaska are the main food for wolves which usually reside in territories (Ballard et al. 1997). When caribou migrated from these territories or occurred at < 0.02 caribou/ km^2, wolves relied on moose. If moose densities were low, approximately 17% of the wolf population migrated with the caribou into wintering grounds and returned to territories at denning time.

There are some instances where wolves appear to have met food requirements primarily with moose without endangering caribou populations. This often occurs where wolf densities are low because of human exploitation or disease (e.g., Ballard et al. 1997). Where wolves had been censused, Bergerud and Elliot (1986) plotted regressions of caribou recruitment and natural mortality rates of adults against wolf abundance. Results indicate that caribou tend to decline at wolf densities that exceed 0.0065 wolves/km^2 (6.5 wolves/1000km^2). To maintain higher densities, wolves must depend on other prey such as moose, deer, and beaver.

Density thresholds lose reliability in heterogeneous landscapes if wolves are more selective where they search for prey, and caribou are able to concentrate in habitats less frequented by wolves. The area component of density is particularly difficult to calculate in mountainous regions that include areas which are mostly uninhabited by wolves and may be occupied seasonally by caribou. Despite the problems associated with prey-wolf ratios, Thomas (1995) suggested that they may be preferable to densities for assessing the effect of mobile predators on clumped prey that use small proportions of the range at any one time. He estimated a population of about 100 caribou would be required to sustain a single wolf if a consumption rate of 2.9 kg/wolf/day was from 50% of the calves providing 5 kg of flesh, and 18% of the adults averaging 50 kg of flesh.

Prey-wolf ratios may be determined from relative densities. Gasaway et al. (1983) considered them useful to assist in evaluating the impacts of predation in relatively simple systems. In a review of six North American studies, Mech (1970) concluded that when ratios were about 11 000 kg prey/wolf or less (about 30 moose/wolf), predation was the main factor limiting prey. In a further review that included 12 studies, Gasaway et al. (1983) described ratios of <20 moose/wolf causing a moose decline, between 20 and 30 moose/wolf controlling moose numbers, and at >30 moose/wolf allowing increases in moose populations. Theberge (1990) summarised the confounding factors described by Mech (1970) and Gasaway et al. (1983) that interfere with the accuracy of prey-wolf ratios as predictors of predation impacts, and he added others. With a large number of difficult-to-measure variables, Theberge (1990) questioned the validity of using ratios in predator-prey management. In his review of 27 studies, Messier (1994) found that moose-wolf ratios poorly reflected predation rate because they did not integrate the functional response.

For boreal regions of North America where moose were the main ungulate prey of wolves, Messier (1994) modelled population dynamics that demonstrate a linkage between wolf density and prey abundance. As moose densities increased from initial low levels, wolf densities were shown to increase sharply and up to 0.65 moose/ km^2, predation was strongly density dependent. Above 0.65 moose/km^2, the predation rate became inversely density dependent and gradually declined. At higher moose densities, wolf density eventually levelled off at an upper asymptote of 0.0587 wolves/km^2 (58.7 wolves/1000km^2). This predator has social intolerances that may limit population density, even if there is abundant prey.

The data summarized by Messier (1994) also suggested that the density of moose would stabilize at approximately 2.0 moose/km^2 in the absence of predators, and 1.3 moose/km^2 where wolves were present. Both equilibria are caused by density dependent food limitation. Population growth decline began when density exceeded one moose/km^2 on Isle Royale (Messier 1991). If moose population growth rate is reduced by less productive habitat or the presence of an additional predator such as grizzly or black bear, equilibria are predicted to be at much lower densities ranging from 0.2 to 0.4 moose/km^2 (i.e., one fourth to one tenth of food carrying capacity).

According to Messier (1994), the effectiveness of wolves in reducing moose population growth at low densities may be explained by moose being well dispersed and spatially predictable for wolves throughout the year. Wolves must depend on moose, even at low density, if other ungulates such as caribou are rare or seasonally unavailable. The high wolf predation rates at low caribou densities and rapidly decelerating kill rates with increasing caribou density observed by Dale et al. (1994) demonstrates a scenario where caribou populations in a multiple prey system must be able to exist above some critical threshold density, or risk extirpation by predation.

Caribou in predator-free environments, such as the Slate Islands in Lake Superior, are capable of achieving densities as high as 4-8/km^2 before they become food limited (Bergerud 1980).

13.0 POPULATION STABILITY

Population sizes of caribou herds have been known to change by several orders of magnitude. For example, the George River herd numbered less than 5000 in 1954 (Banfield and Tener 1958), then approached 800 000 in 40 years (Couturier et al. 1996). Also, a 22-year study of the Delta herd in Alaska followed five phases of population change ranging among rapid growth, slow growth, stability, slow decline, and rapid decline. Since 1960, it has oscillated between 2500 and 10700 (Valkenburg et al. 2002). Changes in calf survival as little as 5% can determine whether a caribou population grows or declines (Griffith et al. 2000). Ferguson et al. (1988) suggest that local populations fluctuate stochastically and are vulnerable to extinction.

The population of the Nelchina caribou herd in Alaska rose from a low of 5000 in 1948 to more than 70 000 in 1962, then plummeted to less than 10 000 in 1972 (Van Ballenberghe 1985). A subject of debate, the cause of the decline was variously attributed to poor range (Doerr 1979), severe winter weather (Van Ballenberghe 1985), and wolf predation (Bergerud and Ballard 1988). According to Eberhardt and Pitcher (1992), the key factor was a sharp reduction in calf recruitment from 1964 to 1967, but there was a lack of frequent and reliable censuses to determine the cause of the decline.

There are difficulties in censusing and delineating caribou populations, and evaluating their stability (Thomas and Gray 2002). Because short-term changes in numbers can be quite variable due to natural factors such as weather events, the International Union for the Conservation of Nature (IUCN) has adopted minimum suitable time frames to evaluate changes in wildlife numbers. It has been recommended that a 20 year span for three generations be used as a standard for all caribou populations. Declines or increases would be defined as at least a 20% change over 20 years. Few populations have been tracked adequately enough to measure such changes. Using collared caribou as a subset of the population may overestimate the mortality rate if the correct proportion of young cohorts is not collared.

Skogland (1991) reviewed the existing knowledge on the effects of predators on large ungulate populations. He defined "regulation as any density dependent process that tends to stabilise populations over time. The process that causes the change(s) in population size is termed limitation." The Rosenzwieg-MacArthur model predicted the following three conditions that would promote stability in a predator-prey system:

- access to alternate prey that could sustain predators when their main prey became scarce
- predators are characterised by low prey-capture efficiency
- predators are limited by factors other than food, such as territoriality.

Skogland (1991) found little supportive evidence that alternate prey facilitated predator regulation of ungulate numbers, whereas many factors strongly lower the predator's prey-catching efficiency. Seasonal nomadism and refuging by caribou could buffer against limitation by predators, which are limited by territoriality, regardless of alternate prey. He stated that there was considerable empirical data that spatial relationships are crucial factors in predator-ungulate relationships, but definitive evidence was generally lacking. Also, to prove wolves regulate caribou numbers, it is not enough to show that wolf removal experiments result in caribou population increases. There may be cases where wolves regulate caribou, but they have not been adequately tested over long enough periods of time. To regulate a population, the limiting effect of wolves must increase when caribou density grows, and decrease when caribou density declines. Skogland (1991) suggested that reducing the prey population without changing the predator population and then studying the recruitment response of the prey population may be the best method to test for regulation.

Sinclair (1979) hypothesized that in heterogeneous environments where prey have opportunity to avoid encounters with predators, prey populations would fluctuate and become food limited, while in more homogeneous environments where they are in closer association, predators could have a stronger impact on prey.

According to Messier et al. (1988), wolves are unable to regulate the George River caribou population because alternate prey are lacking and the caribou find refuge from wolves by migrating. Unlike annual production of herbaceous or shrub forage types used primarily by other ungulates, a standing crop of lichens represents many decades of annual production. During a rapid caribou population increase, there is no immediate feedback if consumption of annual production is exceeded. The carrying capacity may be greatly overshot because of the length of the time lag and the initial rate of population increase. The caribou compensate temporarily by expanding their range, but ultimately there will be a catastrophic decline after all of the food is depleted. Because lichen only grows a few millimetres per year (Pegau 1968), decades are required to restore the standing crop sufficiently to restore caribou numbers. An example of this is St. Matthew Island where 29 reindeer were introduced in 1944. In this predator-free environment, the population peaked at 6,000 by 1963, and then declined to 42 the next year, with no males remaining. Twenty two years later there was only 10% lichen recovery (Klein 1968).

This George River scenario described by Messier et al. (1988) may also true for other forest-tundra herds. Populations that eventually become limited by food may require increased levels of human harvest as a management strategy if dramatic declines are not desirable. However, west of Hudson's Bay muskoxen recovering from over-exploitation in earlier centuries, and muskoxen introduced to northern Quebec, may achieve densities that provide significant potential alternate prey for wolves.

Although wolves are territorial, there is some adjustment of their populations and territory sizes to prey biomass (Packard and Mech 1980; Keith 1983; Fuller 1989; Bergerud and Elliott 1986; Messier 1994; Bergerud and Elliott 1998). In his review of North American studies, Fuller (1989) described a linear relationship between wolf density and *total* ungulate biomass. As Theberge (1990) emphasized, the data points for this relationship were from stable wolf populations whose stability is inherently temporary, and there can be considerable lags in the numerical response of wolf populations to changes in prey density. As ungulate diversity and biomass increase, the predator-prey relationship may become more unstable with the wolf population temporarily growing beyond the sustainable biomass of prey (Bergerud and Elliott 1998). This instability would be particularly apparent if a prey population becomes more vulnerable because of poor physical condition (Boertje and Stephenson 1992), or declining prey populations force hungrier predators to hunt more extensively and less selectively. Intraspecific strife and malnutrition are main factors limiting wolves and a decline in their population may occur long after the prey has declined (Packard and Mech 1980). This loose feedback loop and lag in wolf response can push the prey to very low densities. In assemblages of multiple prey species, ungulate population increases escaping from predation tend to be infrequent and short lived, or cyclic (Gasaway et al. 1983).

Fancy et al. (1994) modelled the growth rate of the Porcupine caribou herd and determined that for population stability, any increase in adult female mortality required approximately a threefold increase in calf recruitment to ensure replacement of the lost females. In this modelled population, growth of the herd was most sensitive to changes in the survival of females three years of age and older, followed by calf production and survival. This is typical of long-lived species. Female caribou that reach adulthood have survived a very risky period of their life. All females are usually breeding by age three and will probably contribute reproductively to the population for several years. In a normal caribou population, loss of breeding bulls would have minimal effect on the population because they are easily replaced from the ranks of surplus bachelors.

Adult mortality rates in many vertebrate species often vary much less through time than immature mortality rates, especially in large-mammal populations (Fowler 1981) and adjustment of juvenile recruitment may be an efficient mechanism to hold populations stable (Charnov 1986). Caribou calf losses may be replaced during the next breeding season, and the population would maintain relative stability if years of poor recruitment are offset by years of good recruitment. Reproductive females are not as easily replaced and excessive mortality will reduce production of future reproductive females. The Porcupine caribou model demonstrates the importance of adult females for population stability.

14.0 VULNERABILITY TO PREDATION

Ungulate vulnerability is closely associated with wolf population dynamics (Keith 1983). A predator that expends considerable time searching for and pursuing prey is expected to be very selective for the easiest individuals to catch (Ricklefs 1979). Studies by Holmes (1982) and Husseman et al. (2003), which compared wolf and cougar hunting strategies, found that the longer chases and lower capture success of wolf packs had a stronger culling effect on disadvantaged prey, than did ambush hunting by cougars.

Murie (1944) provided several accounts of wolves hunting caribou. Many chases were quickly abandoned if no vulnerable individuals were discovered, but if one caribou started to lag others in a group, it seemed to encourage the wolves to press the pursuit. Determining hunting success rates of wolves is difficult because large numbers of observations are not easy to obtain and environmental conditions vary (Mech 1970). On average, wolves killed less than 10% of moose they encountered on Isle Royale (Mech 1966; Peterson 1977), and 15% of caribou encountered in Alaska (Mech et al. 1998).

14.1 Age

For most wildlife species, the period of reproduction is a critical period when environmental factors are likely to be the most limiting (Odum 1971). Very young calves are particularly vulnerable because of there small body size and lack of experience in avoiding predators (Adams et al. 1995a; Mech et al. 1998). Kuyt (1972) and Miller (1975) found that wolves took more caribou calves than any other age class and adults over eight years of age were also heavily preyed upon. Mech et al. (1995) observed that females aged 16 to 30 months had the lowest mortality, and the highest rate was at over ten years of age, mainly by wolves. On Isle Royale, wolves become more successful as a moose population ages and wolf numbers will grow as a result (Allen 1979).

On the caribou calving grounds of Denali, Adams et al. (1995b) made the following observations during their study from 1984-1987 when 226 calves were radio-collared. Grizzly bears were responsible for most of the calf mortality. It was greatest when calves were less than eight days old, and few were killed by bears after calves reached ten days of age. Only two or three wolf packs had calving caribou in their territories. There appeared to be a lag time before calving caribou were detected because wolf predation did not peak until after ten days. Calves averaging 50% larger than those at birth were more profitable for wolves. Approximately two weeks after the onset of calving, intense wolf predation ended abruptly. Caribou calves became more difficult to catch and wolves may have switched to moose and sheep neonates which began to appear at that time. A dramatic decrease in calf mortality occurred through summer and fall. Calves were not selected disproportionately in winter, consistent with other Alaskan studies (Ballard et al. 1987; Dale et al. 1995; Mech et al. 1995).

While research in Denali by Adams et al. (1995a) was carried out from 1987 to 1991, wolves were the main agent of caribou mortality. Neonatal losses to all sources of mortality, including wolf predation, were strongly correlated to average birth weight. Although wolves did not appear to select low birth weight calves within years, few calves were killed after 15 days of age during 1987-1989 when calves were heavier at birth. However, because of severe snow conditions, lighter calves were produced in 1990-1991 and their vulnerability to wolves extended throughout the summer.

From 1986-1992, Mech et al. (1995) observed that the occurrence of wolf predation on caribou calves in Denali was related to accumulated snowfall during the winter they were *in utero*. This was illustrated by the fact that calves were killed by wolves during winters that followed winters of above average snowfall, but after winters of below average snowfall, no wolf-killed caribou calves were found the next winter. Miller (1975) also stated that calves in poor physical condition appeared to be more susceptible to predation than healthy calves in winter.

In a 1983-85 study of calf survival, Whitten et al. (1992) determined that predation was the main cause of mortality for calves older than 48 hours. However, up to 74% of the deaths of calves occurred within 48 hours of birth largely due to factors other than predation. They cautioned that using survival rates of only radio-collared calves and calves of radio-collared females could underestimate mortality and overestimate predation if many calves die of congenital defects, low birth weights etc., before they can be collared.

14.2 Nutritional State

Mech et al. (1995) concluded that the most important common denominator in predisposing Denali prey to wolves was poor nutritional condition. Individuals that lost considerable muscle mass and fat would lack sufficient energy to withstand chases by wolves. The marrow fat content of wolf-killed prey was consistently low despite relatively low snowfall in some years. Mech et al. (1995) noted a major increase in the number of caribou killed during winters when above average snowfall accumulated. Adams (2003) found that weather-induced nutritional effects and predation were density independent. Marrow fat deposition and skeletal growth of calves through 20 days of age were negatively correlated with late winter snowfall that prolonged maternal under-nutrition.

Following 14 years of population growth, adverse weather for four years, combined with high wolf densities, caused Delta caribou population in Alaska to decline (Boertje et al. 1996). Besides deep and prolonged snow cover, adverse weather may also be defined by a short growing season, and an unusually warm dry summer that increases oestrid fly harassment. Excessive biting insects may cause increased caribou energy expenditure and decreased food intake (Boertje 1985). For the Delta herd, Valkenburg et al. (2002) used live weights of calves to determine their nutritional condition. Deteriorating body condition, induced by weather, predisposed caribou to predation. This interaction between weather and predation was considered to be the main determining factor for caribou population size in Alaska. Calf survival largely depended upon their size in fall, area available for winter range, and snow conditions.

Periodic unavailability of forage caused by weather variables is a component of long-term carrying capacity (Thomas and Gray 2002). Caribou have certain tolerance limits to snow if their main forage is terrestrial lichens. When depth, density, hardness or duration of snow tolerances is exceeded, there is an excessive energy cost (Fancy and White 1985). Forage intake and selection may also decrease (Boertje 1990). Caribou may be forced to search for more suitable range or switch to greater use of arboreal lichens (Pruitt 1959; Henshaw 1968; Stardom 1975; LaPerrierre and Lent 1977). In mountain caribou range where snow reaches its greatest depths, these animals rely almost entirely on arboreal lichens during late winter (Terry et al. 2000; Rominger et al. 1996).

In the Red Wine Mountains of central Labrador, Brown and Theberge (1990) studied the effect of extreme snow cover on caribou feeding behaviour. The caribou of central Labrador experience deeper snow than any other populations in North America, except those in southern British Columbia. Brown and Theberge (1990) found that the snow depth and hardness tolerances of the Labrador caribou greatly surpassed all thresholds documented from other caribou populations, which suggests that regional adaptations have developed for overcoming adverse snow conditions.

Thomas (1982) found a positive relationship between fat reserves and fertility in Peary caribou. Although data are lacking in woodland caribou, Thomas and Gray (2002) suggested that female caribou that are nutritionally stressed in late winter or early spring are likely to produce weak calves susceptible to predators. In Minnesota, a 12-year study on white-tailed deer provided evidence of a “grandmother effect” where wolf predation on fawns may be linked to weather conditions from two generations earlier (Mech et al. 1991). As expected, first generation offspring were more likely to be killed by wolves if snow conditions were severe during their mother’s pregnancy. However, predation was also higher on fawns whose grandmothers were in a poor nutritional state, regardless of the nutrition of the fawns’ mothers.

14.3 Season

Winter and spring snow conditions may also have more immediate effects on caribou vulnerability. Compacted or crusted snow that does not support the weight of caribou is energetically costly for movement, and if the snow is deep and the surface supports wolves, they have a distinct advantage in capturing caribou (Thomas 1995).

From the 165 caribou kills sampled monthly during their study, Mech et al. (1995) found that wolves tended to kill females primarily from February through to June, a period when they are most vulnerable because pregnancy and lactation demands are highest. Spring migration and the onset of lactation may cause a negative energy balance among cows (Fancy and White 1986). Also at this time of year, wolves are in peak condition and snow crusting is common (Thomas 1995). Vulnerability of neonates to predation and short growing season require cows to maximize investment in growth of offspring when their own body reserves are lowest (Adams 2003).

Although caribou bulls were the most predominant prey type throughout the year, they were most vulnerable immediately before, during, and after the autumn breeding season (Mech et al. 1995). Rutting ungulates are generally in relatively poor condition at this time because they lessen their food intake and spend considerable time chasing females and fighting rivals. Wolves killed a significantly greater proportion of male caribou than expected based on their fraction of the population (Adams et al. 1989). The mortality of male barren-ground caribou was more than double the rate of females (Miller 1974). Parker and Luttich (1986) found an even sex ratio for caribou killed by wolves in Labrador. When predation rates were high, adult bulls tend to be killed at a greater rate than females (Haber 1977; Bergerud and Elliott 1986). Relatively higher mortality has also been observed with male calves in spring and summer (Bergerud and Ballard 1986; Bergerud and Elliott 1986; Miller 1974; Kelsall 1968; Bergerud 1971), which may be a result of their more precocious behaviour.

14.4 Disease

Necrotic inflammation of the mandible or "lumpy jaw" is a disease of caribou and other ungulates that interferes with eating. Almost one-third of moose taken on Isle Royale by wolves had necrotic inflammation of the jaw (Mech 1966).

Caribou may periodically undergo outbreaks of hoof rot, a debilitating disease of the foot. It is especially prevalent during extended periods of wet weather (Elkin and Zarnke 2001). Crisler (1958) described caribou with hoof disease that were unable to escape from wolves. She also speculated that these animals would not survive the winter because they would be unable to dig feeding craters.

14.5 Parasites

Insects are potentially a major limiting factor for caribou (Thomas and Gray 2002). Effects include parasite and disease transmission, harassment, loss of blood, and immune system reactions, all of which can predispose animals to predation.

Mature woodland caribou are likely to have a relatively high incidence and prevalence of *Echinococcus granulosis* hydatid cysts (Thomas and Gray 2002). A large number of cysts in the lungs could make a caribou susceptible to predators. Crisler (1956) observed wolves killing caribou that were apparently weakened by such tapeworm cysts. Ovsyukova (1984) suggested that wolves single out reindeer weakened by hydatid infection. Wolves and other canids are the main hosts, while intermediate hosts such as caribou are required for this parasite to complete its life cycle. Consequently, hydatid infection of caribou may be particularly high where wolves are common.

The impact of ticks in caribou is not well known. It is thought that white-tailed deer are the primary host of the winter tick (*Dermacentor albipictus*), whereas moose and caribou are secondary hosts, maladapted for coping with infestation. Caribou have been infected in Alberta and Saskatchewan (Rock 1992; Godwin and Thorpe 2000). A warm autumn–late cool spring caused a severe outbreak of ticks and moose declined from New Hampshire to Alberta (Peterson and Vucetich 2003).

A meningeal nematode (*Parelaphostrongylus tenuis*), benign in white-tailed deer, is potentially a limiting factor for woodland caribou in eastern and central Canada (Anderson 1972; Pitt and Jordan 1994). Although infected individuals would be more vulnerable to predation, the effect would be compensatory as the parasite is lethal to caribou.

14.6 Genetic Load

Genetic variation is necessary for evolutionary adaptation to a changing environment. Genetic load is defined as the selective deaths experienced by a population due to genotypes that deviate from the genotype with the maximum fitness. It may increase in closed populations limited to small numbers of individuals over several generations that lose genetic variation. Modelling results from Vucetich and Waite (1999) suggested that small isolated populations undergoing natural fluctuations are prone to massive losses of genetic diversity. They also stated that the importance of this to the extinction risk of populations remains unresolved and contentious.

Random genetic drift occurs when random segregation of genes into gametes and unequal reproduction among individuals results in changes in allele frequency at polymorphic loci. The ability of populations to keep pace with anti-predator devices or immune responses to rapidly evolving diseases may be reduced if loss of alleles and fixation of one allele on a formerly polymorphic locus occurs and overwhelms natural selection for beneficial alleles. In Quebec, Courtois et al. (2003) determined that isolated caribou populations had the lowest mean number of alleles per locus and there appeared to be a general north to south reduction of genetic diversity.

In a normal population, dominant alleles mask deleterious recessive alleles, and may also interact with recessives to express advantage over either homozygote (heterosis). Breeding by close relatives may lead to *inbreeding depression*, whereby fitness is reduced by increasing frequency of recessive phenotypes and decreasing heterosis. This may become particularly apparent after a rapid reduction in population size does not allow time to purge deleterious alleles.

The relationship between decreased genetic variability and fitness is very complex. Evidence has not been well documented in wild ungulates, and some data are available from captive animals. Pemberton et al. (1988) reported that red deer calves homozygous for two alleles did not survive as well as calves heterozygous for both. Also, Ralls et al. (1979) used juvenile survival of ungulates as a measure of inbreeding depression in zoos. Any genetic conditions that potentially reduce optimal fitness of caribou would be expected to increase vulnerability to predation.

15.0 CHANGES IN UNGULATE AND CARNIVORE DISTRIBUTIONS

Climate change and human influences are likely factors affecting changes in wildlife distributions, but not all of these changes are completely understood. Causes of caribou range retraction may vary among populations, and remedial actions will require proper diagnoses of the problems.

Often, caribou range retraction coincides with range expansion of moose and deer. For example, the Red Wine Mountains caribou herd declined (Schaefer et al. 1999) as a moose population expanded across most of Labrador to treeline during the latter half of the 20^{th} century (Chubbs and Schaefer 1997).

Since glacial retreat, wolves and caribou coexisted on the island of Newfoundland. Around 1930, wolves disappeared even though introduced moose provided alternate prey, and the average take for bounty was only between three and four animals per year (Maunder 1991). Since 1985, coyotes have invaded the island (Lariviere and Crête 1993). Formerly, caribou and coyotes coexisted on Isle Royale (Allen 1979). They have now been replaced by moose and wolves. Black bear have extended their range in Labrador during the past century and become a source of caribou mortality. The first report of a coyote in Labrador has occurred recently. Other ungulates such as wood bison and muskoxen may also be expanding in some areas occupied by woodland caribou.

15.1 Climate Change

Subtle changes in climate may have profound effects on wildlife distributions. Peterson (1955) stated that moose appeared to invade northern Ontario and British Columbia since the late 1800s. A shift in predator-prey interaction may have been occurring before widespread anthropogenic influence in northern Ontario (Harris 1999). Spalding (1990) suggested that moose may have been sparsely distributed in central B.C. before undergoing a rapid increase in the 1900s. In a review of moose distribution records from northern Canada, Kelsall (1972) noted a trend of increasing observations of moose near treeline, and on tundra, between Hudson Bay and the Yukon-Alaska border.

This may have been the trend throughout Canada coinciding with the end of the “Little Ice Age” that lasted approximately through the years from 1300 to the mid 1800s, and subsequent global warming. The presettlement range of woodland caribou was also their maximum range at the end of the “Little Ice Age” (Bergerud and Mercer 1989). According to Telfer (1967), a moose/white-tailed deer fauna in Nova Scotia changed to a moose/caribou fauna during this period of global cooling. After it ended, deer reinvaded the province and have generally expanded their range northward and westward. This scenario would probably exacerbate the meningeal nematode problem in caribou. The last ranges they occupied during their disappearance from parts of eastern North America were generally high in lichen cover and these were the last to be invaded by deer (Bergerud and Mercer 1989).

Associated changes in the forest fire regime would certainly have produced a different mix of successional stages and relative amounts of moose and caribou habitat. A major increase in fire frequency began around the mid-1700s, and was followed by a significant decrease since the late 1800s. These changes may be associated with “Little Ice Age” effects on temperature, precipitation, and circulation of air masses (Bergeron and Archambault 1993). Time-since-fire data have shown synchronous changes in fire cycles in many areas of North America, with and without fire suppression, suggesting that climate change is the main cause of these changes in fire frequency (Johnson 1992).

Many experts believe that the current rate of temperature change is unprecedented, and historical patterns will be inadequate to predict future patterns (Brubaker 1988; Payette et al. 1989). Several general circulation models have been developed to simulate future climate if carbon dioxide levels in the atmosphere continue to rise. Most predict that the greatest warming will occur at high latitudes (Flannigan et al. 2000). Over ten years of simulation, the Canadian Regional Climate Model for western Canada predicts that temperatures will increase by five degrees and precipitation will decrease by 20% (Amiro et al. 2001). The expected result would be increases in fire frequency and area burned. Wotton and Flannigan (1993) have calculated that a doubling of carbon dioxide levels would extend the fire season in Canada by 30 days. Eastern Canada may actually experience longer fire intervals because of greater amounts and more frequent precipitation in a warmer climate (Flannigan et al. 1998).

According to Weber and Flannigan (1997), the indirect effects of climate change on vegetation through fire may be more important than direct effects on species distribution, migration, substitution, and extinction. As the favourable climatic region for many species shifts northward, large disturbances that terminate life cycles of the original inhabitants would facilitate the entry of the new competitors. Woodland caribou have adapted to an environment where approximately 40 years is required for lichen to recover from fire (Harris 1996), and where fire intervals are long enough to allow adequate lichen cover to develop as their main food supply. The adaptations of species such as moose, deer, or elk are more suited for environments with shorter fire intervals.

Woodland caribou habitat characterised by sparsely forested peatlands may be intrinsically linked with discontinuous permafrost (Bradshaw et al. 1995). Global warming would probably cause more frequent drought years in central Canada (Price and Apps 1996). Increased desiccation, fire, and mean temperatures that facilitate melting of permafrost could alter the southern limits of peatland caribou habitat.

All caribou populations are vulnerable to climatic warming and greater weather variability, especially small herds on the southern periphery of the range. Besides fire, detrimental effects could also include more adverse snow conditions such as crusting, thermal stress, and changes to food supplies (Thomas and Gray 2002). Because small changes in calf survival can affect population growth or decline, the relationship between calf survival and vegetation biomass and growth rate may be used to predict effects of climate-induced habitat restrictions on caribou populations (Griffith et al. 2000).

15.2 Human Influences

Some species such as coyotes and white-tailed deer have adapted well to anthropogenic landscape disturbances such as agriculture, and thrive along with moose and wolves in areas modified by timber harvesting.

According to Kay (1998), aboriginal people were the ultimate keystone predator before their populations were devastated by introduced diseases. They were more efficient predators than wolves and could rely on a vast array of alternate food when meat was scarce. There is growing evidence that humans limited moose, bison, elk, deer, and muskox populations at very low levels in historical times. Perhaps woodland caribou benefited because they were less profitable to hunt, and humans suppressed populations of alternate prey, thereby keeping wolves at low densities.

Cultural use of fire to modify the environment was very widespread in aboriginal societies (Pyne 1982). Use of fire in the boreal forest included improving habitat for preferred species such as moose (Lewis 1982), but impacts on woodland caribou have not been documented.

Hunting activities of aboriginal people in northwestern Ontario were found to have minor impacts on boreal caribou because moose were more dependable (Hamilton 1984). Accordingly, humans may have had significant effects on the local abundance of these two species for the past several thousand years.

16.0 CONSERVATION ATTEMPTS

16.1 Hunting Restrictions

As forest-dwelling woodland caribou population declines became apparent, most provinces enacted more stringent legislation. Non-aboriginal hunting was banned in Ontario in 1929, followed by Alberta in 1981, Saskatchewan in 1987, Manitoba in 1992, and Quebec in 2001. Recreational hunting in Newfoundland and Labrador, Northwest Territories, B.C. and Yukon is restricted by various means such as no-hunting zones, bag limits and limited-entry seasons. Hunting by indigenous people is largely uncontrolled.

16.2 Reintroductions

Some translocations of caribou into former range, such as at Michipicoten Island in Lake Superior. have been considered successful. Others have not been as encouraging and no reintroductions have succeeded where high white-tailed deer populations exist with meningeal worm (Bergerud and Mercer 1989). Augmentation of existing endangered populations along the southern parts of former range has not been as successful as hoped for either. For example, the failure to reverse caribou decline in Idaho may be attributed to an increased cougar population resulting from an expanded white-tailed deer prey base, and loss of habitat (Zager et al. 1996).

16.3 Predator Control

Bounties had been instituted for wolves and other large carnivores in most jurisdictions in the past, but they have been generally deemed ineffective (Kelsall 1968). However, more organised government control programs have been quite effective in reducing wolf predation on caribou, at least in the short term. These measures have attempted to arrest or reverse declines in caribou herds, and assist population rebound from prolonged low densities. There are many examples of increased calf recruitment and adult survival following wolf reductions (e.g., Farnell and McDonald 1986; Bergerud and Elliot 1998; Valkenburg et al. 2002), and coyote reductions (Crête and Desrosiers 1995).

From the mid 1950s to the early 1960s, all winter ranges of barren-ground caribou were baited with poison (Kelsall 1968), and considerable portions of these ranges were shared by woodland caribou. After 11 000 wolves were killed over a ten year period in Northwest Territories, Saskatchewan, and Manitoba, caribou were able to attain high numbers. Subsequently, recovering wolf populations in these areas have coincided with caribou declines. Thomas and Gray (2002) recommended that the atypical caribou population highs in the 1960s, when wolves were reduced to artificially low numbers, should not be considered as current objectives.

Reproductive attributes of prey populations have evolved, among other factors, in association with predator pressure (Ricklefs 1979). Removal of predators places the prey species in an environment it is not adapted to. After abnormally high population growth, the species is forced by other mortality factors such as disease or starvation to return to lower levels compatible with resources. In a study by Kie et al. (1979), the white-tailed fawn:doe ratio increased in an experimental area where predators were removed. After three years, there were signs of malnutrition and winter mortality of fawns compensated for earlier losses to predators. After five years, adult deer were succumbing to parasites and densities dropped to the same level as the time before predators were removed.

There has been experimentation with more socially acceptable and indirect forms of predator control (e.g., Spence 1998; Boertje and Gardner 2000; Valkenburg et al. 2002). These include reducing the moose food base for wolves, encouraging trappers to focus efforts on wolves, diversionary feeding of predators in calving areas, sterilization of breeding male wolves, and captive rearing of caribou cows and calves during a few weeks around parturition.

Reducing the moose population by increased hunter harvest was modelled by Weclaw (2001) for an area of northeastern Alberta. Computer simulations showed this to be a more efficient method to sustain caribou than direct predator control. Courtois et al. (2003) modelled a similar best management measure for Quebec. Such strategies may be beneficial in some localities with low potential for other land use conflicts, and if wolf populations had sufficient time to adjust their numbers without being forced to compensate by including more caribou in their diet.

16.4 Parks and Protected Areas

Parks such as Woodland Caribou and Wabakimi in Ontario and the Grands-Jardins Conservation Park in Quebec have been created primarily for caribou. Many other parks that function in the interests of caribou conservation were originally established with multi-purpose goals. In order to conserve habitat adequately, many parks, reserves, and other protected areas should be assessed to determine whether they are meeting that objective. Some may need to be expanded, or the surrounding region must have compatible goals.

16.5 National and Provincial Recovery Strategies

Federal and provincial governments must implement a recovery process and adhere to timelines under the Federal Species at Risk Act. Following the COSEWIC designation, formation of Recovery Teams, development of Recovery Strategies, input into a National Recovery Process, Public Review and Approvals are required.

Land use policies that apply to caribou conservation have been developed in many provinces. Some examples are A Strategy for the Recovery of Mountain Caribou in British Columbia; West Central Alberta Standing Committee Industrial Guidelines; Boreal Caribou Committee Strategic Plan and Industrial Guidelines; and Forest Management Guidelines for the Conservation of Woodland Caribou: a Landscape Approach–for Use in Northwestern Ontario.

17.0 FOREST MANGEMENT IMPLICATIONS

17.1 Caribou Habitat and Commercial Forest

Stands of late successional forest are often preferred by both woodland caribou and the forest industry. Because distance to markets is a major factor determining forest merchantability, the commercial viability of logging in much of the caribou range may be sensitive to the price of lumber and technological improvements in wood processing.

Age of forest is considered a main quality of habitat suitability for woodland caribou (Apps and Kinley 1998; Higgelke and MacLeod 2000; Palidwor and Schindler 1995; Szkorupa 2002). However, boreal forests begin to lose their terrestrial lichen component after about 110 years (Ahti 1977) as canopy closure shifts light, temperature, humidity, and litterfall conditions to an understory environment more favourable for feathermosses (Kershaw 1978; Thomas and Armbruster 1996). In southeastern Manitoba, the oldest stands of 160 years showed the lowest productivity for lichen forage and disturbance such as fire is required to maintain optimal lichen resources (Schaefer and Pruitt 1991). Skogland (1986) suggested that lichen growth is adapted to intermediate levels of reindeer grazing pressure. Without grazing, lichen mats stop growing and succession is reversed to favour shrubs.

Along a latitudinal gradient through the Quebec-Labrador peninsula, production of preferred forage exhibits a clear north-south increase for moose, and a decrease for caribou (Crete and Manseau 1996). This implies a general decline in caribou habitat quality towards the southern portion of the boreal forest where merchantable timber is most abundant (Wedeles et al. 1995). Forest types containing white spruce (*Picea glauca*), larch (*Larix laricina*), and deciduous species develop on moist rich soils that produce little lichen (Brown et al. 2000). On the southern periphery of the caribou range, there are populations that have unacceptably low probabilities of persistence into the future because of diminished numbers, isolation from other herds, and proximity to habitat favoured by moose.

Direct negative effects of forestry on caribou habitat vary according the ecological setting. Studies in many regions have shown that caribou avoid or underutilize clearcuts (Freddy 1979; Darby and Duquette 1986; Rettie and Messier 2000; Smith et al. 2000; Chubbs et al. 1993; Hillis et al. 1998; Courtois et al. 2004). In west-central Alberta, Smith et al. (2000) observed no avoidance of areas during the initial stages of logging activity, followed by 12 years of significant avoidance of harvested areas. Rettie and Messier (2000) suggested that decreased use of cutblocks as they improve as moose habitat may be a wolf avoidance strategy. In Newfoundland, Chubbs et al. (1993) found that caribou movements away from clearcuts in summer appeared to be mainly in response to ongoing operations, and some individuals seemed to habituate to the harvest activity.

In many areas, caribou select lowland black spruce (*Picea mariana*) peatlands which contain raised xeric substrates suitable for terrestrial lichens. Merchantable timber is generally associated with upland sites that are likely to become prime moose habitat after harvest. In northeastern Ontario, Wilson (2000) concluded that areas used most by caribou had relatively low stand densities and may be less valuable as sources of timber. According to Bradshaw et al. (1995), pulpwood harvest in northeastern Alberta targeting aspen (*Populus tremuloides*) stands does not appear to directly affect caribou range. Studies in this region by Bradshaw et al. (1995) and Fuller and Keith (1981) showed that caribou appeared to use denser timber stands during periods of high snow accumulation. This tendency has also been observed in west-central Alberta (Edmonds and Bloomfield 1984) and southeastern Manitoba (Darby and Pruitt 1984).

Terrestrial lichens may also be abundant on well-drained soils or very shallow soils with exposed bedrock that are not likely to produce prime moose habitat. On such sites, vascular plants are sparse and grow more slowly, and pines (*Pinus* spp.) dominate (Topham 1977; Racey et al. 1999). Coarse textured soils that promote lichen production are often poor growing sites for trees (Seip 1993). Caribou of west-central B.C. tended to select mature forested habitats on sites of low nutrient quality (Cichowski 1989).

In west-central Alberta, caribou preferred highly merchantable stands in some winter ranges, especially when snow was deep (Hervieux et al. 1996). Szkorupa (2002) determined that the highest preference was for stands with 70-100% crown closure, where lichen was not abundant. This may be explained by predator avoidance, snow interception, or dense lichen at finer scales even though it was sparse at the coarser scale. Most cratering was in moderately dense stands of 50% canopy closure. Bjorge (1984) found caribou selected "medium density" stands, but this is not directly comparable to the crown closure results of Szkorupa (2002).

The mountain/arboreal ecotype of caribou occupies mature coniferous forests during winter, where they feed almost exclusively on arboreal lichens. This ecotype requires a higher proportion of mature and old forests, uneven-aged stands, small cutblocks, and mature forest connectivity than other forest-dwelling ecotypes (Seip 1998). Some of these stands are also valuable sources of timber and may improve as moose habitat after cutting.

In the northern Cariboo Mountains of British Columbia, forests with moderately high timber volumes were used most often by caribou during early winter, but only in proportion to availability. They mainly used open-canopy subalpine fir (*Abies lasiocarpa*) stands later in the winter, characterised by low stocking and inoperable timber volumes (Terry et al. 2000). This suggests less overlap between caribou habitat and commercial forest than in other parts of southern British Columbia.

17.2 Roads

Caribou may be affected by roads in many ways, including changes in predator behaviour. In Alberta, considerable research and modelling have been carried out on impacts of linear corridors, mainly associated the oil and gas industry, that may have some relevance to forestry roads.

It has been speculated that roads may result in greater penetration of wolves into caribou habitat as easy travel routes if there is limited human activity (Bergerud et al. 1984; Edmonds and Bloomfield 1984; Thurber et al. 1994; Seip and Cichowski 1996; Stuart-Smith et al. 1997; James and Stuart-Smith 2000). As part of a long term study of woodland caribou in northeastern Alberta, James (1999) radio-tracked wolves and caribou and examined their relationship to linear corridors. In caribou habitat, wolf locations were found to be closer to linear corridors than random. Based on straight line distances between telemetry locations, wolves travelled almost three times faster on linear corridors than in the surrounding forest and this was calculated to increase the encounter rate with caribou by up to 72.8%. The results supported the hypothesis that roads provide wolves more direct access into caribou habitat and allow them to penetrate further into caribou range. Although caribou mortality appeared to be random across the study area, wolf kills were closer to linear corridors than live caribou locations. This suggested that caribou near roads were at a higher risk of predation.

In a study of disturbance of woodland caribou in northeastern Alberta, Dyer (1999) found that caribou responded mainly to the vehicular traffic associated with development. Total avoidance was most apparent on heavily used roads (600-800 vehicles per day).

After conducting studies near Lake Nipigon, Cumming and Hyer (1998) suggested that chronic or severe disturbance, such as log hauling through prime winter range, could displace animals into poor habitat or closer proximity to moose and wolves.

Roads also have negative impacts on wolves such as human-caused mortality and disturbance. In a study by Thiel (1985), wolf packs in Wisconsin were unable to persist at road densities above 0.58 km/km^2. Observations by Jenson et al. (1986) in Ontario and Michigan, and Mech et al. (1988)

in Minnesota supported Thiel's model. In Alaska, Thurber et al. (1994) found that human presence without mortality was sufficient to cause avoidance of roads.

17.3 Harvest Pattern

Of key importance to predator-prey relationships is the spatial arrangement of habitat types and timber harvesting at the landscape level. Although fen/bog complexes in northeastern Alberta that caribou selected lacked valued timber resources, James (1999) stated that timber harvesting in upland sites close to fen/bog complexes may increase predation on caribou. In this scenario, regenerating browse immediately after logging would cause elevated moose densities in cutovers that may persist for decades, and some "spill over" of moose into fen/bog habitats. The numerical response by wolves would result in more frequent encounters with caribou.

A mosaic of small cutovers carried out over a long period of time could potentially produce the edge and young growth to sustain high moose and wolf populations. In west-central Alberta, two and three pass logging systems, producing a checkerboard pattern of cuts and reserve blocks, were designed in the mid-1980s for the purpose of maintaining adequate caribou habitat. Instead, they resulted in undesirable effects for caribou (Hervieux et al. 1996). In addition to loss of habitat that concentrated caribou in remaining areas, the distribution and abundance of moose, elk, white-tailed and mule deer increased uniformly across the landscape. This expanded alternate prey base for wolves may have caused a corresponding increase in predation on caribou.

Woodland caribou have adapted to a boreal forest landscape dominated by effects of fires that are able to reach thousands of square kilometres in size. In order to more closely mimic a typical fire event, a large irregular cut, or a series of contiguous small cuts are recommended in some regions such as northwestern Ontario (Racey et al. 1999) and central Quebec (Courtois et al. 2004) for the purpose of eventually producing the extensive even-aged mature forest beneficial for caribou.

Kuzyk (2002) found that 31wolves radio-collared from eight packs in west-central Alberta preferred non-forested natural habitat (beaver meadows and shrublands) and forest cutblocks. Least preferred habitat consisted of non-forested anthropogenic clearings. He suggested that planning cutblocks away from prime caribou habitat, or close to non-forest natural habitat preferred by wolves, may prevent excessive wolf predation on caribou.

In mountains, large cutblocks are not appropriate because they eliminate arboreal lichen and create favourable moose habitat. The Cariboo Chilcotin Land Use Plan Mountain Caribou Strategy recommended modified harvest and no-harvest zones (Armleder et al. 2000). Lodgepole pine reforestation is discouraged in favour of other conifers that potentially provide more arboreal lichen biomass.

17.4 Lichen Retention

Intensive conifer silviculture may be compatible with lichen production and reduce the production of moose browse. Lichens are intolerant of shade, and do not compete well in soils with a well developed duff layer that holds moisture and provides a substrate for vascular plants. Disturbances that remove vascular plants and alter growing conditions by exposing mineral soil can enhance a site suitable for lichen regeneration (Nash 1996; Brown et al. 2000). Lichen growth is often most abundant where fire burns away duff layer completely (Brown et al. 2000). Herbicides that do not target lichen may also be useful.

In the northern interior of B.C., woodland caribou rely on terrestrial lichen (Seip 1993). In lodgepole pine stands of this region, Coxson and Marsh (2001) observed that in blocks cut during summer persistence of lichen was less apparent, and there was a problem with invasion of vascular plants. Furthermore, logging residue piled or mixed in soil promoted vascular plant growth.

17.5 Fire Control

Fire suppression to protect timber resources will also conserve caribou habitat, at least in the short term. Control of fire in much of the boreal forest has only been in place since the late 1940s, and large conflagrations still occur (Johnson et al. 1998). In a review of time-since-fire studies, Johnson et al. (1998) noted that boreal landscape mosaics across North America are generally comprised of large areas of younger forest resulting from the most recent large fires, and these contain small patches of remnant old forest from past large fires. They concluded that virtually all areas of the boreal forest will have burned within a 300-400 year time period. Forests older than 200 years rarely exceed 5-10% of the total landscape (Johnson et al. 1995).

In Ontario's unmanaged boreal forest where fires are not suppressed, Boychuk et al. (1995) also found that younger age classes dominated the landscape. In his assessment of the province's managed boreal forest, Euler (1998) calculated that 75% of stands were older than 40 years. Combined disturbance by fire or logging per year amounted to less than 40% of the average annual burn during pre-settlement times. In managed forest, burn area is limited by fire suppression and forest fragmentation resulting from activities such as agriculture.

In central Saskatchewan, Weir (1996) found that large fires (> 100 hectares) account for over 99% of total area burned, and this pattern may be similar to any part of the boreal or montane forest. Although small fires may occur at high frequency, they are spatially rare and constitute a small proportion of the landscape (Johnson et al. 1998).

Prime woodland caribou habitat may not have been as widespread in historic times as commonly assumed. Extensive stand replacing forest fires that periodically occurred would concentrate their effects on parts of the overall landscape, and caribou adapted by temporarily abandoning those parts of their range. An exception to this scenario may be caribou habitat consisting primarily of fen/bog peatlands where moisture and fuel characteristics are usually not conducive to intense fire.

Limiting the annual percentage of caribou habitat allowed to burn has been recommended in some jurisdictions (e.g., Ferguson 1983), but it is a difficult objective to achieve because of the uncontrollable nature of fire weather. Habitat of isolated populations restricted in range may require virtually complete protection from fire to prevent their extinction.

18.0 SUMMARY OF STUDIES

The number of research articles in the form of reviews, studies, and commentary included in this report that addressed aspects of caribou predation totals 149. With most, the main focus of research was on subjects other than caribou predation. Multiple reports using duplicate data are often published following a single study, and in some cases, data sets are duplicated in expanded studies. There are many areas of Canada where the effect of predation on caribou populations has received little investigation, or important data have not been published. Most of the conclusions from studies in this review are deductive and observational.

Wildlife scientists have identified many problems associated with predator and ungulate prey research that are often difficult to remedy (Hebblewhite et al. 2002). These problems include a) difficulty of separating simultaneous effects of predation and other limiting factors; b) small sample sizes and low statistical power; c) model selection uncertainty; d) correlative nature of models where alternatives to null hypothesis testing are appropriate; and e) difficulty of applying classic experimental design. The main purpose of experimental design (replication, random sampling, controls etc.) is to produce an unambiguous result in the presence of confounding factors. In contrast, inferences from observational data are weak because uncontrolled variables have confounding effects and it cannot be determined which variables are causing the observed effects (Caughley and Gunn 1996). Hebblewhite et al. (2002) stated that the only consistent advice from researchers has been to take advantage of natural experiments where variation in predator and ungulate densities allow comparison of population processes across the range of densities.

In the tables below, 31 studies described the environment where wolves are the main predator of caribou. Early reports from studies that were continued and progress reports were not included if final reports became available. Papers with duplicated data sets were also excluded. It was found that less than one third of these studies exceeded 5 years in duration, some of the long term studies collected data at irregular intervals, sample sizes ranged widely, some investigations continued throughout the year while others were conducted seasonally, and study areas were subjected to varying degrees of human exploitation of wolf and ungulate populations.

Table 18.1 outlines 12 studies of forest-dwelling caribou carried out from central Labrador to the foothills of west-central Alberta. They are usually distributed at low density across broad landscapes or isolated into small herds (10s or 100s). These relatively sedentary caribou appear to have relatively few options to avoid wolves. The Gaspesie caribou may exhibit movement and foraging behaviour more similar to forest-alpine ecotypes of western North America. The habitat of herds in central Labrador may more closely resemble the transitional zone between forest and tundra.

Forest-alpine ecotypes occur in mountainous regions of the western cordillera. The 14 studies in Table 18.2 are comprised of ten from western Canada and four from Alaska. Herds tend to be fairly discreet because of mountain-valley constraints and their numbers may range from less than 100 to tens of thousands (Mallory and Hillis 1996). They are able to avoid wolves at calving by ascending to higher elevations.

Forest-tundra caribou generally occur at higher latitudes than other ecotypes. Most of the herds in the studies in Table 18.3 have undergone high amplitude population changes in the hundreds of thousands. These caribou spend part of the year in the forest and migrate long distances to calving grounds on the tundra where there are fewer wolves.

Table 18.1 Studies That Examined Predation Relationships of Forest-Dwelling Caribou Ecotypes

Study	Region	Duration	Spatial Dynamics	Predation
Schaeffer et al. 1999	Central Labrador	1993 - 1997	Red Wine Mountains herd mainly sedentary Some emigration to George River herd	Recent arrival of moose expanded prey base for wolves Wolves main mortality factor of the population declining during 1990s
Brown et al. 1986	Central Labrador-northern Quebec	1982 - 1984	Females dispersed and did not use common calving grounds	Increased migratory caribou and moose sustain more wolves Population declines of sedentary herds
Mosnier et al. 2003	Southeastern Quebec	1998 - 2001	Recruitment higher for Gaspesie caribou calving at highest elevations away from coyotes	Coyotes have recently become a major source of mortality
Bergerud 1985	Central Ontario	1975 - 1979	Lake Superior shoreline at Pukaskwa refuge from wolves	High wolf densities inland limit caribou range expansion
Ferguson et al. 1988	Central Ontario	1978 - 1982	Pic Island in Lake Superior refuge from wolves	High wolf densities inland limit caribou range expansion Low predation on island resulted in forage competition
Cumming and Hyer 1998	Northwestern Ontario	1990 - 1993	Small scale spatial separation disrupted by human disturbance	Increased mortality for caribou displaced outside of normal winter range
Cumming et al. 1994	Northwestern Ontario	1980 - 1984	Caribou-moose habitat partitioning put greater distances between caribou and wolves	Predation proximate limiting factor Refuge habitat ultimate limiting factor
Rettie and Messier 1998	Central Saskatchewan	1992 - 1996	Females spaced out and calved alone	High mortality of calves and adults limits population
Fuller and Keith 1981	Northeastern Alberta	1976 - 1978	Wolves and moose in Birch Mountain study area at low density Calving females dispersed alone or in small groups	Caribou population apparently stationary or declining Wolf predation light in summer Lynx density high and hare population in rapid decline, and winters of deep snow during study period
James 1999	Northeastern Alberta	1991 - 1997	Fen/bog habitat away from wolves Avoidance of good quality habitat because of human disturbance	Linear corridors facilitate wolf travel speed and penetration into caribou habitat increasing encounter rates
Kuzyk 2002	West-central Alberta	2000 - 2001	Restricted wolf movements in moose habitat reduced encounters with caribou of the Little Smoky Herd	Presumed to be limiting to the population
Edmonds 1988	West-central Alberta	1979 - 1984	Little Smoky and Berland-Simonette caribou herds more sedentary than adjacent alpine ecotype	Predation primary factor limiting growth of caribou herds

Table 18.2 Studies That Examined Predation Relationships of Forest-Alpine Caribou Ecotypes

Study	Region	Duration	Spatial Dynamics	Predation
Kuzyk 2002	West-central Alberta	2000 - 2001	Restricted wolf movements in moose habitat reduced encounters with A la Peche and Prairie Creek caribou herds	Wolf predation presumed to be limiting
Edmonds 1988	West-central Alberta	1979 - 1984	Mountain caribou migrated to high elevations and became widely dispersed during calving	Predation primary factor limiting growth of caribou herds Small groups may become isolated in mountainous areas
Edmonds and Smith 1991	West-central Alberta	1987 - 1989	Calving in 1989 less dispersed at lower elevation caused by late snow cover	Calf survival in 1989 lower than long term mean
Seip 1992	Southeastern British Columbia	1984 - 1989	Wells Gray population separated from wolves year round in high elevations Quesnel population separated only in winter	Wells Gray population increased, while Quesnel population declined
Seip and Cichowski 1996	West-central British Columbia	1985 - 1988	Itcha-Ilgachuz-Rainbows females calved on large alpine plateaus Tweedsmuir-Entiako females calved at high and low elevations and on islands	Calves born at high elevations and islands had high survival Tweedsmuir-Entiako calves born at low elevations had low survival
Poole et al. 2000	Central British Columbia	1996 - 1998	Takla caribou occupied higher mountain elevations than wolves and moose	Population may have used more low elevation habitat before wolf and moose densities increased earlier in century
Bergerud et al. 1984	Northern British Columbia	1976 - 1977	Spatsizi females dispersed in high south slopes of mountains to avoid wolves during calving	Anti-predator tactic only relatively successful, and calf mortality still high
Bergerud and Elliot 1986	Northern British Columbia	1976 - 1982	Females dispersed in high elevation calving grounds where predation influenced by presence or absence of wolf dens	Calf survival increased in Horseranch Mountains where wolves were reduced Calf survival decreased in control areas
Hayes et al. 2000	East-central Yukon	1990 - 1994	Finlayson herd temporarily available to wolves for a few months each year	Recovering wolf population killed more moose even when caribou more plentiful Abundance of young moose may have been more profitable
Gauthier 1984	Southwest Yukon	1978 - 1982	Burwash caribou calving grounds away from high wolf densities	Wolf predation during rut and winter most important limitation for slowly increasing or stable growth of the herd Weather may be a factor some years
Ballard, et al. 1987	South-central Alaska	1975 - 1982	Most Nelchina caribou unavailable to wolves during calving season Caribou usually wintered in poor moose habitat where wolf density lowest	Predation rate varied according to location of caribou wintering areas

(Continued on next page.)

Table 18.2 Continued

Study	Region	Duration	Spatial Dynamics	Predation
Mech et al. 1995	Interior Alaska	1986 - 1992	Denali caribou adjusted distribution to avoid wolf activity and adverse snow conditions	Losses of calves to wolves related to birth weight When wolf population doubled, exposure of calves to predation did not increase
Valkenburg et al. 2002	Interior Alaska	1979 - 2000	Calving areas and female dispersal varied among years	Population fluctuations related to interaction of food competition (in larger herds), weather and predation
Barten et al. 2001	Interior Alaska	1994 - 1995	Mentasta maternal females used high elevation sites with fewer predators	Low density population similar to other Alaskan herds limited by large carnivores

Table 18.3 Studies That Examined Predation Relationships of Forest-Tundra Caribou Ecotypes

Study	Region	Duration	Spatial Dynamics	Predation
Messier et al. 1988	Northern Quebec-Labrador	1954 – 1985 review of surveys	Long distance migration of George River herd from wolf denning areas	Year-round alternate prey to sustain high wolf densities lacking Predation could not halt growth of the herd leading to forage exploitation and range expansion
Heard and Williams 1992	Northwest Territories	1976 – 1990 included previous surveys	Most wolf dens within 50 km of treeline occupying only 25% of calving areas of all mainland migratory caribou populations	Caribou populations growing Wolves easily hunted by snowmobile and their fur valuable
Fancy et al. 1994	Northeastern Alaska-northern Yukon	1983 - 1992	Porcupine herd females calved north of foothills to avoid wolves and bears	Highest mortality when calving closer to foothills and snowmelt late
Dale et al. 1995	Northern Alaska	1989 - 1990	Spatial distribution important influence on predation rate	High wolf predation regardless of number of caribou
Ballard et al. 1997	Northwest Alaska	1987 - 1992	Some wolves followed migrating caribou of the Western Arctic herd when moose densities low	Caribou main prey of wolves when present Switched to moose when caribou scarce Wolves limited by hunting and trapping did not strongly limit caribou population

19.0 CONCLUSIONS

- Predator-prey interactions are dynamic and pervade forest management activities in caribou range.
- Although some generalizations are possible, there is little comparability among studies. Ecological components of caribou ranges can be so different that good site-specific information is critical for management.
- The smaller and more isolated populations are, the more vulnerable they will be to all mortality factors, including predation.
- Spatial separation from alternate prey such as moose is one of the most important conditions for caribou to reduce their profitability to wolves. Where caribou and moose habitats are separate and extensive, core areas of caribou distribution may be sufficiently remote to escape the impacts of adjacent moose habitat. In other ecological settings where long narrow riparian zones and other small patches of moose habitat are embedded throughout extensive areas of caribou habitat, or small patches of prime caribou habitat are embedded throughout extensive areas of moose habitat, the adverse impacts on caribou may be profound.
- The least viable woodland caribou populations tend to be sedentary and available as year-round prey for wolves.
- The most viable caribou populations escape wolf predation for at least part of the year by migrating to relatively safe calving areas.
- Insular or migratory caribou that escape limiting effects of predation may become food limited, resulting in population oscillations of great amplitude.
- If wolves regulate some caribou populations at low densities, management strategies such as predator control will produce temporary results.
- When evaluating winter severity in relation to caribou condition, snow density, hardness, duration and depth of snow need to be examined.
- Viability of caribou populations in some localities may be inherently restricted by environmental factors such as snow conditions that regularly exceed tolerance limits, or lack of secure calving areas.
- Regular monitoring of populations is required to verify long-term or changing demographic trends.
- Changes in caribou distribution may be the result of many complex factors.
- Varying degrees of overlap exist between caribou habitat and commercial forest.
- To meet some caribou population objectives, reducing quality of moose habitat must be considered.
- Knowledge of critical threshold densities and predator-prey ratios is important for resource managers, but their reliability depends on many variables.

- Habitat components such as refuge from predation or disease should not be overlooked when evaluating habitat quality.
- Some populations that are too small and precarious for experimental treatments require adaptive management strategies.

20.0 RESEARCH AND MANAGEMENT NEEDS

To manage woodland caribou better and to maintain a viable forest industry, decision makers require more accurate information as outlined below.

- more long-term caribou, moose, and wolf demographic studies to account for changes in forest succession, weather, disease prevalence, and human exploitation
- silvicultural techniques for minimising production of moose browse and enhancing production of lichen and other forage species generally used only by caribou
- nutritional requirements of caribou at the population and individual animal level
- importance and most critical period for predation on caribou calves for each region
- impacts of other predators such as black bears and lynx
- caribou and wolf responses to roads in varied ecological settings
- habitat alteration thresholds for caribou populations
- experimental intervention to manipulate moose densities (hunting pressure) to test wolf and caribou population responses
- consequences of declining moose populations on caribou predation
- conditions affecting wolf encounter rates with caribou
- coarse- and fine-scale levels of prey selectivity in caribou-moose-wolf systems
- optimal juxtaposition and geometry of cutblocks in relation to caribou habitat and travel routes of wolves
- effect of habitat quality and enhancement on resilience of caribou populations to withstand wolf predation
- standardization and further classification of ecotypes
- intraspecific morphological variation in caribou, wolves, and moose and its effect on predator-prey relationships
- adaptive environmental assessment and management processes to organize agencies and stakeholders to use knowledge and models for resource management decision making

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