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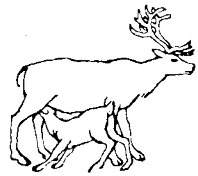

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Preface

The 7th North American Caribou Conference was held August 19-21 1996, in Thunder Bay, Ontario, Canada where 136 registrants participated in 3 days of sessions and subsequent field tours. The first day of the conference provided a forum for the presentation of new knowledge about the biology of woodland caribou. Four evening sessions promoted discussion on selected themes including caribou as indicators of ecosystem health of the Lake Superior basin; GPS collars for caribou telemetry studies; conserving woodland caribou in the managed forest; and caribou foraging and use of second growth managed fotests. The second day featured presentations on the status and management of caribou across Canada and the continental United States. A barbecue was held in the evening and promoted casual discussion and networking. The third day corresponded with the Canadian Institute of Forestry annual meeting and a joint day with the CIF provided an opportunity fot a total audience of over 350 people to hear presentations and arguments about woodland caribou and forest management.

Two field tours followed the conference. A van-load of participants traveled to the Armstrong caribou wintering area and had many valuable discussions about lichen ecology, caribou habitat use in northwestern Ontario, forest management guidelines for caribou, and related conservation issues. Thirty people took advantage of a multiple day excursion to the Slate Islands, home of the highest density woodland caribou herd in the world. Under the able leadership of Mr. Bill Dalton, participants wete able to explore the unique floral and faunal communities on the islands.

The conference achieved a primary objective of raising the profile of woodland caribou issues in Ontario among the scientific community, the forest industry and the general public. These proceedings include papers that provide a permanent record of some of the presentations and discussions from the conference. The editors thank the planning team and the participants for making the conference a success and the authors and reviewers for theit efforts in producing and reviewing these papers.

The Seventh North American Caribou Conference,
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What does it mean to put caribou knowledge into an ecosystem context?

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Abstract: Ecosystems are envisioned as integrated, complex systems with both living and non-living components, that are linked through processes of energy flow and nutrient cycling (Bowen, 1971; Ricklefs, 1979). The ecosystem approach seeks to describe the components of this system, the pathways through which energy and nutrients move, and the processes that govern that movement. The goal is a better understanding of the role or effect of each component (abiotic or biotic) within the system. Theoretically, the more we know, the better we can predict the future behaviour of the ecosystem and therefore manage the system on whatever sustainable basis we deem appropriate. Caribou (*Rangifer tarandus*) presently inhabit two ecosystems, tundra (arctic and alpine) and taiga (or boreal foresr), both characterized by relatively low productivity and diversity (Bowen, 1971; Bliss, 1981; Bonan, 1992a). As increased anthropogenic impacts are expected in these ecosystems through the next century, our ability to ensure the continued survival of caribou requires that we pay increasing attention to the processes that drive these systems. In this endeavour, an awareness of rhe effects of both spatial and temporal scale, in borh ecosystem processes and our research programs to understand those processes, is crirical.

Key words: climate, succession, wildfire, Pleistocene, boreal forest, taiga, tundra, conservarion, *Rangifer tarandus.*

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The principal defining feature of an ecosystem approach is scale, which can vary along several dimensions. Spatially, an ecosystem can range from a single organism (i.e., a tropical forest tree with its associated epiphytic flora and fauna) to the entire earth (i.e., the Gaia hypothesis) (Usher, 1973). In general, however, ecosystems are described at intermediate scales, defined by their dominant plant communities: desert, scrub, grassland, shrubland, woodland, and forest (Caughley & Sinclair, 1994). Each of these can be subdivided into increasingly similar floras (i.e., forests in general into tropical, temperate and boreal forests) and these in turn can be further divided. The boundaries between neighbouring ecosystems, at whatever level of analysis, represent relative rather than absolute divisions of the natural world.

Ecosystems also vary temporally, representing the continuity of time from yesterday to today and Tertiary to Quaternary. As the time frame lengthens, change shifts from stochastic to evolutionary processes. Year to year changes in species' abundance due to vagaries in rainfall give way to longer term successional changes which in turn yield to evolutionary changes as some species become extinct and other are modified by natural selection. Thus change of a dynamic nature, and not stasis, is expected in an ecosystem approach.

Subordinate features of scale in ecosystems include diversity, productivity and stability. As human activities have increasing impacts on a variety of ecological processes at all levels of scale throughout the earth's ecosystems, incorporating an ecosystem outlook into caribou science means keeping an awareness of these aspects of scale, periodically reassessing our current focus to avoid losing sight of important ecological processes that may be operating on another level of scale.

Spatial scale

The vegetation communities that distinguish ecosystems are products of five factors: parent material (substrate), topography (especially elevation, aspect and slope), climate, the biota, and time (Viereck *et al.*, 1986). The first three factors set the basic spatial boundaries of the ecosystem, influencing the biotic possibilities within a specific area. These factors, in essence, set the stage that is later "fleshed out" by the biota over time (Kimmins & Wein, 1986). As the stage changes, opportunities for the biota also change.

Boundaries between adjacent ecosystems are relative rather than absolute, with one replacing another through a transition of intermediate habitats (Payette, 1983; Sirois, 1992). Even ecosystems that seem relatively well defined, such as the terrestrial, aquatic and marine ecosystems of arctic tundra biomes may have unexpected interconnections. Power & Barton (1987) proposed that caribou may have a significant impact on arctic char (*Salvelinus alpinus*) populations in Ungava Bay, Quebec. Areas of summer range grazed heavily by caribou have reduced lichen cover and consequently retain less water during spring melt and summer rains, causing a drop in ground water levels. During dry spells in late summer, stream flows may be insufficient to allow char to migrate upstream to spawn. Thus during periods of high caribou numbers, char populations may be depressed or even lost from the most severely affected streams.

Caribou presently inhabit ecosystems along both the northern limits of land and the higher elevation sites of mountains. Thus in one direction, caribou have no place to go should the boundaries of their ecosystem move north or to higher elevations with global warming. Whitehead *et al.* (1982) proposed that a rapid 75% decline in the area of boreal forest between 11,000 and 8,000 yr BP, likely caused by a 7 °C increase in global temperature at the end of the Pleistocene (Hoffmann & Taber, 1967), significantly reduced mastodon (*Mammut*) populations, making them vulnerable to stochastic events and leading to their eventual extinction.

Caribou exploit spatial aspects of their arctic and alpine tundra ecosystems in predator avoidance (Bergerud & Page, 1987). To pay off, this strategy requires an adequate distance between calving grounds and areas of wolf activity (Heard & Williams, 1992). Extensive loss of tundra habitat, expected in some models of global warming (i.e., Solomon, 1992), could make this strategy less viable.

Boreal forest is also expected to retreat northward with global warming (Kullman, 1983; Solomon, 1992), displacing tundra in the process (Payette, 1983). Such change in itself does not necessarily mean a decline in the areal extent of the forest, although one estimate sees it declining by 25% (Solomon, 1992). At present, however, boreal forest is being affected by forestry practices, which at best return the forest to an earlier successional stage and at worst lead to fragmentation and degradation through export of biomass (Freedman, 1989) with an increased risk of local extinction for species with small populations (Diamond, 1984).

Space is also employed in predator avoidance by woodland caribou, which disperse to reduce predation on calves (Bergerud & Page, 1987; Ferguson *et al.*, 1988). The success of spacing out appears to be dependent on predator density, which is likely affected by distance from habitat used by other ungulates (i.e., moose and white-tailed deer (*Odocoileus virginianus*)) (Thomas, 1995). Thus changes in ecosystem spatial distributions can influence the viability of spacing out, and caribou population dynamics as a result.

Temporal scale

The characteristics of an ecosystem at any given time are determined by three sets of successional (temporal) processes: allogenic, autogenic and biogenic (Kimmins & Wein, 1986). Allogenic processes are external to the biota but have significant impacts on it, such as seasonal or global climate change, wildfires or other perturbations. Some may follow specific time courses (i.e., annual temperature and solar cycles), but many are unpredictable. Wildfires in black spruce taiga, for example, may occur today at 60-120 yr intervals, *on average*, but variation is great (Dyrness *et al.*, 1986; Payette, 1992). In the past, wildfires have occurred at both significantly longer and shorter intervals (Johnson, 1983).

Wildfires release nutrients and destroy a portion of the above ground biomass, allowing earlier successional flora to recolonize (Dyrness *et al.*, 1986; Kimmins & Wein, 1986). Soil temperature, a primary determinant of productivity in northern areas (Van Cleve & Yarie, 1986; Bonan, 1992b), rises for a number of years following a fire, accelerating both the growth of a palatable post-fire vegetation (Bryant & Chapin, 1986) and the decomposition of its litter (Van Cleve & Yarie, 1986). As Dyrness *et al.* (1986:84) comment, "it is essential that we view fire as in ecosystem process in taiga communities rather than as a catastrophic event", as "fire can be interpreted as an essential agent of renewal." Thus climatic and anthropogenic factots that influence fire rate can have far-reaching affects on an ecosystem in both the short term and the long term.

Autogenic processes are those generated by the biota that change the physical environment of the ecosystem (Kimmins & Wein, 1986). Over several decades following a fire or other major disturbance in the boreal forest, slower growing plants characteristic of later successional stages overtake the pioneer species, and an important autogenic process comes into play. Late successional plants invest more heavily in defense than those in the post-fire flora (Guthrie, 1984; Bryant & Chapin, 1986). The combination of increased canopy cover and thicker layer of toxic litter leads to soil cooling, movement of permafrost toward the surface, a shorter growing season, and decreased decomposition of litter, thus lowering productivity and reducing the availability of nutrients for future growth (Guthrie, 1984). Whatever growth is produced, being unpalatable, is largely unavailable to consumers. Thus the late successional community modifies the environment to favour its long-term survival, at least until the next wildfire or other disturbance.

As Larsen (1980) noted, calling the late successional flora a 'climax' community may be misleading, as few communities remain free from disturbance for any long period. Also, some subclimax communities remain relatively stable for long periods in arctic and boreal habitats. Where the environment is very harsh, competition among plants may be unimportant, so any plant that gains a foothold can survive, and succession to a climax community characteristic of more benign environments does not occur. The ecosystem that we see before us is thus a product of both general successional rules and special historical circumstances.

Biogenic processes involve the web of direct interrelationships among species within the ecosystem (Kimmins & Wein, 1986). Ecological processes such as population growth, competition, predation and parasitism, and species adaptations to these processes (as well as failures to adapt) (Ricklefs, 1979), give a dynamic form to the biotic community of the ecosystem.

Diamond (1984) has shown that ecological (biotic) stasis on relatively short time scales (i.e., years to decades) resides more in the human mind than in nature. Studies of birds and invertebrates have shown that species composition typically varies from year to year as some species disappear while others reappear. The probability that a species will disappear from a local habitat, or an ecosystem, is dependent on its population size and area occupied and is greater for carnivores than hetbivores, larger than smaller species, and specialists rather than generalists (Diamond, 1984). Thus remnant populations of caribou in fragmented boreal forest are vulnerable to extinction. On the other hand, the smaller populations of their predators are even more vulnerable, as the Isle Royale moose-wolf system demonstrates (Peterson, 1995). During the late-Pleistocene, caribou comprised about 5% of the large ungulate fauna in numbers of individuals, but only a fraction in terms of biomass (Guthrie, 1968). Could persistent low density have allowed caribou then, and today (Bergerud, 1992), to wait out their predators, and see them disappear first?

On a longer time scale, ecosystems change as their biota respond to stochastic and selective pressures. The alpine and arctic tundra biomes are likely the youngest of terrestrial ecosystems, originating at the end of the Tertiary (Hoffmann & Taber, 1967; Bliss, 1981). Caribou appeared during the mid-Pleistocene, about 2.0 m-yr ago, likely originating in central Asia (Anderson, 1984) in taiga-tundra environments (Bergerud, 1974). Until the late Pleistocene, caribou shared tundra, boreal forest and grassland ecosystems with a variety of other often more numerous and larger herbivores, including horses (*Equus caballus*), moose (*Alces alces*) and musk oxen (*Ovibos moschatus*), as well as the now extinct woolly mammoth (*Mammuthus primigenius*), giant bison (*Bison priscus*), woolly rhino (*Coelodonta*) and ground sloth (*Megalonyx*) (Guthrie, 1968; Caughley & Sinclair, 1994). In one now-vanished ecosystem, the mammoth steppe, they typically ranked a distant third or fourth in abundance behind bison, horses and mammoths (Guthrie, 1968; 1984; 1990). Where did caribou fit within this broad array of herbivores? How did caribou fare against a predatoty guild of wolves (*Canis lupus*), lions (*Felis*), brown bears (*Ursus arctos*) and the occasional sabre-toothed cat (*Smilodon*)? What affect did the late-Pleistocene extinctions have on caribou?

The cause or causes of the late Pleistocene megafaunal extinctions are still debated, with climate change one strong contender pitted against the "overkill" hypothesis (Martin & Klein, 1984). Climate-centred hypotheses are ultimately grounded in ecosystem change, arguing either massive changes in plant abundance or composition (i.e., Whitehead *et al.*, 1982) or changes in the relative investment made to growth and defense as plants responded evolutionarily to changes in climate (Guthrie, 1990). Even Martin's (1984) "over-kill" hypothesis is rooted in an ecosystem change: the arrival of a new predator to which a number of species had inadequate defenses. Whatever the case, caribou have distinguished themselves for another 10,000 years by surviving in the face of this new predator, even though highly sought after throughout their range (Anderson, 1984).

We, along with caribou, stand poised to witness what many believe may become a major extinction event (Wilson, 1988). Habitat change caused directly (i.e., deforestation) and indirectly (i.e., global warming) by human activity is likely to have far-ranging effects on ecosystems well into the future. How will caribou fare as these changes unfold?

Caribou and their knowledge of ecosystems

Like any species, caribou have evolved an array of adaptations which have thus far enabled them to meet the various selective challenges provided by the ecosystems they have inhabited. In addition to morphological and physiological traits, their behavioral repertoire has been shaped by natural selection to enable them to respond adaptively to the spatial and temporal heterogeneity of boreal and tundra environments. This environmental variation includes both the unpredictable and patchy distribution of food and predators and the stochastic vagaries of climate. An attempt to understand caribou ecosystems from a caribou perspective, that is, to understand how caribou make decisions about foraging sites, calving areas, and movements both localized and migrational, will better enable us to understand both the evolution of their behaviour and the consequences of ecosystem change on their future behaviour and survival.

Caribou and ecosystem management

A recent development in wildlife conservation is ecosystem management (i.e., Seip, this issue). Rather than developing a variety of specific management programs focused on individual species, this approach seeks to preserve biodiversity by mimicking the natural disturbances that historically were responsible for the development of the ecosystem and the evolution of the species in its biota. Thus we might hypothesize: if an ecosystem (forest, tundra, etc.) continues to function, spatially and temporally, as it did in the past, species of that ecosystem, such as caribou, will continue to exist. This approach has great promise, but two aspects of ecosystem history need to be kept in mind when applying it.

First, stochastic processes have long been at play in ecosystems. If, for example, timber harvesting is to substitute for wildfire in perpetuating forest ecosystem structure, we must realize that beyond characteristics of the forest (i.e., species composition, age, site) and recent climate (i.e., rainfall, winds, thunderstorms), chance played a major role in determining where fires would start and how long and wide they would burn once started. Thus we must be careful to ensure our management plans retain that natural element of chance, despite the cost in terms of economic gain from timber harvest or other human endeavour. We must be wary about placing an unnatural human-derived pattern on the ecosystem, lest we lose important random features, including local extinctions, which may have allowed rare species like caribou to survive through the past.

Second, we need to remember that the ecosystems we study and seek to preserve are unique in the history of life. Their present form is the result of a long series of evolutionary and stochastic events stretching far back in time and poised to continue far into the future. But just as change has been a dominant characteristic of ecosystem form and function in the past, it will continue to be so in the future. One factor often lacking from our considerations of ecosystems is change and its inevitability, and a failure in this regard is our exclusion of humans, both local and global, as driving forces in this change. Thus it is not sufficient to manage ecosystems based on the unique historical processes that gave them their current form. We must place humans into the ecosystem and manage adaptively, based both on past processes and a sensitively to how humans are changing those processes.

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Needed: less counting of caribou and more ecology

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Abstract: Most aerial surveys designed to estimate numbers of caribou (*Rangifer tarandus*) lack clear objectives, are inaccurate and imprecise, lack applicarion, and often are doubted by the public. Sources of error in surveys are bias (inaccuracy) and sampling error (imprecision) caused largely by sampling units (strips, sections of strips, quadrats, or photographs) being inappropriate for highly variable group sizes and distributions. Many visual strip surveys of caribou on calving grounds were inaccurate by 136-374%. Photographic surveys of calving caribou are more accurate but usually have coefficients of variation (*CV*) of 20-40%, whereas a *CV* of about 15% is required to detect a 50% change in population size between surveys. Extrapolation of such counts to population size produces unacceptable accuracy and precision. Consequently, no conclusions can be made about changes in population numbers between or among surveys because even large natural fluctuations fall within confidence limits. These problems combined with difficulties of managing caribou populations in remote areas of northern Canada indicate that scarce funds may be better allocated to ecological studies.

Key words: accuracy, bias, census, precision, *Rangifer tarandus,* surveys.

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Introduction

As a member of a caribou management board, I became concerned that population estimates of two large herds of caribou (*Rangifer tarandus*) were inadequate for management. Additionally, board members did not understand the reliability of survey results or how they were obtained. An attempt at a simple explanation for the board grew into this review of caribou surveys.

There are few experimental studies that explore accuracy and precision of caribou surveys because of high costs in remote areas. Therefore, I use experimental results for moose (*Alces alces*) in forest cover and pronghorns (*Antilocapra americana*) in open and shrub habitats to most-closely simulate what may be expected from caribou surveys in those cover types.

I briefly review survey terminology, examine accuracy and precision of some current methods, recommend improvements in design, and examine alternatives to surveys. This paper is not a review of all survey methodology. Most comments refer only to strip transect and photographic surveys of the Beverly and Qamanirjuaq herds of caribou. *The focus is on problem definition and potential solutions.*

First of all we must define terms and become familiar with statistical terms and sample design. Bookhout (1994) provided a good review, using examples from wildlife studies. Consult statistical texts for further information.

Accuracy

Accuracy is closeness of a measured or computed value to its true value (Sokal & Rohlf, 1981). Accutacy can only be measured if the number of caribou in a prescribed area is known. An accurate survey method is one that will reliably estimate the actual number of caribou in an area on average when repeated many times (Eberhardt, pers. comm.).

Bias (departure from reality) in counting, sampling, and analysis results in inaccuracy (Jolly, 1969b). There are many sources of bias in visual strip surveys (Caughley, 1974; Heard, 1985; Crête *et al.*, 1991; Couturier *et al.*, 1996). High and variable bias causes density estimates to vary considerably among observers in the same aircraft (Thomas, 1969; Heard, 1985).

Precision

Precision tells us nothing about survey accuracy. The amount of variation in normally-distributed measurements is *variance* or its square root, *standard deviation* (*SD*). In surveys, it is a measure of variation in numbers of caribou in each of the sample units (areas). *Precision* is sampling error as measured by *standard error* (*SE*). The *SE* is standard deviation divided by the square root of sample size (*n*) or *n* -1 if *SD* is calculated using *n* and not *n*-1 (Bookhout, 1994). Sampling error is zero if the same number of caribou occur in each sample unit. A knowledge of how precision is derived can guide surveyors in sample design, i.e., reduce variation in caribou numbers among sampling units and increase sample size to reduce *SE*. For example, with constant variance, *SE* is reduced by half as *n* is increased from 16 to 64.

The *SE,* when combined with a probability (*P*) level, yields *confidence limits* (*CL*) and their interval, the *confidence interval* (*CI*). At $P = 0.90$ (alpha = 0.1), it is incorrect to state that there is a 90% chance that the actual number of caribou in a survey area is within the *CI*. Rather, assuming no bias, the *CI* is likely to contain the true population size in 90% of surveys of the same type and intensity.

Survey results should consist of an estimate, confidence limits (*CL*), probability level, and sample size. Presenting results as the sample mean ± *SE* is not meaningful to people who cannot calculate approximate *CL* from *SE* values.

Statistical texts define confidence interval (*CI*) as the interval between *CL*s (Steele & Torrie, 1960). Caribou biologists (e.g., Goudreault, 1985; Farnell & Gauthier, 1988; Crête *et al* , 1991; Couturier *et al* , 1996) refer to estimates ± "*CI*" but the *CI* is half textbook definitions. For example, the 1976 estimate for the George River herd was 63 463 ± 30% ($P = 0.90$") (Goudreault, 1985). This example points to the need to define terms (Bookhout, 1994).

Precision is also measured by a coefficient of variation (*CV*). It is standard deviation divided by the estimate and usually expressed as a percentage. To confuse matters, *CV* is also defined as *SE* divided by the estimate and expressed as a fraction or a percentage. It should be designated as CV_{se} to distinguish it from CV_{sd}. The CV_{sd} is the preferred index of precision for comparisons among surveys because it is relative to population size and independent of probability and sample size.

Randomness

Most surveys are random or systematic. Many statistics are based on an assumption that samples are drawn randomly from a normal distribution. Systematic surveys generally are efficient and may produce suitable estimates but they can produce biased estimates of *SE* (Caughley, 1977; Cochran, 1977). All survey statistics and sampling designs are based on assumptions about distribution, variance, randomness, and independence of samples (Eberhardt, 1978a, b). Often, assumptions are ignored but rarely with reason. For example, a recommendation to sample in two directions (Cochran, 1977; Couturier *et al.*, 1996) can complicate sampling designs and inflate variance if caribou are in linear groups. Constraints of caribou movements, costs, weather, aircraft availability, and personnel means that the best theoretical sampling design may be impracticable.

Stratification

Stratification is division of a survey area into two or more parts (strata) based on density, degree of clumping, or some other attribute. Its purpose is to reduce variance and therefore *SE* and *CL.* In *optimum allocation,* sample units are proportioned to estimated variance or density in each stratum. The purpose is to get a precise count of a high proportion of a population. Survey biologists urgently need guidelines regarding thresholds of density and degree of clumping beyond which any sampling design will produce imprecise estimates. Post-survey stratification may be done in certain types of systematic surveys (Jolly, 1969a; Anganuzzi & Buckland, 1993) but with caution (Caughley, 1977). Post-survey stratification of systematic quadrats might produce the most-precise estimates and be cost effective.

Stratification can result in lower precision if it unduly partitions sample size. Surveyors should attempt to achieve a large sample size in each stratum because *SE* decreases with sample size whereas power increases. However, an estimate of required sample size is necessary to achieve a cost-efficient survey.

Stratification within systematic surveys with 50% coverage produced some erratic estimates of pronghorns (Kraft *et al.*, 1995). Confidence intervals did not contain the known population size half the time. Even some precise (CV = 13%) designs produced CIs that did not contain the known number of pronghorns.

A minimum total count may be necessary in part of a caribou distribution because aggregations of widely differing numbers are unevenly distributed. Variance is likely to increase sharply as clumping increases. It may also be necessary to change the size and shape of sampling units to reduce variance and edge bias. Stratification is difficult when sizes and shapes of indiscrete caribou groups are constantly changing in response to environmental variables and a distribution is moving over landscapes with few defining landmarks. One potential solution is for an independent observer to stratify distributions during a survey based on relative densities and degree of clumping. The boundaries would be logged using a geographical positioning system.

Coverage

Coverage (proportion of area sampled) and sample size usually are directly related and consequently the relative effect of each on reported CVs is unclear. That explains why data on the effect of coverage on accuracy and precision can be contradictory. For example, coverage of 0.23% produced relatively accurate (*vs.* July photography) but imprecise estimates of population size (Couturier *et al.*, 1996). Conversely, coverage below 33% produced accuracy below 80% in 1.6-km-wide strip surveys of caribou on tundra (Cameron *et al.*, 1985). In contrast, strips 100 m wide on each side of an aircraft and covering <4.4% of an area gave much more accurate estimates of pronghorns than strips 1.6 km wide and covering 35% of a survey area (Pojar *et al.*, 1995). However, CVs of pronghorn estimates decreased progressively with coverage of 16%, 33%, and 50% (Kraft *et al.*, 1995). Acceptable average CVs (11-13%) were achieved only with stratification and 50% coverage, similar to surveys for muskox (*Ovibos moschatus*) (Graf & Case, 1989). If coverage of 50% is required for precise estimates, then perhaps a minimum total count should be considered.

A finite population correction factor is necessary where coverage is high (Eberhardt, pers. comm.). Variance is reduced by the coverage fraction, i.e., 50% if half the population is surveyed.

Survey objectives

Objectives must include survey justification and accuracy/precision components. Justification may include: (1) monitoring, (2) management, (3) population analysis, and (4) hypothesis testing (Eberhardt, 1978b). Generally, the need for greater accuracy and precision increases in the order listed.

A CV of 12-15% was considered necessary for management (Gasaway *et al.*, 1986; Crête *et al.*, 1991). However, a CV of <10 is required to detect a 30% difference between two surveys at P = 0.90 (Heard, 1985). Only a 50% change would be detected with a CV of 15% (Heard, pers. comm.). Some surveyors wish to detect a 15% difference between surveys (Pojar *et al.*, 1995) necessitating a CV of <5. A CV of 13% was considered precise by Kraft *et al.* (1995), relative to a mean CV of 29% for several designs.

Much emphasis is now placed on power and calculation of required sample size. The greatest conservation concern is not detecting a significant decline in numbers, which is a Type II error. Power is 1 minus the probability of a Type II error. Heard (pers. comm.) suggested that power of detecting population change should be 90% (beta = 0.10). Surveyors should carefully define their objectives and calculate required accuracy, precision, power to detect change, and required sample size (Eberhardt, 1978b). For example, 100 radio-collared caribou are required to detect a 20% change in mortality rates with 80% power (Walsh *et al.*, 1995).

Examples of accuracy and precision from surveys

Viewers tend to underestimate numbers in large groups. For example, visually estimated numbers were low by 21% for 27 groups containing 114 to 796 caribou clearly visible in large photographs (Thomas, 1969).

Failure to detect caribou can be a major source of bias but rarely is it measured. A correction of 20% (estimate x 1.25) was adopted for many surveys in Canada (Thomas, 1969; Heard, 1985) but case studies in survey literature reveal that bias often is much higher. Intensive searches for caribou within quadrats in forested habitat yielded 33% and 74% more caribou than "normal" searches (Farnell & Gauthier, 1988).

Data for moose illustrate detection problems in forest cover. For example, only about a third of moose were seen in narrow strips in conifer forest

Table 1. An example, selected because of unusually low coefficients of variation (*CV*), of results of visual strip and photographic surveys of caribou on the calving grounds of the Qamanirjuaq herd in June 1988.

Survey type	Sample size	Estimate	*CV*	90% *CL*[1]
Visual strip	20	56 000	11	45 000 - 67 000
Photo	15	160 000	13	123 000 - 197 000

[1] *CL* = confidence limits = estimate ± $SE \times t_{0.1}$. Data from Heard & Jackson (1990b).

cover (Gasaway *et al.*, 1985; Anderson & Lindzey, 1996).

Relatively precise visual strip and photographic surveys of caribou on a tundra calving ground produced concurrent estimates that differed by a factor of 2.9 (Table 1). The average factor for seven such paired comparisons was 2.34 (1.4-3.7) (Heard & Jackson, 1990a & b). Visual strip surveys produced caribou population estimates about half those obtained from quadrats (Fong *et al.*, 1985). Similarly, visual estimates of pronghorn numbers based on two strips 0.8 km-wide were half of estimates from quadrats (Pojar *et al.*, 1995).

The CV_{se}s of 13 visual strip surveys over calving grounds averaged 12.4% (Heard & Jackson, 1990a, b; Heard, pers. comm.). The *CV*s of stratified strip surveys of tundra caribou on Southampton Island were 29.1% and 34.7%; those of random quadrats 11.6% and 16.3% (Heard & Ouellet, 1994). Those differences in CVs relate in part to a larger sample size for quadrats (35 & 48 *vs.* 18 & 24). Estimated *CV*s of sightability-corrected quadrat samples of two woodland caribou herds in Yukon were 24.2% and 14.8% (Farnell & Gauthier, 1988).

Sampling errors (precision) associated with photographic surveys of caribou on calving grounds often are unacceptably large (Table 2). Wide *CL*s do not permit firm conclusions about population trends (Fig. 1). Photographic samples of caribou on calving grounds generate *CV*s of 5% to 32%, which progressively increased with each of three ratios used to estimate population size (Table 3). In NWT, long-term average ratios with estimated *CV*s of 10% are used for the second and third ratios (Heard & Jackson, 1990a). In any 1 year, those ratios may each be inaccurate by 10%, adding further uncertainty to estimates. Photographic surveys of calving grounds have produced unusable population estimates in 2 of 13 surveys (Table 2).

Discussion and recommendations

Objectives and sampling design

Survey objectives must be clearly stated and include components of management, accuracy, precision, and trend detection. Surveyors must either learn about the complexities of survey design or consult a biometrician with experience in aerial surveys.

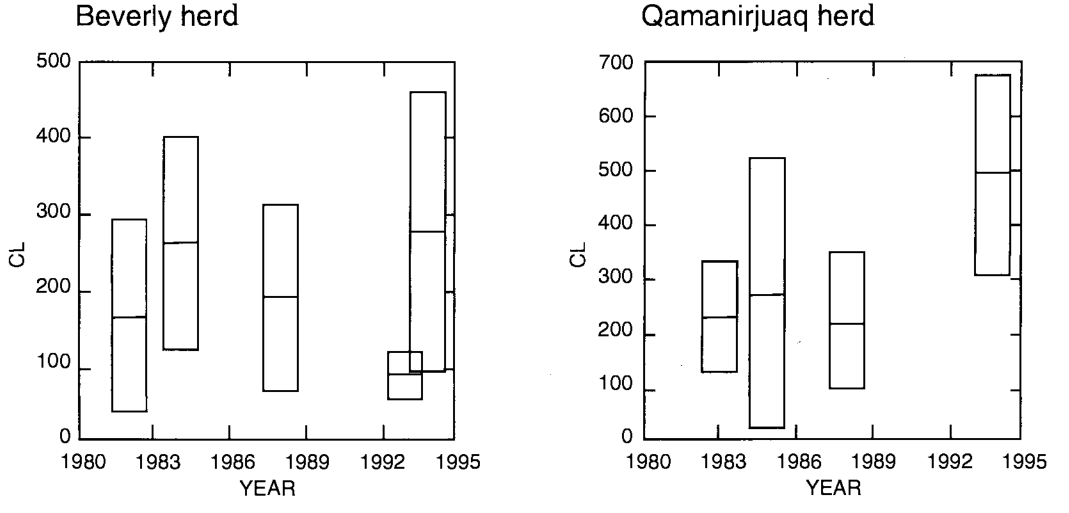

Fig. 1. Estimated 90% confidence limits of (*CL*) population estimates (x 1000) for the Beverly and Qamanirjuaq herds derived from 1982-1994 photographic surveys of calving grounds. Data from Heard & Jackson (1990a, b) and Gunn (this issue).

Table 2. Precision of herd estimates (X 1000) obtained by photographic surveys of the calving grounds of the Beverly and Qamanirjuaq herds from 1982 through 1994.

Year	Estimate[1]	*SE*[2]	90%*CL*[3]	Source[4]
Beverly herd				
1982	164	72	38 - 290	1
1984	264	81	123 - 404	1
1988	190	71	66 - 313	1
1993	87	18	56 - 118	2
1994	277	107	91 - 462	3
Qamanirjuaq herd				
1983	230	59	126 - 334	4
1985	272	142	22 - 522	4
1988	221	72	94 - 349	4
1994	496	105	310 - 682	3
George R. herd[5]				
1984	644	97	483 - 805	5
1986	283	66	173 - 394	5
1988	682	147	437 - 928	5
1993 (adult method)	982	135	759 -1204	6
1993 (calf method)	749	151	501 - 998	6

[1] Population estimate = caribou on calving grounds x proportion of parturient cows x (1/pregnancy rate) x (1/proportion of cows in adult population) (Heard, 1985).

[2] SE = standard error. It is the *SE* of caribou on the calving grounds and the *SE*s associated with 3 ratios used to extrapolate to a population estimate (Heard & Jackson, 1990a, b).

[3] Confidence limits (*CL*) as mean estimate ± *CL* at P = 0.90 (alpha = 0.10).

[4] Soutces: 1: Heard & Jackson, 1990a; 2: Williams, 1995; 3: Gunn, this issue; 4: Heard & Jackson, 1990b; 5: Crête *et al.*, 1991; 6: Couturier *et al.*, 1996.

[5] Values are for all caribou in October.

Surveyors must design surveys that are expected to produce acceptable accuracy and precision. If costs do not justify benefits, then a survey should be canceled.

Perhaps surveys of caribou should be designed only by survey specialists because the field biologist is unlikely to become competent in this complex methodology. Sampling design is highly technical, complex, and controversial. For example, there are many methods of analyzing trend data (Hatfield *et al.,* 1996).

Detection of a 10% or 20% difference in population size between surveys is not possible with common survey sampling methods. In fact, only a change of 50% between surveys is detected by most photographic samples of all caribou on calving grounds (Heard, pers. comm). Frequent surveys are too costly and long survey intervals are insensitive to short-term fluctuations in numbers. Detection of a significant change in population size may be delayed many years if several surveys are required to detect a trend. Variation is a critical component of nature and we must recognize limitations in attempting to compartmentalize it statistically.

Counts of forest-tundra caribou

I favor attempts at total counts of aggregations during July (Valkenburg *et al.*, 1985; Parker, 1972; Heard & Jackson, 1990b; McLean & Russell, 1988; Couturier *et al.*, 1996). Photography of July aggre-

Table 3. Coefficient of variation (CV = 100 *SE*/estimate) for photographic surveys of adult caribou on calving grounds, for parturient females on calving grounds, and extrapolated total population size of the Beverly, Qamanirjuaq, and George River herds of caribou.

	Coefficient of variation (%)		
Population/ year of survey	Calving grounds	Parturient females	Total population
Beverly herd[1]			
1982	19.5	41.7	44.0
1984	25.5	27.1	30.6
1988	25.9	34.7	37.4
1993	11.6	15.1	20.6
1994	32.3	35.9	38.6
Qamanirjuaq herd[1]			
1983	17.5	21.6	25.8
1985	12.3	50.3	52.3
1988	13.0	29.6	32.8
1994	NA	15.9	21.3
George River herd[2]			
1984	4.8	7.2	15.0
1986	17.9	21.0	23.4
1988	13.7	16.8	21.6
1993 A[3]	11.8	12.0	13.7
1993 C[3]	NA	19.0	20.1

[1] Data from Heard & Jackson, 1990a, b; Williams, 1995; Gunn, this issue.

[2] Column 3 is adult cows (not parturient females) and total population includes calves of the year. Data from Crête *et al.* (1991) and Couturier *et al.* (1996).

[3] A and C are esrimates based on numbers of adult females and calves, respectively.

Table 4. Generalized and subjective rating of the accuracy and precision of some surveys used to enumerate large forest-tundra herds of caribou.

No.	Survey type	Accuracy	Precision	Relative cost
1	Systematic visual strip (transect)	Often poor	Fair-good	Low
2	Random quadrat	Good	Poor-fair	Moderate
3	Photo: caribou on calving ground	Good	Good	High
4	Photo: adjust #3 results to ad. females	Good	Fair-good	Very high
5	Photo: adjust #3 to parturient females	Fair	Poor	Very high
6	Photo: adjust #5 to total population	Poor-fair	Poor	Very high
7	Photo: total count & intensive search	Excellent	Excellent	Moderate
8	Photo: partial count + radio ratios	Excellent	Good	Extreme
9	Photo: partial count + strip surveys	Good	Good	High
10	Total visual count	Variable	Variable	Wide range

gations that contain all sex and age classes usually produces estimates of adequate accuracy and precision, unlike most other types of surveys (Table 4). Use of a minimum real population size is a conservative approach to management. Accuracy is high and variation is almost nil if a near-total count is achieved. It is low if an adjustment must be made for a small proportion of "missing" caribou, as the variation may only apply to 5-10% of the population. Caribou outside photographed aggregations can be surveyed or estimated by ratios of radio-collared caribou (McLean & Russell, 1988; Couturier *et al.*, 1996). Radio-collared caribou in post-calving aggregations led biologists in Alaska to 87-90% of all caribou found through extensive searching (Valkenburg *et al.*, 1985). A photographic count of July aggregations is less costly than calving grounds surveys and associated sampling, which can cost up to $200 000 (Crête *et al.*, 1991). That technique is improved with radio-collared caribou but I agree with Valkenburg *et al.* (1985) that they are not essential.

If a *CV* of 10% is considered adequate for photographic samples on calving grounds, then only 1 of 12 surveys have achieved that precision for estimates of all caribou on calving grounds and for parturient females (Table 3). If a *CV* of 15% is deemed adequate, then 6 of 12 surveys achieved that objective for all caribou on calving grounds and 2 of 12 for parturient females. However, *CV*s of 10% and 15% still only permit detection of population changes of 30% and 50%, respectively (Heard, pers. comm.). Furthermore, a significant proportion of adult cows in the George River herd were not on the designated calving ground in 1 year (Couturier *et al.*, 1996). It would be necessary to put more than 100 radio-collars on cows to accurately adjust for those absent (Couturier *et al.*, 1996). In contrast, <4% of radio-collared females were outside the "core" calving grounds of the Qamanirjuaq herd from 1985 through 1988 (Heard & Stenhouse, 1992).

Extrapolation of population size from photographic estimates of caribou on calving grounds is not justified. There is unknown or poor accuracy and precision of three ratios used in such calculations. Further, there is no agreement on what sampling units or scale should be used for photo surveys (Heard, 1985; Crête *et al.*, 1991; Couturier *et al.*, 1996). Only Crête *et al.* (1991) adjusted photo counts for sightability bias.

Precision of calving ground surveys and others can be increased with attention to caribou distribution followed by adjustment of sampling units and stratification. A sampling objective is to stratify optimally and to construct sampling units within strata that will have the least variation. In reality, stratification is difficult and no unit size or shape will avoid sampling error. Kraft *et al.* (1995) warn potential surveyors of the danger of estimating abundance of aggregated populations.

Improved visual surveys

The accuracy of visual strip surveys can be improved. All caribou must be readily detected within viewing strips or sightability bias must be measured. One method of correcting for visibility bias is to compare caribou density in strips (belts) at several distances from an aircraft. Distance of caribou groups can be calculated from aircraft altitude and angle to the horizon, preferably measured by a second observer on each side of an aircraft. Adjustments for sightability vary among many factors, consequently correction factors should be developed for average conditions encountered in each survey.

Fewer caribou are missed by people experienced in scanning for animals under survey conditions. Observers should be trained to count aggregated caribou in photographs before a survey. Larger groups must be photographed. Counts of observers with low sightability should be adjusted to those with high sightability. Surveys should be conducted when caribou are in open habitats and contrast between caribou and background is high. Radar altimeters improve estimation of altitude and coverage. Sample size required to achieve a specified CV should be calculated as a survey progresses. In reality, the goal may not be achievable if the variance is large.

The multiplier effect of biases results in some gross underestimates of population size. Surveyors will readily admit that they may miss 20% of caribou and they may undercount numbers in groups by 20% but they are reluctant to increase their estimate by 1.56 to account for both biases. Every surveyor should attempt to measure accuracy in several sampling units in their survey area.

Credibility

The 1980 visual strip survey of the Qamanirjuaq herd produced an estimate of 38 000 ± 26 000 (90% *CL*) caribou. Such surveys subsequently were found to underestimate populations by an average of 234%. The estimate evoked a crisis herd situation when none existed and credibility of biologists was lowered.

Low estimates for caribou populations also led biologists to speculate without evidence that emigration and calving ground infidelity was the cause (Gates, 1985; Heard & Calef, 1986; Williams, 1995). Most female caribou in forest-tundra populations return to the same calving grounds annually and there is little emigration or immigration (Parker, 1974; Heard, 1983; Goudreault, 1985; Heard & Stenhouse, 1992; Valkenburg, this issue). Even when bias is reduced, as in sharp photographs of adequate scale, surveyors should first suspect that the real population size may be outside the confidence interval of anomalous survey results.

Another problem arises when improved or more-intense sampling produces higher population estimates when a decline may be occurring. Past estimates are subject to veneration with repeated uncritical use over time. Most historic estimates of forest-tundra caribou based on visual strip surveys were biased, probably by factors of 2-3. The consequences of inaccurate and imprecise estimates, and weak attempts to explain them, is that a growing number of resource users simply reject survey results.

In remote areas of northern Canada, management of caribou is not possible unless hunters agree that a problem exists. Data from herd monitoring was not used by the caribou board I sit on except to recommend slight changes to resident and commercial quotas.

Because surveys are inaccurate and imprecise, it is misleading to announce a population estimate as say 4312. Rounding is required to the nearest 1 or 2%.

A need for ecological studies

Even if caribou numbers could be estimated accurately and precisely, the data are not useful unless ecological studies indicate causes of population fluctuations or there is an ability to reduce harvest or natural mortality. The relative importance of limiting factors is not known for most populations because comprehensive ecological studies are expensive and mortality statistics are unreliable. Ecological studies generally are piecemeal responses to proposed developments in parts of caribou ranges. The best approach is to identify important habitats and attempt to protect them from activities that would be unacceptably detrimental. Without adequate safeguards on habitat, caribou populations will dwindle. An understanding of survey inaccuracy and imprecision may cause biologists to direct resources to other forms of population analysis, such as estimates of fat reserves, pregnancy rates, and recruitment, and to habitat use and requirements.

Conclusions

1. Main sources of error in caribou surveys based on sampling methods are bias (inaccuracy) and sampling error (imprecision) caused by highly variable group sizes and distributions relative to sampling units.
2. Visual strip surveys of caribou on calving grounds were inaccurate by an average factor of 2.3 relative to photo based estimates, however, most surveys of caribou are of unknown accuracy.
3. Most visual and photographic survey estimates are imprecise, having coefficients of variation (*CV*) of 10-50%, whereas 5-10% is required to detect changes in population size of 15-30% required for management.

4. Limitations of surveys must be explained to the public and estimates always expressed with lower and upper confidence limits along with any additional uncertainty. Variability in nature limits our ability to precisely quantify it.

5. Only minimum total counts, particularly photography of aggregations in July, produce results acceptable for conservative management of caribou.

6. Other indices of caribou population "performance" such as pregnancy rates, calf survival, and body condition and growth indices may be preferable to inaccurate and imprecise estimates of population numbers.

7. Many surveys for population size should be replaced by ecological studies that focus on habitat requirements in relation to limiting factors that affect reproduction and survival.

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Will ecosystem management supply woodland caribou habitat in northwestern Ontario?

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Abstract: Ecosystem management is emerging as an important concept in managing forests. Although the basic conceptual idea is not new, important defining principles are developing that elucidate some of the specific attributes of ecosystem management. These principles include: the maintenance of all ecosystems in the managed forest, the emulation of natural disturbance patterns on the landscape and the insurance that structure and function of forested ecosystems are conserved. Forest management has an impact on woodland caribou (*Rangifer tarandus caribou*), although the presence of wolves (*Canis lupus*) and moose (*Alces alces*) in the same northern ecosystems also affects the caribou-forestry interacrion. Specific management for caribou as a featured species has been proposed, based on managing large landscape blocks. Ecosystem management would also produce habitat in a manner that might accomplish the goal of conserving woodland caribou as well as maintaining other important ecosystem functions.

Key words: forest management, wildlife, biodiversity, ecological management.

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Purpose

The purpose of this paper is to briefly review the concept of ecosystem management and to consider how ecosystem management might affect woodland caribou (*Rangifer tarandus caribou*) habitat in Northwestern Ontario. The idea in this paper is a management hypothesis which must be tested before it is implemented. Establishing management hypotheses is a vital step in effective resource managment policy.

Meeting the needs of wildlife in forest management

A major problem faced by forest managers concerns how to deal with the complex and varied needs for maintaining wildlife habitat. Traditionally, management agencies have concentrated on a few commercially valuable species. The assumption behind this approach is that these species have economic value and if managed carefully can be sustained for long periods of time.

As concern for forest health increases in the public mind, more species get added to the management list of interest. Kimmins (1995) has reviewed the stages of forest management and terms the current stage "social forestry". In this stage, more species of plants and animals, both commercially valuable or as indicators of forest health, are added to the list that managers must accommodate.

In Ontario, the progression from commercially important species to species of broader interest is well underway. White-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) dominated managers' thinking for the last several decades. However, as more people become interested in forest management, and value other wildlife species, managers have had to expand their concern to include a larger number of wildlife species.

As the list of wildlife species of concern to managers gets longer, the complexity of management increases dramatically. Ontario management policy now mandates that several species be "featured" in forest management plans. In Northwestern Ontario, white-tailed deer, moose, American marten (*Martes americana*) pileated woodpecker (*Dryocopus pileatus*) osprey (*Pandion haliaetus*) great blue heron (*Ardea herodias*) bald eagle (*Haliaeetus leucocephalus*) black bear (*Ursus americanus*) and woodland caribou are all supposed to have habitat provided in forest management plans. As well, pressure is mounting for managers to conserve biodiversity, meet sustainability certification requirements and address habitat needs for additional wildlife species such as wood warblers.

The complex and sometimes contradictory habitat requirements of wildlife species leads to a virtually impossible task. No forest manager, however skilled, can develop a forest management plan that explicitly deals with habitat needs of all wildlife species. The best that can be accomplished, if an individual species is "featured", is to provide habitat for that featured species. Some benefits will accrue to non-featured species, but these are byproducts of the main goal.

Woodland caribou in northwestern Ontario

In Northwestern Ontario, attempts to develop and implement specific habitat management for caribou (Racey *et al*, 1991) have been frustrating. The large scale logging disturbances needed to eventually create extensive tracks of old forest are difficult for the public to accept. The issue of wood supply and caribou habitat is also difficult to reconcile. Other criticism is based on caribou and moose partitioning their habitat (Cumming, 1996), thus avoiding the predator pit problem espoused by Bergerud (1983).

Rather than focusing directly on woodland caribou habitat, and continuing to contribute to the piecemeal approach to managing wildlife habitat, the more general ecosystem management approach might be more successful. Although a general approach does not explicitly provide habitat for any species, it may provide the best opportunity to meet the needs of a variety of wildlife species, while conserving biodiversity and meeting the objective of sustainability. Ecosystem management should also provide for the needs of woodland caribou.

The emerging concept of ecosystem management

The Crown Forest Sustainability Act in Ontario and policy documents of the Ministry of Natural Resources (e.g. Ontario Forest Policy Panel, 1993) have outlined Ecosystem Management as the new policy in forest management. As outlined by Carey & Curtis (1996) ecosystem management should help conserve biodiversity, maintain viable populations of wildlife and meet reasonable needs for human use of forest products.

The concept of ecosystem management of natural resources is gaining prominence with natural resource management agencies and in the literature of forest management (Gerlach & Bengston, 1994; Slocombe 1993). Although recent discussions have increased its profile, the fundamental idea was envisaged several decades ago. Grumbine (1994) listed Aldo Leopold and Victor Shelford as "visionary ecologists" who began advocating the ecosystem concept in natural resources management in the 1930's and 1940's. Even though ecosystem management is not a new idea, implementing it in forest management is new. The present intensity of timber harvest and the concern for maintaining healthy forests has prompted development of new approaches to forest management (Kimmins, 1995).

There is no universally accepted definition for ecosystem management, although the core idea expressed by nearly everyone is similar. Ecosystem Conservation, New Forestry and Natural Landscape Management all convey the essential elements of a comprehensive approach to forest management. For this paper, the term ecosystem management will be used, as it seems to be used most often in the literature.

Grumbine (1994) summarized much of the ecosystem management literature and defined ecosystem management. His definition is: *"Ecosystem management integrates scientific knowledge of ecological relationships within a complex sociopolitical and values framework toward the general goal of protecting native ecosystem integrity over the long term."* The U.S. Forest Service has been developing policy on ecosystem management for some time (Salwasser & Tappeiner II, 1988) and in 1992 adopted ecosystem management as a policy for the Service. The definition accepted there was *"The use of an ecological approach to achieve multiple-use management of the national forests and grasslands by blending the needs of people and environmental values in such a way that the national forest and grasslands represent diverse, healthy, productive and sustainable ecosystems."* (Salwasser, 1992).

Principles of ecosystem management

The fundamental principles of ecosystem management are still evolving, with some important ideas evident in all approaches to this management technique. The principles of ecosystem management listed by Grumbine (1994) include: a hierarchical context, appropriate ecological boundaries, adaptive management and managing for integrity of ecosystems. Kimmins (1995) spoke of the need to maintain ecosystem health and integrity, retain old-growth stages, use low disturbance harvesting systems, and above all else, protect biodiversity. Booth *et al.* (1993) emphasized the need to maintain a continuing supply of all natural forest ecosystem types, the importance of basing forest management on sound knowledge of forest science, and the need to address a diverse range of interests in planning.

While the principles of ecosystem management are still evolving, the universal goal of ecosystem management is to sustain the integrity and health of ecosystems, while meeting society's need for a sustainable supply of forest products, and other forest attributes to which social and cultural values are attached.

Characteristics of ecosystem management

The emerging paradigm in forestry clearly includes concern for both conservation of biodiversity and sustainable harvest of forest goods and products. Conservation of biodiversity and sustainable harvest represent conceptual ideas that are important but difficult to measure. However some goals and objectives of ecosystem management are measurable and these should give guidance to managers who are implementing the concepts.

Grumbine (1994) found that most of the discussion of ecosystem management focused on five main goals.

1. Maintain viable populations of all native species in situ.
2. Represent within protected areas, all native ecosystem types across their natural range of variation.
3. Maintain evolutionary and ecological processes (i.e. disturbance regimes, hydrological processes, nutrient cycles, etc.).
4. Manage over periods of time long enough to maintain the evolutionary potential of species.
5. Accommodate human use and occupancy within these constraints.

These goals represent a fundamental change from the goal of providing goods and services to humans to the maintenance of the integrity of ecosystems. Success is measured by the fact that ecosystems continue to evolve and change, but are not subject to degradation by human activity. The integrity of the forest itself is more valued than the monetary value of the goods and services that are supplied by the forest.

Ecosystem management and caribou habitat in northern Ontario

Changes in policy occur slowly. As the Ontario Ministry of Natural Resources moves from Featured Species Management to Ecosystem Management some different results can be expected in the forest. Would a forest managed under Ecosystem Management support woodland caribou populations in Northwestern Ontario?

Woodland caribou in Ontario

Woodland caribou habitat has been discussed extensively in many papers, (e.g. Cumming & Beange, 1993; Cringan, 1957; Darby & Pruitt, 1984). Predation and its impact on woodland caribou and moose has also been the subject of intense discussion and speculation, (e.g. Bergerud, 1983; Seip, 1991; Cumming, 1996). While these are important topics, they would not be the major concern in an ecosystem approach to managing northern forests. Instead, managers would consider how to maintain the natural ecosystems in the forested areas of concern. The assumption is that if natural ecosystem processes are conserved, and woodland caribou have evolved historically under those conditions, they have the best opportunity to continue to exist and remain healthy, under these same natural conditions.

Maintaining ecological processes

There are, of course, many ecological processes in any ecosystem. Predator-prey relationships, decomposition of organic matter, disturbance events of several kinds, such as fire or wind storms are all normal parts of ecosystem process and function.. However, only a few basic processes can be affected by forest management as keys to an ecological approach.

The key ecosystem processes that can be manipulated by foresters, in most cases, are:

– Use of logging to mimic the patterns that fire, wind, and insects create on the landscape,

– Managing selected attributes of biodiversity to ensure that biodiversity is conserved in the management processes,

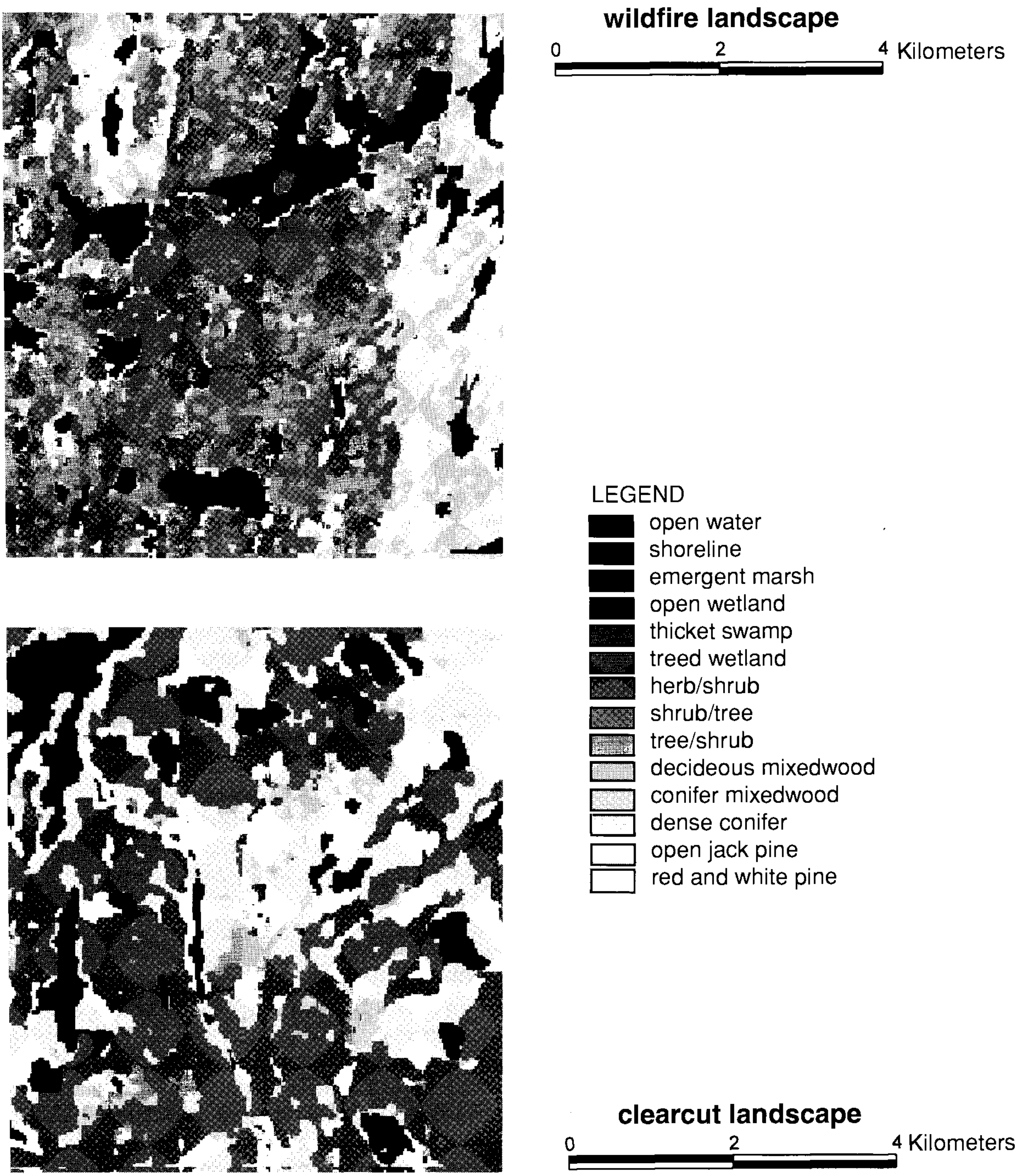

Fig. 1. Illustration of the different landscape patterns between a clear-cut and wildfire (Gluck & Rempel, 1996).

– Maintaining the age class distribution of commercial tree species similar to natural evolution of forests.

Mimic the pattern

The distribution of plant species on the landscape is important to wildlife species living there. If the pattern on the landscape after logging is similar to the natural disturbance pattern, then wildlife species and biodiversity conservation goals have the best chance of being achieved. While the pattern left by logging cannot duplicate exactly the pattern left by natural disturbance events, it should be as similar as possible.

Gluck & Rempel (1996) compared the structural characteristics of post-wildfire and clear-cut landscapes in the Boreal forest near Dryden Ontario. They found that the clear-cut landscape tended to have larger, less dense patches than the wildfire, the patches in the clear-cut were more irregular in shape with greater amounts of edge and core areas than those in the wildfire, whereas the wildfire had more interspersion between patch types at the broader scales, Fig. 1.

Under ecosystem management, the size of clearcuts is important, and the size of wildfires is a useful guide to planning the size of clearcuts. Li *et al.* (1996) found that the size of wildfires was quite variable, and did not always follow a particular mathematical distribution. A common pattern of wildfire size distribution, in Northwestern Ontario, based on a 10 km by 10 km area, is illustrated in Fig. 2. Hunter (1993) found a similar pattern in eastern Canada. Fig. 2 describes a useful guide in developing logging plans that are consistent with the idea of ecosystem management.

With the advent of remote sensing, GIS systems and models of disturbances, (e.g. ON-FIRE as described in Li *et al.*, 1996) forest harvest plans that mimic the pattern of natural disturbances are within the reach of most forest managers. If practiced over 80 to 100 year rotations, and at the scale of a large area such as Northwestern Ontario, ecosystem management should contribute to maintaining the normal ecological processes that were present before major human exploitation of the forest started. This in turn should provide the habitat caribou need to remain healthy.

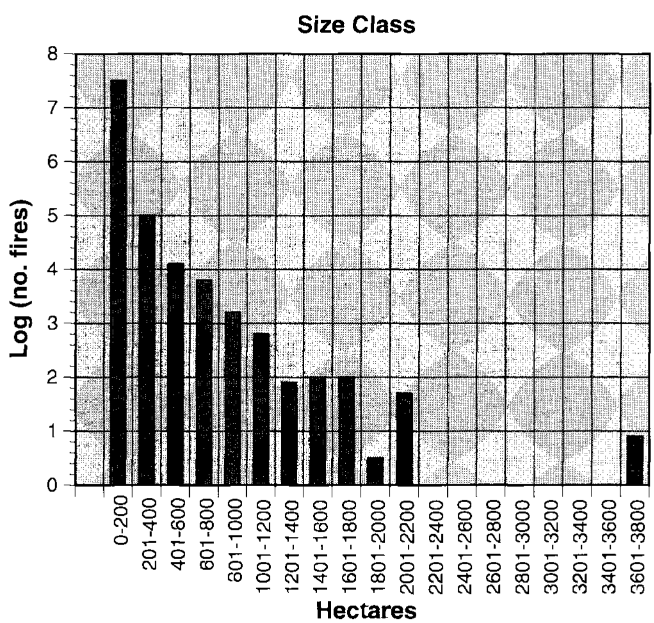

Fig. 2. Size distribution of wildfires in Northwestern Ontario (from Li *et al.*, 1996).

Selected aspects of biodiversity

The concept of biodiversity has come to mean all the aspects of life in ecosystems. The species present, the interaction among species, the generic variability, indeed virtually any component of an ecosystem can contribute in some way to the idea of biodiversity. Forest management may change the biodiversity of the landscape or it may not, depending on the harvest techniques used.

Under ecosystem management the goal should be to maintain the diversity of the managed area reasonably close to the diversity present before management began. This goal is both scale and time dependent and must be considered at relatively large scales. However, the diversity maintenance goal is a practical and realistic way to measure the impact of logging on the landscape and assure the public that forest management is consistent with biodiversity conservation (Carey & Curtis, 1996).

Baker (1993) describes how one aspect of diversity can be measured in areas disturbed by wildfire. Although Baker did not compare the wildfire landscape to a logged landscape, it would not be hard to do that comparison. In Baker's example, from the Boundaries Waters Canoe Area in northern Minnesota, he used patch age to calculate, using Shannon's index, the diversity of patch ages on the landscape. He demonstrated how fire suppression increased the patch age diversity of the landscape over the presettlement forest. The idea that fire suppression would increase some measures of diversity of the

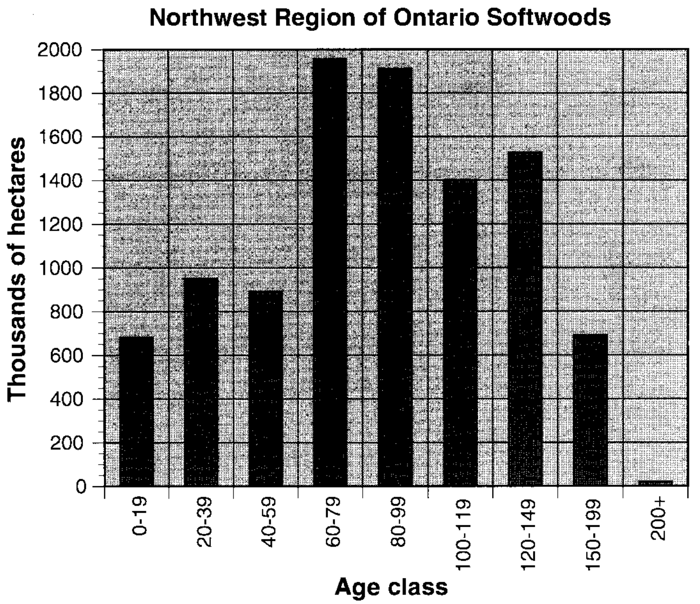

Fig. 3. Age class distribution of softwood trees in Northwestern Ontario.

landscape may seem counter-intuitive, and illustrates the importance of actually measuring the impact of major human activities on the landscape.

Managing age classes of trees

The third area that forest managers manipulate in the process of logging and fire suppression is the age class structure of commercial trees. As with the other goals of ecosystem management, the goal is to try to approximate the age distribution that has evolved in the boreal forest.

In an unmanaged and unlogged boreal forest, with forest fires unsuppressed, average disturbance frequency is usually in the range of 70 to 100 years. Van Wagner (1978) proposed that the resulting age class distribution is exponential. Boychuk *et al.* (1995) reviewed theoretical age class distributions in the Boreal Forest and concluded that the exponential model was common, although significant variations can occur. The age class distribution is not fixed, and will vary depending on scale and climatic factors. However, in virtually every case in Boychuk *et al's* data a larger area of the forest is in younger age classes and less is in older age class. Forested boreal ecosystems, evolving in a disturbance environment, typically show age class distributions with considerably more area in younger rather than older forests.

The managed boreal forests of Ontario, in contrast, are dominated by older age classes. For example, in a status report from the Ontario Ministry of Natural Resources (Ontario, 1994) the following analysis is given:

In terms of age structure, Ontario's forest are dominated by mature and overmature forests; fully three quarters of the province's productive forest are over forty years old. The age class distributions of Ontario's forests result from 77 years of organized forest fire control in the north and 250 years of post-colonial settlement in the south. Forest fires disturb an average of 80 000 hectares of managed forest every year. In the pre-suppression (pre-settlement) era approximately 700 000 hectares of forest were consumed by fire. If one adds the area harvested each year (170 000 hectares) to the average area burned, the total area affected is 250 000 hectares. This represents less than 40% of ave-

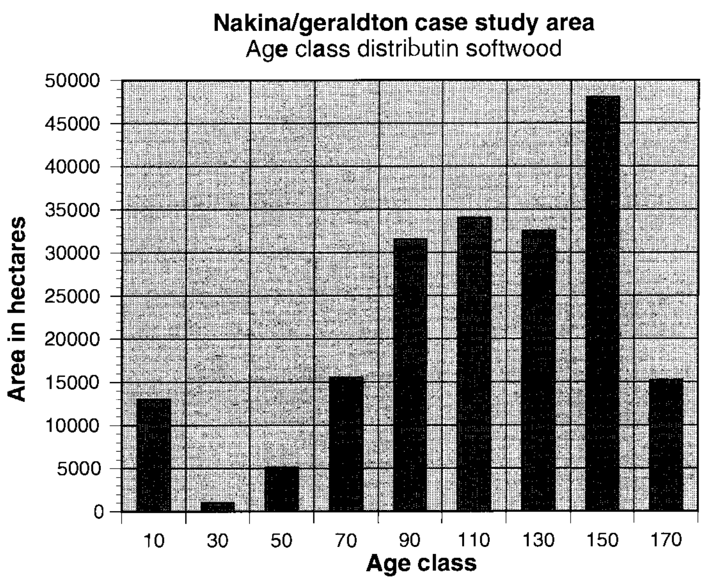

Fig. 4. Age class distribution of commercial tree species from the Nakina management unit in Northwestern Ontario.

rage area disturbed annually in Ontario's forests before European settlement.

Figs. 3 and 4 illustrate typical examples of this distribution.

To change the age classes distribution of commercial tree species towards a more evolutionary pattern, Boychuk *et al.* (1995) provide some useful guidelines. The goal is fewer trees in older age classes than is there now, met either by less fire protection or selective logging.

Affects on woodland caribou habitat

A Boreal Forest area managed under ecosystem management would have large scale disturbances, sometimes dozens of square kilometers in size. Old forests would be relatively rare; perhaps 5 to 10% of the landscape would be in these old stages. The landscape would not be as diverse, because most human activities tend to increase the diversity of the landscape, (e.g. Baker, 1993; Gluck & Rempel, 1996). Wide spread management for moose and other popular game animals that respond to edges and disturbed areas, has left a more fragmented forest than that which evolved under fire, insects and wind storms. The net result would be a forest with attributes that resemble the forest that evolved before people began to intensively manage the area. Because caribou evolved under these conditions it seems logical that the habitat portion of woodland caribou management would be satisfied by this approach.

The next step should be to use computer models of forest management and develop a specific example of how the landscape would change following an ecosystem management strategy. Gooding & Van Damme, for example, (1996) used a computer model to compare hauling costs of wood harvested in both conventional and ecosystem management regimes. The same approach would be beneficial in studying the potential impact of ecosystem management on caribou habitat.

Summary and conclusions

Moving from a featured species approach to ecosystem management is a difficult process that will be hard for many people to accept. There is a strong bias to search for specific solutions to problems encountered by selected species. When any wildlife species is considered endangered, whether it is bald eagles or woodland caribou, there is a strong impetus to develop specific solutions to the specific problem. The problem with the species by species approach is that the palate of individual problems accumulates to such a degree that it becomes impossible to solve in any realistic sense. In Ontario, for example, there are some 30 or 40 "guidelines" that managers are supposed to follow in developing forest management plans. In addition, there are several criteria for measuring sustainability that managers are supposed to include. The net result is that managers, no matter how sincere or hardworking, cannot follow the sometimes contradictory, sometimes obscure, guidance from these documents. In response, they build plans based on the particular biase they bring to the planning process.

In ecosystem management, a few basic principles are followed that provide the best opportunity to maintain viable populations of all species on the landscape, that will conserve biodiversity at the appropriate levels, and will sustain the fundamental processes that are important to ecosystem function. In that scenario, the needs of woodland caribou would seem to be protected to the best possible degree.

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Defining the Pen Islands Caribou Herd of southern Hudson Bay

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Abstract: In this paper, we describe the Pen Islands Herd of caribou, the largest aggregation of caribou in Ontario (it also occupies a portion of northeastern Manitoba). Photographic counrs showed the herd had a minimum population of 2300 in 1979, 4660 in 1986, 7424 in 1987 and 10 798 in 1994. Throughout the 1980s, the Pen Islands caribou exhibited population behaviour similar to migratory barren-ground caribou herds, although morphology suggests they are woodland caribou or possibly a mixture of subspecies. The herd had well-defined traditional tundra calving grounds, formed nursery groups and large mobile post-calving aggregations, and migrated ovet 400 km between tundra summer habitats and boreal forest winter habitats. Its migtation took it into three Canadian jurisdictions (Ontario, Manitoba, Northwest Territories) and it was impottant to residents of both Manitoba and Ontario. It is clear that the herd should be managed as a migratory herd and the critical importance of both the coastal and variable large winter ranges should be noted in ensuring the herd's habitat needs are secure.

Key words: woodland caribou, Ontario, Manitoba, migration, population size, annual range.

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Introduction

Woodland Caribou (*Rangifer tarandus caribou*) are found throughout northern Ontario north of about 50°30' north latitude (Darby *et al.*, 1989). The Hudson Bay Lowlands contains the majority of the province's caribou, including aggregations that occur along the Hudson Bay coast (Fig. 1). In the late 1970s and early 1980s, evidence accumulated about increasing numbers of caribou summering near the Ontario-Manitoba border (Thompson & Abraham, 1994). It was thought that this summer aggregation might be the source of the increasing number of observations of caribou in winter in the boreal forest of extreme northeastern Manitoba and northwestern Ontario. In addition to the many questions of biological interest raised, the discovery of so many caribou had several implications for harvest by the Cree people of the area, tourism and jurisdictional management. These implications provided the impetus for the Ontario Ministry of Natural Resources (OMNR) to undertake a 3 year study to document the characteristics of the herd.

The objectives of this paper are: 1) to review the history of caribou occupation of the Hudson Bay Lowlands between Ft. Severn, Ontario and York Factory, Manitoba; 2) define the size of this herd during the 1980s and early 1990s, and 3) to delineate the annual range and seasonal use areas.

Study area

East Pen Island lies offshore from Ontario and is thus part of the Northwest Territories. West Pen Island, formerly an island but now a peninsula of the Ontario coast, lies to the southwest of East Pen Island, within 5 km of the Manitoba border (Fig. 1). Because these islands are near the longitudinal centre of the calving and summer range where the first evidence of a large summer aggregation was obtained, we named this group of caribou the Pen Islands Herd.

The study area comprised an area of approximately 80 000 km^2 in extreme northwestern Ontario and northeastern Manitoba (Fig. 1). It is bounded on the east by the Severn River, on the north by Hudson Bay, on the west by the Nelson River, and on the south (at approximately latitude 55° N) by God's Lake, Edmund Lake, Kistigan Lake

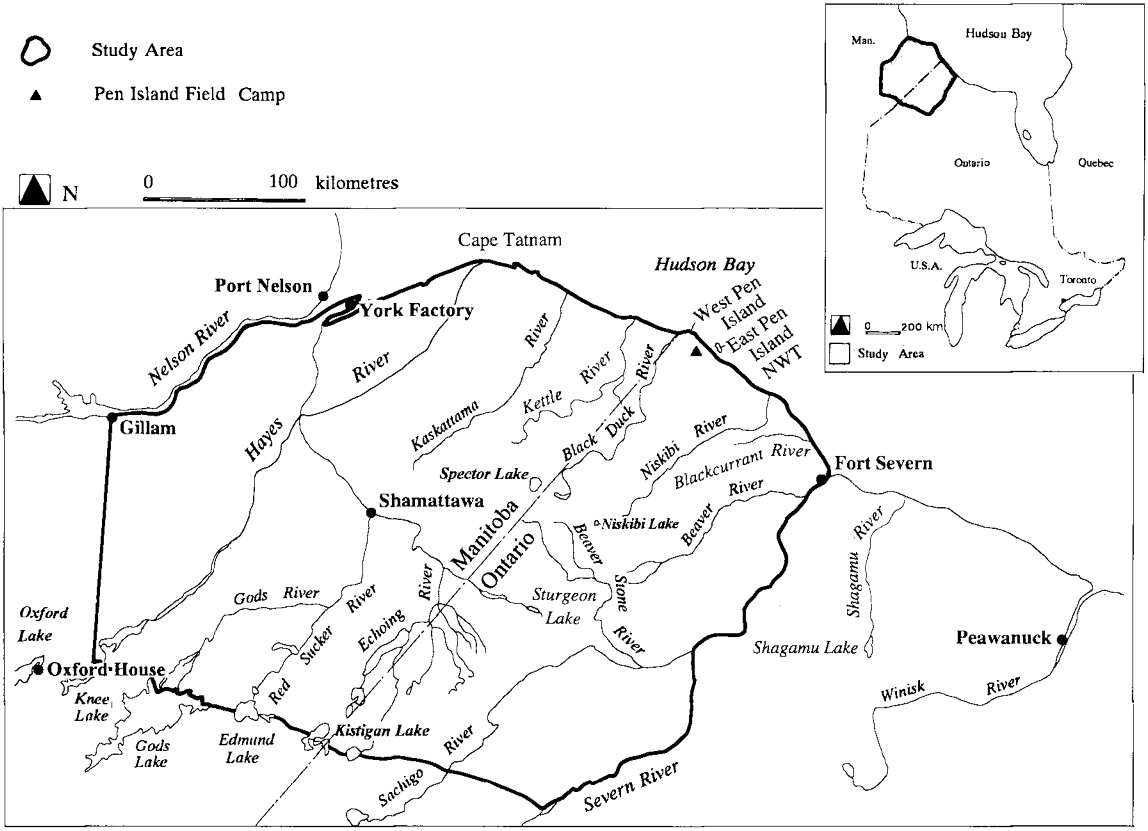

Fig. 1. Pen Islands caribou study area in Ontario and Manitoba and southern Hudson Bay coast showing places of caribou groups and movements described in text.

and the upper reaches of the Echoing River watershed. The majority of the study area is in the Hudson Bay Lowland physiographic region (Hutchison, 1982) and the remainder is on the Canadian Shield (Rowe, 1972). Within this broad study area, spring, summer and fall studies were concentrated between the Niskibi River, Ontario and Cape Tatnam, Manitoba and within 20 km of Hudson Bay (the Forest-Tundra zone of Rowe, 1972). Winter radio-tracking and aerial surveys defined the inland extent of the study area.

Methods

Historical information on caribou numbers, distribution and harvest was assembled from published and unpublished reports, OMNR and Manitoba Department of Natural Resources (MDNR) files, researchers' notes and Lowland residents.

Visual and photographic aerial surveys were flown in the coastal portion of the study area to locate important areas and to estimate population size in summer. We conducted a total of 26 reconnaissance and photographic aerial surveys on a subjective schedule between 25 May 1987 and 13 June 1989. Aggregations were photographed to obtain total population surveys on 11 July 1986, 25-26 May, 22-23 June and 14 July 1987 and 20 July 1988.

Caribou were captured and collared or tagged in two separate time periods. The first session was during the rut from 28 September to 5 October 1987 when 21 females and 2 males were captured and fitted with radio-collars. The second session was from 7 to 14 June 1988 just after calving when 4 females (all collared) and 23 males (13 collared, 10 ear-tagged) were captured. We conducted a total of 25 telemetry surveys between 28 October 1987 and 27 March 1990, approximately bi-weekly during winter to locate collared caribou. The annual ranges of the 23 caribou tagged during the rut in September-October 1987 and the 27 caribou tagged during early aggregation period in June 1988 were overlapping and indicated that both sets of captured animals did come from the same population. Therefore, these two groups are combined for analysis and discussion of the Pen Islands Herd characteristics. Annual range was estimated by creating an outer convex polygon of locations of radio-marked caribou each year.

A detailed description of methods is provided in an OMNR internal report by Thompson & Abraham (1994).

Historical perspective on caribou in the Pen Islands area

Relatively little quantitative information is available on the historic numbers, distribution or behaviour of caribou in the Hudson Bay Lowland, particularly along the Hudson Bay coast. The earliest written records are from the period of Hudson's Bay company settlement in the 1700s. Andrew Graham (in Williams,1969:14-16) describes "reindeer" as being "several kinds" and "very numerous" in the 1770s along the Hudson Bay coast. He mentions their great importance in the diet of Indians and in the local economy. He also provides a vivid description of their "southward" migratory movement in May along the coast past the "York Fort" (now York Factory) and "Severn" (now Fort Severn) settlements and their return "northward" migratory movement in September. Finally, he notes them as "rarely seen within eighty or one hundred miles of the coast" between November and April. Other early accounts of caribou in this area by S. Hearne, N. Jérémie, and J.B. Tyrrell were summarized in Banfield (1961:85); these noted migration between forested interior areas and coastal tundra. Banfield (1961) also raised a question of taxonomic status of "the herds that formerly inhabited the southern Hudson Bay coast from Cape Henrietta Maria, Ontario to Cape Churchill, Manitoba". The question he posed (and left unanswered) was whether they were "migratory woodland caribou" or the "southernmost tundra caribou". Despite rapid reduction of the herds through heavy killing in the eighteenth century, apparently a few migratory bands still existed as late as 1912. The caribou that Banfield himself examined in northeastern Manitoba in 1949 "appeared to be woodland caribou" but interestingly, he noted that the area was "overrun by migrating tundra reindeer" at the time. Despite the observation, he offered qualified conclusions that "reduction of local populations has apparently curtailed the migratory habit" and that the area was a "possible ... area of intergradation between the subspecies." de Vos & Peterson (1951) stated that woodland caribou occurred widely in scattered herds but also noted that they were "absent from a fringe along the Hudson Bay in the northwestern part" of Ontario.

In the 1950s and 1960s, a series of surveys of the Hudson Bay Lowland was made during summer, fall and winter. Winter surveys (Simkin, 1962; 1964; 1966; 1967) and interviews with Cree living in the area revealed that the coastal zone was virtually unoccupied in winter, just as Graham had noted so much earlier, except that there was a small group north of Sutton Lake toward Cape Henrietta Maria (de Vos & Peterson, 1951; D. Simkin, pers. comm.). Simkin found caribou in winter (January to March) 50-100 miles inland from Hudson Bay and showed winter densities in these interior Lowland forests to be similar to densities in the bulk of Ontario's boreal forest. Occasional winter surveys conducted between 1959 and 1982 by Ontario and Manitoba provincial employees documented caribou distribution and densities in parts of our study area. Although winter concentration areas were mapped, neither month to month movements nor annual variation in areas occupied were known and no population estimates were made that could be related to the entire study area we defined. Thompson (1986) presented results of a survey conducted from 1981-1983 and summarized all previous winter caribou surveys from the Ontario Hudson Bay Lowland. The 1981-83 surveys re-confirmed the absence of caribou from the coastal zone in winter, and documented significant wintering concentration areas at the habitat boundary of the Hudson Bay Lowlands Forest and the Northern Boreal Forest (terminology of Rowe,1972) particularly around Sturgeon Lake, Ontario and the upper reaches of the Echoing River near the Manitoba border.

Simkin's (1959) interviews with Cree residents provided accounts of caribou movement inland in November (i.e., away from open tundra areas to forested areas) and coastward in February and March, a pattern that appears to have held true for the entire Hudson Bay coast. During our community visits from 1987-90, Fort Severn hunters related their accumulated knowledge of caribou in their areas of activity. They reported that caribou were thinly scattered over this portion of the Lowland about 50 years ago. In more recent years, they noted the migratory nature of these animals, particularly an east to west movement to the coast in April when the snow is crusted (J. Stoney, pers. comm.) and an increase in summer numbers on the coast. Fort Severn hunters distinguished three types of caribou within and near their hunting grounds: small caribou north of the Nelson River called "little white ones", the Pen Islands animals, and larger "woodlands" caribou. Their caribou harvesting habits incorporated a shift from mainly inland hunting to coastal harvesting in the early 1970s.

Independent discussions we had at this time with Shamattawa, Manitoba, Cree hunters revealed similar information. They also distinguished three types. Shamattawa hunters began to see and hunt the migrating caribou in about 1980 (possibly the Pen Islands Herd) in addition to the more usual resident "woodlands" caribou and the Cape Churchill caribou with thinner hides and "pelage like a rabbit". Corresponding reports from Manitoba Department of Renewable Resources (S. Kearney, pers. comm.) suggested increases in winter use of the boreal forest in extreme northeastern Manitoba near the Ontario border, including the Shamattawa area and the Echoing River watershed, during the early 1980s. Movement patterns reported by Shamattawa Cree hunters were westward movements in the fall towards Oxford House (Fig. 1) and return movements in winter and towards the coast in spring.

Information from both Fort Severn and Shamattawa revealed an awareness that beginning in the early 1970s, caribou seemed to concentrate in summer near the Pen Islands. Interestingly, neither community was aware of the location of calving. Taken as a whole, the information from Fort Severn and Shamattawa pointed either to an increasing herd in the Pen Islands area or, alternately, a range shift (from the interior or further north along the coast?) and increased use of coastal areas in spring and summer and interior areas in winter in extreme northwestern Ontario and northeastern Manitoba. We cannot distinguish between these alternatives.

Generally missing from both the technical and Native accounts is a comprehensive understanding of numbers, distribution and behaviour of caribou in the Lowland during the snow-free seasons. In summer surveys, Simkin (1959; 1961; 1965) recorded small bands along the Hudson Bay coast from Cape Henrietta Maria to the Manitoba border. The largest summer group he recorded was 41, with averages from 6 to 9 depending on month and year; these data are mostly from the Hudson Bay coast east of the Winisk River. From the Winisk River west to the Shagamu River, he found no evidence of large groups, nor tracks of more than 2 together. West of Severn, near the Niskibi River he found "heavy track concentrations" but few caribou. Simkin (1965) found no specific coastal calving grounds.

During 20 coastal polar bear (*Ursus maritimus*) surveys conducted between 1963 and 1990, no large caribou aggregations were recorded (G. Kolenosky and others, unpubl. reports). However, most of these surveys were conducted between late August and early September and covered only the area within 5 km of the high tide line. Our study indicates that the large aggregations disperse by late July and that smaller bands of caribou probably move into the treed ridges and fen areas some distance from the coastline. This probably resulted in polar bear surveyors seeing few caribou, even in years when the population was growing.

In the 1970s, observations and photographic documentation of caribou in summer along the Hudson Bay coast were obtained by biologists conducting waterfowl surveys. The existence of a large herd west of Fort Severn was first suggested by the observations of H. G. Lumsden (pers. comm.) in 1973. During July waterfowl surveys, he observed tracks in tidal mudflats along the coast strongly suggestive of large numbers of caribou. R.K. Ross (pers. comm.) recorded many small groups (1-40) near the Pen Islands between May and October 1977, but he also found mixed sex groups of 150 and 300 in July 1977. The first photographs confirming large caribou aggregations (totalling 2300 animals) in the Pen Islands area were taken on 6 July 1979 by Lumsden near the mouth of the Black Duck River at the Ontario-Manitoba border.

As a result of heightened awareness, OMNR employees were encouraged to regularly report and if possible, photograph caribou they observed along the coast. In 1983, we began systematic attempts to collect numerical population data on caribou summering in this area, with variable success. However, by 1985, we knew unequivocally that summer post-calving aggregations containing a few thousand caribou occupied the coastal tundra west of Fort Severn, but we did not have a reliable estimate of numbers. Finally, a count of 4,666 caribou of both sexes and all ages was obtained from photographs of three large aggregates found between Black Currant River and the Pen Islands on 11 July 1986. We did not search west of the Kettle River, Manitoba on this date so it is possible that other similar groups were not located. On 27 March 1987, approximately 400-500 animals were observed in a 4-6 km area approximately 10 km from the Pen Islands (D. McKnight, pers. comm.). At this time, we knew little else about this population of animals, including their connections, if any, to Manitoba and Ontario winter concentrations (Thompson,1986).

This was the information that led us to the working hypothesis that a group of migratory caribou occupied coastal tundra areas centered at the Pen Islands in spring and summer and moved to inland forested areas in winter. The "herd" appeared to straddle the Ontario-Manitoba border and seemed to be both large and increasing in size.

The intensive study from 1987-1990 allowed us to define the general population behaviour of the Pen Islands Caribou Herd. Although subsequent population growth and other events may have changed this picture, we offer the following information as the first definitive description of the Herd.

Subspecies identity

The subspecies identity of the Pen Islands caribou is not certain. Pen Islands animals are larger than barren-ground caribou and resemble woodland caribou in external body and skull measurements and antler position, but antler characteristics are more similar to barren-ground caribou (Thompson & Abraham, 1994). Genetic studies may help resolve the question posed by Banfield (1961) about whether the herd has a mixed subspecies origin.

Population size 1987-1989

Aerial photographic surveys of summer aggregations containing both sexes and all ages were conducted in 1987 and 1988 to determine population size. We located the aggregations by flying parallel low altitude transects over the entire coastal calving and summer range and few single caribou were observed. On 14 July 1987, we found and photographed 7 distinct groups on intertidal flats and beach ridges near the coast, totalling 7424 caribou. Surveys before and after this date in 1987 indicated that this was the peak of aggregation and this survey gave us the largest count obtained during the three year study. Other counts at peak aggregation yielded as few as 3190 (20 July 1988). Thus, we recognize that the photographic technique we used is only able to provide a minimum population estimate and that scattered individuals, small bands and in some years, even large aggregates could have been missed. However, the aggregating behaviour was consistent among years and provided an annual opportunity in mid July to record the majority of caribou in the Herd.

Population size since 1990

The techniques we established were used to conduct photographic counts after the intensive study. Delean (1993) photographed 5113 caribou in aggregates, primarily between Kaskattama River and Cape Tatnam, Manitoba. Scholten (1994) photographed 10 798 caribou in 12 aggregates across virtually the entire described summer range from Cape Tatnam, Manitoba to Niskibi River, Ontario. We interpret the difference between years (a two fold increase) as a problem with the visual location of aggregates in 1993, similar to our earlier experience, rather than real population change. Simultaneous ground observations made by us in 1993 indicated over 500 caribou along the coast between the Severn River and the Winisk River. We have not previously associated this portion of the coast with the Pen Islands herd summer range, chiefly because of the lack of observations of caribou near Ft. Severn between 1987 and 1990 and because of the physical barrier to eastward travel that the large Severn River and the community of Ft. Severn might pose. However, it is possible that as the herd has grown such factors as their own habitat impacts, increased human disturbance and coincidental increases in other herbivores (e.g. snow geese) may have induced the herd to move farther eastward than during our initial study. An alternative explanation is that the caribou bands near the Shagamu River and Shagamu Lake have increased in parallel with the Pen Islands Herd. Regular observations have been made of small summer bands near the river mouth and winter concentrations near the lake.

In summary, the known number of caribou summering in the Pen Islands area has risen steadily from at least 2300 in 1979 to at least 10 800 in 1994.

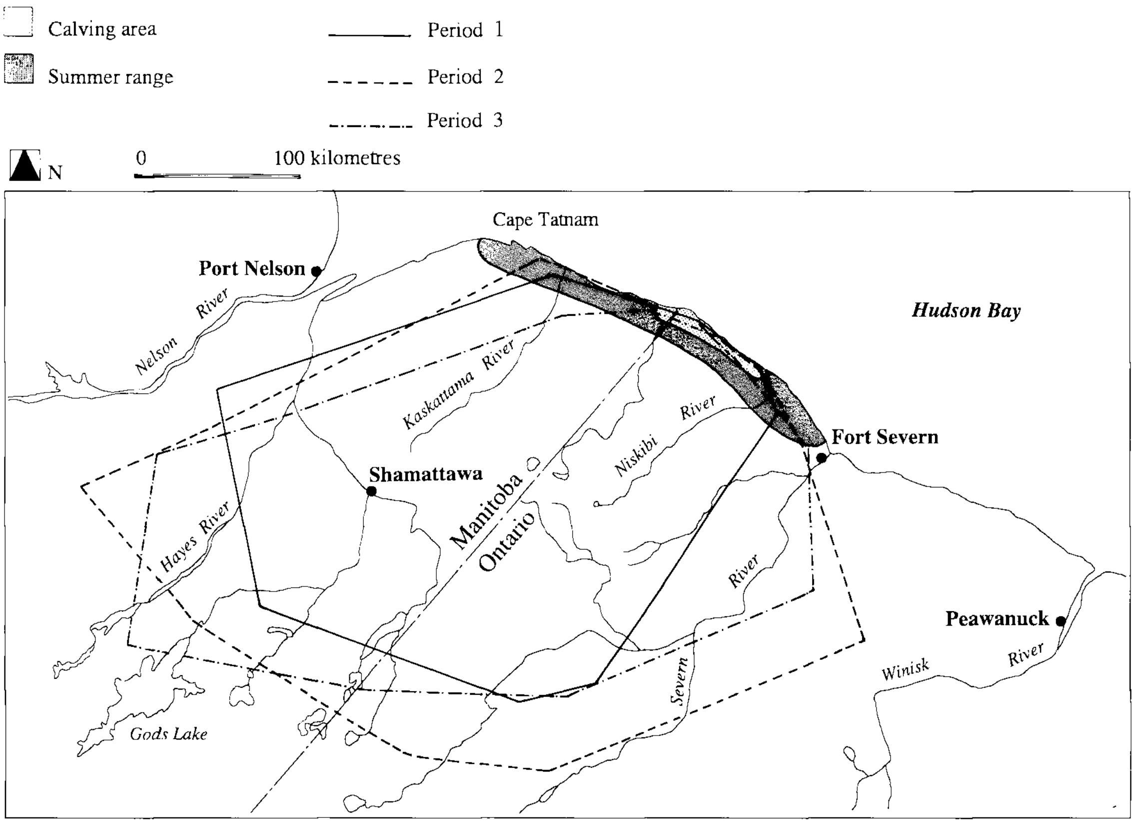

Fig. 2. Annual range of Pen Islands caribou herd showing calving area and summer areas and outer convex polygon of all fall-winter radio telemetry locations in each year (Period 1= Sept.1987- June 1988; Period 2 = Sept. 1988 - July 1989; Period 3 = Sept. 1989 - March1990).

Annual range

Spring

The Pen Islands Herd calving area extended from the Niskibi River, Ontario (56°56' N, 89°22' W) westward to the Kettle River, Manitoba (56°30' N, 88°09' W), was approximately 90 km in length and caribou were observed using these same grounds during all 3 years of study (Fig. 2). This was also where R. K. Ross (pers. comm.) noted calving caribou in 1977. There was nearly complete segregation of the sexes during the peak calving period from the 17-21 May. Most bulls were presumed to be in forest and forest-tundra areas south of the calving grounds. Thus, the Pen Islands herd exhibited a pattern of dispersion during calving and traditional use that is characteristic of migratory barren-ground herds.

Summer

Summer aggregations occupied the Forest-Tundra zone from the Black Currant River, Ontario to Cape Tatnam, Manitoba and were usually found within 5 km of the coast. Cow-dominated "nursery" groups formed immediately after calving (surveys from 24-28 May) and contained up to 764 animals. Bull-dominated groups at this time usually contained 10 or fewer individuals although groups of up to 50 were found. Beginning in early June, all age and sex classes came together to form larger, loosely-knit aggregations and by mid-June, these mixed groups predominated (81%) and a few contained over 500 animals and the largest was 1465. The peak aggregation period occurred in mid July each year when virtually the entire Pen Islands population was found in a few large groups, some containing 2000 animals. By late July and throughout August, these large mixed groups could not be found, despite extensive searches. Apparently they fractured into small bands or solitary social units, including cow-calf pairs. Caribou were rarely encountered in the immediate coastal area. Limited observations of caribou in the fens and bogs up to 40 km inland from 1993 to 1996 suggest they retreated to the spruce-lichen ridges and wetlands of the interior.

Autumn

Telemetry surveys in early to mid-September showed that 79% of caribou were within 30 km of the coast. Small groups were more widely distributed over the available Forest-Tundra and edge of the Hudson Bay Lowlands Forest than during the calving and aggregation periods. The rutting period of the Pen Islands Herd was from mid-September to mid-October. Back-dating from calving, the peak rutting period in all years was estimated to be the last week of September and the first week of October. This back-dated estimate was supported by observations of behaviout and condition during tagging operations.

Winter

After spending approximately 6 months in the open tundra and forest-tundra transition near the coast, the Pen Islands caribou moved southward and inland in late October. No narrowly defined fall migration routes were detected during the study, instead, the movement occurred across a broad front. The infrequency of our radio locations (2-4 weeks apart) precluded defining whether movements occurred along river drainages.

The pattern in each of the three years was for the herd to move gradually inland during November and December, reaching the most distant points from the coast by mid-January and February, then returning slowly to the coast in March and arriving in April. They used substantially different areas in each year: in the 1987-88 they straddled the Ontario-Manitoba border throughout the fall and winter as they moved inland and back toward the coast. In 1988-89, they concentrated in Manitoba in early fall, shifted eastward into Ontario in November, moved back into Manitoba in December through late winter, then east into Ontario for spring. In 1989-90, they moved inland in Manitoba during early fall but then moved eastward into Ontario in December where they remained for the rest of the winter. The Pen Islands Herd showed no consistent preference for either the Northern Coniferous or Hudson Bay Lowlands forest types. Instead, they showed a complex movement and habitat use pattern among months and years. Our data indicate that bulls and cows shared the same winter range over the three years.

The maximum area occupied in each year (including all locations for collared caribou plus summer observations) is shown in Fig. 2. Similarity of annual ranges is evident, however, variation in extent of inland movement is present among years, possibly associated with differences in snow fall or other environmental factors such as timing of freeze up on lakes and rivers, or altered habitat due to the previous summer's forest fires.

Conclusion

Migratory caribou herds that occupy tundra habitats in summer and move into forested habitats in winter have been documented from northwestern Alaska continuously to Manitoba (Baker, 1980:207; Calef, 1981: 16-17). The migratory George River Herd (Couturier *et al.*, 1990) occupies the Ungava peninsula in Quebec. A notable gap in southern Hudson Bay has been filled by our documentation of the range and behaviour of the Pen Islands Herd.

The herd's usual range has been documented by this study. Although it is small in population and range relative to most of the migratory herds, it is similar to them in behaviour, population characteristics and habitat use and appears to be in a rapid growth phase (Thompson & Abraham, 1994). Exceptional movements that probably involved the Pen Islands Herd (e.g., large numbers of caribou were located west and south of Gillam, Manitoba in winter 1991-92, C. Elliott, pers. comm.) have subsequently been noted. Further assessments will be required to monitor annual variation in size of the summer and winter range and location of additional use areas. Management policy must address the herd's need to respond positively to a variety of environmental factors and to vary its use of extensive pottions of the land base. Management plans must also account for increased human awareness, use and activity in the herd's known range.

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Survival, persistence, and regeneration of the reindeer lichens, *Cladina stellaris, C. rangiferina*, and *C. mitis* following clearcut logging and forest fire in northwestern Ontario

Abstract: The responses of the teindeer lichens (*Cladina stellaris, C. rangiferina,* and *C. mitis*) to logging and fire were compared in lichen-rich forest stands in northwestern Ontario. In the summer of 1992, reindeer lichen cover, in total and by species, was visually estimated and detailed notes were taken on reindeer lichen conditions, modes of reproduction, and substrate use on 34 undisturbed, burned, or logged sites. While virtually no reindeer lichens survived forest fire, much of the reindeer lichen cover remained after logging. Reindeer lichen cover increased with time since fire. Total reindeer lichen cover was not cotrelated with time since logging. Fragment growth was found to be an important mode of reproduction on logged sites, and occurred with gteater frequency on logged sites than on burned sites. Colonization of organic substrates by reindeer lichens was observed on both logged and burned sites.

Key words: woodland caribou, timber harvest, reindeer lichens, *Cladina* spp., forest fire, terrestrial lichens.

Rangifer, Special Issue No. 10, 41–47

Introduction

Fire-produced reindeer lichen-rich forest communities serve as late winter habitat for woodland caribou (*Rangifer tarandus caribou*), and the reindeer lichens, *Cladina stellaris* (Opiz) Brodo, *C. rangiferina* (L.) Harm, and *C. mitis* (Sandst.) Hale and Culb., are their primary late winter fodder (Simkin, 1965; Darby & Pruitt, 1984; Cumming & Beange, 1987; Morash & Racey, 1990; Schaeffer & Pruitt 1991). Reindeer lichens are adapted to recurrent forest fire, and reindeer lichen-rich stands in northwestern Ontario are almost exclusively of fire origin (Ahti & Hepburn, 1967). Where logging has replaced forest fire as the most prevalent type of large-scale disturbance, an understanding of the effects of logging on reindeer lichen ecology is relevant to issues of timber and woodland caribou management.

Post-fire ground cover succession in reindeer lichen-rich stands is well documented. Although the effects of fire vary depending largely on the intensity of the fire, in reindeer lichen-rich communities, forest fire almost always consumes the ground cover (Viereck, 1983; Morneau & Payette, 1989; Schaeffer & Pruitt, 1991). Post-fire lichen and bryophyte succession follows a general progression, first described by Ahti (1959) and documented throughout the boreal forest in Canada (Maikawa & Kershaw, 1976; Carroll & Bliss, 1982; Clayden & Bouchard, 1983; Foster, 1985; Morneau & Payette, 1989). Domination of the ground cover is first by crustose lichens, then cup lichens (*Cladonia* spp.), and finally, reindeer lichens: first *Cladina mitis,* then *C. rangiferina,* and ultimately *C. stellaris.*

Until recently there has been little documentation of reindeer lichen survival and regrowth on logged sites. Speculation on the fate of reindeer lichens in the complex process of vegetation regeneration on logged sites has often been contradictory. Ahti & Oksanen (1990) predict that drier, more extreme soil-level microclimates after logging may produce a lichen-rich successional stage in normally bryophyte-dominated forests. Darby *et al.* (1989) note that deciduous trees and shrubs often increase after logging, and reindeer lichens may be replaced by vascular plants. Racey *et al.* (1992) suggest that clearcut logging, like fire, acts as an ecosystem renewal mechanism, allowing young vigorous vegetation, including reindeer lichens, to replace older forests. Recent studies have documented that reindeer lichens are abundant for more than 40 years after logging in some forest stands in northwestern Ontario (Harris, 1996; Racey *et al*, 1996) and that some of these stands are being used by woodland caribou as winter habitat (Racey *et al.*, 1996).

Observations on reproductive modes and substrate use were made in an attempt to understand the reasons behind trends in reindeer lichen abundance. Lichens are known to reproduce through fragment growth, specialized reproductive structures containing both fungal and algal cells, and the conjunction of the fungal and algal components in situ. Lichen regeneration in natural settings has been rarely observed, and the relative importance of each mode of reproduction in various settings is not known.

Methods

In the summer of 1992, 34 stands near Armstrong and Sioux Lookout, Ontario were surveyed: 12 undisturbed sites, 8 sites burned 3-16 years prior to observation, and 14 sites logged 2-16 years prior to observation. The study sites were identified from aerial photographs as lichen-rich or lichen-rich prior to disturbance. The times since logging and fires were calculated from Ontario Ministry of Natural Resources records. Stand boundaries as defined on Ontario Ministry of Natural Resources Forest Resource Inventory maps were used as stand boundaries in this study.

Reindeer lichen-rich jack pine (*Pinus banksiana*) and/or black spruce (*Picea mariana*) stands occur on dry, nutrient-poor sites in this region, most commonly on shallow soils over bedrock or deep sand dunes or outwash deposits (Sims *et al*, 1989). Both shallow soil and deep soil sites were included.

At each site the percent cover of each species of reindeer lichen was visually estimated in 20 50 X 100 cm quadrats randomly distributed along a 100 m transect. Each transect began 10 m from a stand boundary and its direction was determined by random number. Six uneven percent cover classes were used: <2%, 2-5%, 5-25%, 25-50%, 50-75%, and >75%. The midpoints of the percent cover categories were used for statistical analysis. The data points in the figures in this paper represent the average reindeer lichen percent cover for each study site, since the category nature of the data does not lend itself to graphical representation of quadrat percent cover values.

Detailed notes on the ground cover of each quadrat were taken, and photographs were taken at most sites. Reindeer lichens were placed in 3 categories: 1) undisturbed, 2) fragment, or 3) new. The presence or absence of each reindeer lichen species in each category was noted for each quadrat at all but the first four sites. Reindeer lichens which had established prior to logging or fire and remained in their pre-disturbance orientation were classified as "undisturbed". Reindeer lichens grew either in a continuous carpet of 1 or more species or as individual podetia interspersed among moss. The "fragment" category included reindeer lichens which had established prior to logging or fire but were no longer intact. The fragments ranged in size from < 1 mm to several centimeters in diameter. Some fragments had only live tissue; some had both live and dead tissue. This category also included pieces of carpet that had shifted from their original locations and were no longer anchored to the substrate. Reindeer lichens in the "new" category had established since disturbance from propagules too small to be seen by eye. The new reindeer lichens had fewer annual branches than there were years since disturbance. Although there were no visible lichen fragments, the mode of dispersal was unclear. Dispersal may have occurred through thallus fragments too small to be observed, specialized reproductive structures, or the conjunction of the fungal and algal components *in situ*. Undifferentiated primary thallus was apparent at the bases of many of the newer podetia. The new reindeer lichens had fewer annual branches than there were years since disturbance. Collected reindeer lichens were examined under a dissecting microscope for further observations on fragment growth and establishment of new podetia.

Results

Reindeer lichen abundance

No undisturbed reindeer lichens were found on burned sites. *Cladina rangiferina, C. mitis* and total reindeer lichen cover increased with time since forest fire (Table 1, Fig. 1). *C. stellaris* was present in small amounts (average of 0.05% cover) on only two of the three sites burned 15 or more years prior to observation. The average total reindeer lichen percent cover for the three sites burned 15-16 years

Table 1. Correlation coefficients and P values for reindeer lichen percenr covers and years since disturbance.

Reindeer lichen species	Pearson's correlation coefficient	P=
burned sites		
all *Cladina* spp.	0.301	0.0001
C. rangiferina	0.183	0.0212
C. mitis	0.299	0.0001
logged sites		
C. rangiferina	0.203	0.0006
C. stellaris	-0.151	0.0116

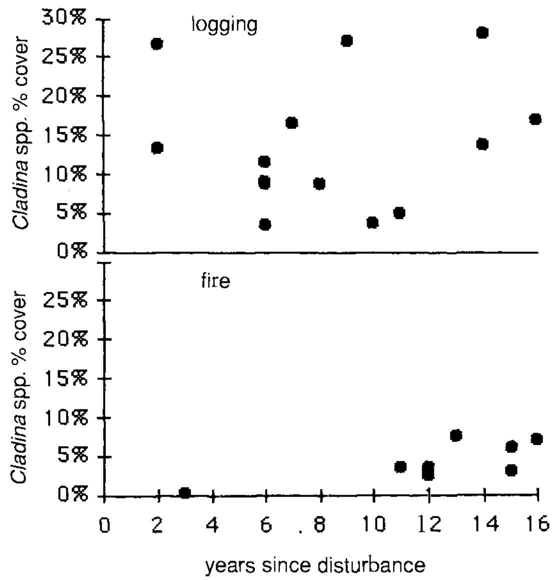

Fig. 1. Total reindeer lichen percent cover for logged and burned sites versus time since logging or fire. Each point represents the mean of 20 percent cover measurements at each site.

prior to observation was 5.3% as compared to 25.2% for all undisturbed sites and 19.7% for the three sites logged 14-16 years prior to observation.

Logging, unlike forest fire, spares much of the ground cover. All three *Cladina* species were present on 13 of the 14 logged sites. The average total reindeer lichen percent cover of the two sites logged 2 years prior to observation was 37.7% of the average reindeer lichen cover on unlogged portions of the same stands. Undisturbed and/or fragmented reindeer lichens which predated logging were present on all logged study sites.

While total reindeer lichen cover was found to be uncorrelated with time since logging, in contrast to time since fire (Fig. 1), *Cladina rangiferina* cover increased with time since logging, *C. stellaris* cover decreased, and *C. mitis* cover was uncorrelated (Fig. 2, Table 1). If the high *C. mitis* percent cover of site 4 (logged 2 years before observation) is considered to be an outlier and removed from analysis, then *C. mitis* cover also is found to be positively correlated with time since logging (Pearson's correlation coefficient 0.254, $P \leq 0.0001$).

Undisturbed reindeer lichens on logged sites

On logged sites, reindeer lichens that had established prior to logging were either: 1) undisturbed, 2) fragmented, or 3) buried beneath overturned soil or deadfall. The buried reindeer lichens, in every case, were dead. Virtually all of the mosses in the ground cover died within the first two years after logging.

With the exception of heavily shaded reindeer lichens and some unshaded *Cladina stellaris,* the

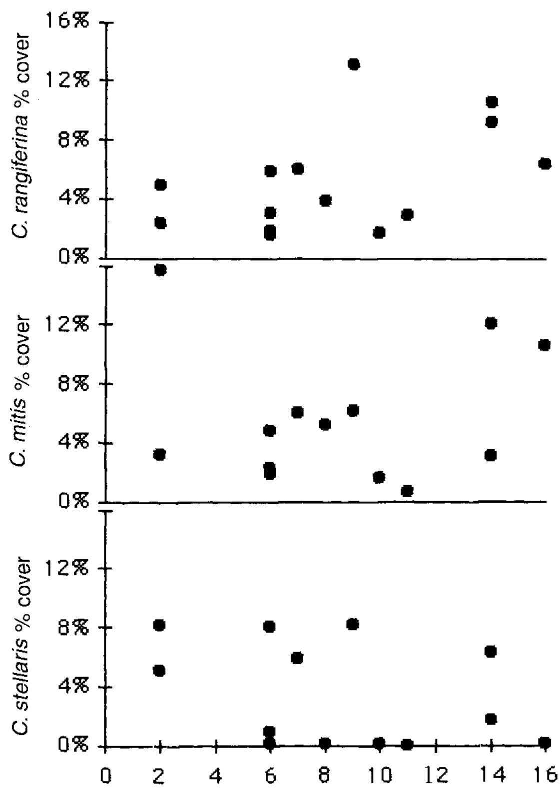

Fig. 2. Reindeer lichen percent cover by species versus rime since logging. Each point represents the mean of 20 percent cover measurements at each site.

growth rate of living tissue and rate of death of basal portions appeared unaffected by logging. Although the surfaces of *C. rangiferina* which received the most insolation after timber harvest changed in color from ash gray to a darker gray-brown, the tissues remained firm and appeared healthy, and the annual growth rate did not appear to be reduced. The death rate of the basal portions of some undisturbed *C. stellaris* appeared accelerated, and the annual growth increments appeared shortened when compared to *C. stellaris* on adjacent unlogged sites.

Scarification by barrels and chains produced a distinctive pattern of disturbance to the ground cover on several of the deep soil sites studied. The ground cover on the ridges between the scarification trenches was generally undisturbed. In the trenches was exposed mineral soil. The ground cover removed to create the trenches was overturned on the sides of the ridges; the overturned ground cover, including reindeer lichens, was dead. Scarification ridges and trenches were well defined and relatively clear of debris 2 years after logging. Over time the scarification ridges settled. Mineral soil shifted down slope undercutting and fragmenting the ground cover mats on the ridge tops. Pieces of the ground cover mats and windblown reindeer lichen fragments and organic debris collected in the trenches. Undisturbed reindeer lichens persisted on the tops of scarification ridges. The effects of scarification were still discernable 14 years later. Rows of reindeer lichen carpet as well as microtopography indicated scarification ridge tops. Observations of resettling and fragmenting of carpet suggest decline in the abundance of undisturbed reindeer lichens over time.

Most of the shallow soil sites surveyed were not scarified. Because of the lack of scarification and the uneven topography typical of these bedrock outcrops, the patterns of ground cover disturbance were not as simple as on the scarified deep soil sites. On shallow soil sites there appeared to be less undisturbed reindeer lichen. The shortest interval between logging and observation on shallow soil sites was 6 years. It is possible that much of the ground cover survived logging intact and succumbed to erosion subsequently. In some areas with steep slopes reindeer lichen mats had slid down the underlying rock until they were caught in the branches of *Vaccinium* spp. and other dwarf shrubs at the bases of the slopes.

Table 2. Mean frequency per site by site disturbance category of reindeer lichen reproductive modes. The presence or absence of each reproductive mode for each of 3 species in each of 20 quadrats was noted (maximum possible score = 60).

disturbance (*n*)	undisturbed lichen	fragmented lichen	new lichen
fire (8)	0	3.1	23.1
logging (12)	5.0	30.0	17.5
undisturbed (10)	26.6	0.7	0.4

Colonization

New *Cladina mitis* and *C. rangiferina,* those colonizing by means of ptopagules too small to be seen, were observed on all sites burned or logged 6 or more years prior to observation. New *C. stellaris* were observed, less often: on two sites burned 15 or more years before observation and on three sites logged 6, 8, and 14 years before observation. The frequency of new reindeer lichen occurrence on logged sites was not significantly different from that on burned sites (Table 2).

New reindeer lichens were observed almost exclusively on organic substrates, including conifer needles, conifer cone scales, bark pieces, and wood ranging in size from small twigs to logs and stumps. There were some organic substrates colonized on logged sites which were not present on burned sites including: dead moss; overturned ground cover; very fine windblown organic matter collected in some scarification trenches; and organic soil on shallow soil sites exposed when dead ground cover or reindeer lichens shifted down slope. Reindeer lichens established directly on organic substrates or on crustose lichens on organic substrates. Smaller pieces of organic litter on which new reindeer lichens were established were often caught among mosses or other lichens, especially on shallow soil sites. Reindeer lichens were not observed colonizing mineral soil. A few cases of *C. rangiferina* colonizing coarsely textured rock faces were observed.

Fragment growth

Reproduction by fragment growth was observed on all disturbed sites except the most recent burn, but occurred on logged sites significantly more frequently than it did on burned sites (t=5.787, $P\leq0.0001$) (Table 2). Three types of fragment growth were observed: 1) continued growth of the apical tissues, 2) formation of new branches in the

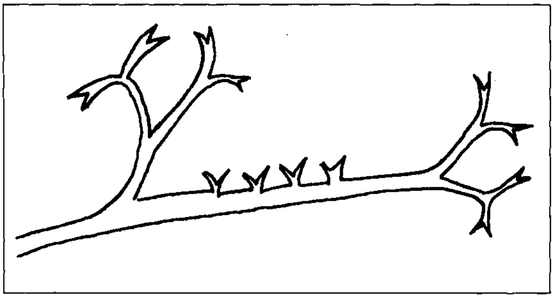

Fig. 3. New branches form on the internode between pre-disturbance branches on the surface which receives the most insolation in the post-disturbance orientation of the lichen fragment.

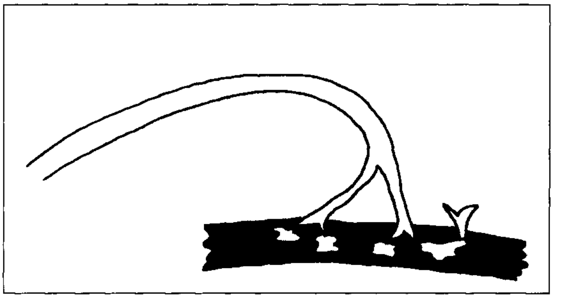

Fig. 4. Undifferentiated thallus spreads from the points of contact of the reindeer lichen fragment and the organic substrate. New podetia form from the undifferentiated thallus.

internodes between pre-disturbance branches, and 3) growth of new podetia from undifferentiated thallus that spread from the point of contact of a reindeer lichen fragment and organic litter.

Reindeer lichen fragments continued to grow from those apical tissues that were oriented toward the sun in the post-disturbance position. Accelerated death of tissues, including apical tissues, which received less insolation in their post-disturbance positions was observed.

Many fragments which were on their sides following logging formed new branches in the internodes between pre-disturbance annual branches on the surface of the internode which received the greatest insolation (Fig. 3). On older fragments the tissue of the original fragment was dead, in some cases making it difficult to distinguish between "new" and "fragment" reproduction. Thickening of the internodal tissue was the earliest indication of the branch formation. This thickening was most noticeable on tissue that was in the transitional zone between live and dead tissue. The formation of new branches in this zone suggests that lack of insolation as well as the age of the tissue, may explain the death of the basal portions of reindeer lichen podetia.

The spread of undifferentiated thallus from reindeer lichen fragments to organic substrate at the points of contact of the fragments and the substrate was observed. This occurred when a fragment was lying on an organic substrate as well as when small pieces of organic matter were caught within a lichen fragment. By 10 years post-logging, new podetia had differentiated from the tissue that spread from fragments (Fig. 4). Adhesion to a substrate seems to diminish the likelihood of further fragmentation and determine the pattern of growth by fixing the orientation of the fragment. Adhesion of fragments also seems to promote the lateral spread of lichen growth, since new podetia grow from the undifferentiated thallus that spreads from the points of contact between the fragment and the substrate.

Discussion

This study found that when reindeer lichen-rich stands are logged, much of the reindeer lichen survives logging and continues to grow, and that reproduction by fragment growth and colonization of organic substrates occurs, but that total reindeer lichen cover is not correlated with time since logging. The different responses of the 3 reindeer lichen species to logging likely accounted for the lack of correlation between total reindeer lichen abundance and time since logging. The decline in *Cladina stellaris* suggests that the *C. stellaris* which survives logging is reduced over time by erosion and/or accelerated death of *C. stellaris* tissue and is not replaced through colonization or fragment growth. The decline in *C. stellaris* is likely due to the increase in insolation at the ground level as a result of logging. *C. stellaris* tolerates a relatively narrow range of light conditions, and is less abundant where excessive light is available such as in arctic and alpine regions (Ahti, 1961). *C. stellaris* is the slowest growing of the reindeer lichens and the last to regenerate on burned sites (Ahti, 1961). Increase in *C. rangiferina* cover could be attributed to continued growth of undisturbed or fragmented *C. rangiferina* and to colonization of the disturbed site. As with *C. stellaris*, the abundance of *C. rangiferina* is also reduced, but not as sharply, in habitats with intense light (Ahti, 1961). *C. rangiferina* is fast growing and is the most successful of the reindeer lichens on humus-rich soils (Ahti, 1961). The relationship of *C. mitis* cover and time since logging was unclear. *C. mitis* is more successful earlier in the successional sequence than *C. rangiferina* or *C. stellaris,* but later its growth rate slows relative to other reindeer lichens suggesting that *C. mitis* is ecologically suited to disturbed sites (Ahti, 1961). Site 4 (logged 2 years prior to study) was the only logged site with well defined, relatively unstable sand dunes which may have led to *C. mitis* cover that was uncharacteristically high before logging for this set of sites and hence a relatively high *C. mitis* cover after logging. When site 4 was eliminated from statistical analysis, then *C. mitis* cover was positively correlated with time since disturbance as would be expected.

None of the relationships between reindeer lichen cover and time since disturbance in this study were strong. Much of the variability likely comes from: 1) differences between the sites compared other than type of disturbance and time since disturbance, and 2) a quadrat size too small to accurately capture reindeer lichen abundance. Type of disturbance and time since disturbance are only two of many factors such as slope, aspect, soil moisture, and canopy closure that influence reindeer lichen abundance. Logging adds variables such as time of year of logging, weather at time of harvest, seeding, method and timing of site treatment, and others, which affect reindeer lichen competitors as well as reindeer lichens themselves. It was not possible to control for or even identify all of these factors. Soil depth (deep sand or organic mat over bedrock) did not explain the variation in reindeer lichen abundance. The quadrat size, 50 X 100 cm, was small relative to the size of the patches in which mosses and reindeer lichens grow; therefore, there was high variability in estimated reindeer lichen percent covers among quadrats within sites.

Reindeer lichen fragment growth was found to be an important mode of reproduction on logged sites. Reproduction by fragment growth was more prevalent on logged sites than on burned sites, probably because of the greater abundance of lichen fragments on logged sites. Fragments on logged sites presumably result from the mechanical break-up of existing reindeer lichens by timber harvesting and site preparation activities (Harris, 1996). This study and Harris (1996) found that reindeer lichens which were undisturbed by timber harvest and site preparation persisted and were still evident on the oldest logged sites.

Colonization of organic substrates by propagules too small to be seen occurred on logged sites as it did on burned sites. This study, like Harris (1996) and Racey *et al.* (1996), found that reindeer lichens grow on substrates created by logging activities including stumps, slash, and haul roads. The persistence of undisturbed reindeer lichens and growth of reindeer lichen fragments, however, likely accounted for the higher cover of reindeer lichens on burned sites than on logged sites of the same age since disturbance. Harris (1996) found that microsites where mineral soil had been exposed during site preparation had significantly fewer reindeer lichens than where the ground cover had not been disturbed, suggesting that minimal disturbance to the ground cover of reindeer lichen-rich communities during harvest and site preparation will promote reindeer lichen persistence after logging. Similar observations were made in this study.

Racey *et al.* (1996), however, found in a 40 year old cutover near Nakina, Ontario, that reindeer lichen abundance was highest where the majority of the organic material had been removed from the mineral soil, for example on haul roads. Racey *et al.* (1996) argue that while severe fire removes the feather mosses and much of the humus layer, the humus, feather moss, and slash left after logging create a wetter, more nutrient-rich ground-level microenvironment which allows the feather mosses to continue growing and overtake the reindeer lichens. On the most recently logged sites observed in this study (logged 2 years before observation), however, virtually all of the feather mosses had died. It is seems likely that the sites observed in this study and by Harris (1996) were drier than those observed by Racey *et al.* (1996).

There is concern among wildlife managers, foresters, and others that logged sites may not produce sufficient abundance of reindeer lichens to support woodland caribou in the winter (Racey *et al.,* 1996). Although some trends in reindeer lichen cover with respect to time since logging were found, the long term fate of reindeer lichens on logged sites cannot be predicted from this study, nor is it possible to suggest silvilcultural treatments which will uniformly increase reindeer lichen abundance on logged sites. It is important to note that the trends observed were only for reindeer lichen cover which is not necessarily equivalent to reindeer lichen abundance. It is clear that even in areas which were lichen-rich before logging there is no simple relationship between reindeer lichen abundance and time since logging.

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Demographic characteristics of circumpolar caribou populations: ecotypes, ecological constraints, releases, and population dynamics

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Abstract: Data on the status of caribou (*Rangifer tarandus*) herds throughout the circumpolar region during the last 20 years were obtained from the literature and personal communication with researchers. Information was analysed in relation to ecotype (insular, montane, barren-ground, and woodland/forest), population status (increasing, stable, decreasing), herd size, human impact, and temporal change in number. The data support the conclusions (1) that each ecotype is exposed to different ecological constraints and releases, which influence the demographic characteristics of their populations, (2) that subspecific (genotypic) classification does not explain the demographic characteristics of caribou populations, (3) that insular and montane ecotype populations are relatively stable, (4) that barren-ground ecotype herds are currently experiencing synchronous population growth throughout the circumpolar region and may undergo population cycles, (5) that in North America, the woodland caribou subspecies (genotype) forms the largest barren-ground ecotype herd in the world and is not endangered nor at risk, (6) that populations of woodland/forest ecotypes are declining and threatened throughout the circumpolar region, possibly due to the interaction of human disturbance and predation, and (7) that no relationship exists between herd size and risk of being classified as threatened by researchers.

Key words: caribou, reindeer, ecology, demography, status, subspecies.

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Introduction

Banfield (1961) hypothesized that extant caribou and reindeer evolved from three forms that survived in isolation during the last Wisconsin glaciation. These Holarctic subspecies include; the arctic forms evolving in tundra refugia north of the continental ice-sheets on the Queen Elizabeth Islands and Greenland, the continental tundra forms originating in Beringia (eastern Siberia/Alaska/Yukon), and the woodland or forest forms that survived in temperate refugia, south of the continental ice-sheets.

Reindeer and caribou (*Rangifer tarandus*) have been divided into subspecies based on morphological (Banfield, 1961) and genetic analysis (Røed *et al.*, 1991). The Arctic Island subspecies include the Svalbard reindeer, *R. t. platyrhynchus*, and the Peary caribou, *R. t. pearyi* from Canada. The continental tundra subspecies include, the Eurasian tundra reindeer, *R. t. tarandus*, the Alaska caribou, *R. t. granti*, and the Canadian barren-ground caribou, *R. t. groenlandicus.* Woodland caribou/reindeer subspecies include the Eurasian forest caribou, *R. t. fennicus*, and the American woodland caribou, *R. t. caribou.*

Although these taxonomic designations may reflect evolutionary events; they do not appear to reflect current ecological conditions. In numerous instances, populations of the same subspecies have evolved different demographic and behavioural adaptations, while populations from separate subspecies have evolved similar demographic and behavioural patterns.

For example, in North America populations of the woodland caribou subspecies typically form small isolated herds in winter, but are relatively sedentary and migrate only short distances (50 - 150 km), during the rest of the year (Euler *et al.*, 1976; Seip, 1992). Gravid females most often calve in the spring on islands or in bogs separate from the rest of the population and frequently remain solitary until mid-winter. In contrast, the caribou of the George River herd, Quebec, Canada, which morphologically and genetically belongs to the woodland caribou subspecies, represents the largest caribou herd in the world (Williams & Heard, 1986), migrating thousands of kilometers from boreal forest to open tundra, where most females calve within a three week period (Messier *et al.,* 1988). This behaviour is typical of most barren-ground caribou/reindeer subspecies, which inhabit the Northwest Territories and northern Eurasia.

For wildlife managers dealing with caribou across a wide range of habitats and continents, understanding the ecotype in relation to existing ecological constraints and releases may be more important than the taxonomic relationships between different populations.

For these reasons, the primary objectives of this study were:

(1) to review demographic data on caribou/reindeer populations throughout the circumpolar region,

(2) to analyse the data in relation to ecotype (insular, montane, barren-ground, and woodland/forest), and

(3) to analyse the data in relation to population status (increasing, stable, decreasing), herd size, and temporal change in number.

Table 1. Circumpolar herds classified as insular caribou[1] ecotypes: I = increasing; S = stable; D = declining; TH = threatened.

No.	Name	Trend	Population Estimate	Location
1	Slate Is.	D	250	Ontario
2	Belcher Is.	I	700	NWT
3	Coates Is.	S	2 100	"
4	Southampton Is.	I	1 100	"
5	Banks Is.	S	5 000	"
6	Inglefield Land	I	<100	Greenland
7	Orlik Fiord	I	300	"
8	Nienavik	D,TH	400	"
9	Nusussuaq	I	300	"
10	Qegertassuaq	I	250	"
11	Nassuttuup	D	3 300	"
12	Sismut	D	5 500	"
13	Nuuk	D	10 200	"
14	Qoornoq	S	75	"
15	Ameralek	S	2 000	"
16	Sermilik	S	400	"
17	Qassit	S	300	"
18	Neria	S	500	"
19	Tasiilaq	S	120	"
20	Iceland	S	3 000	Iceland
21	Svalbard Is.	S	4 500	Svalbard Is.
22	Svalbard Is.	S	500	"
23	Svalbard Is.	S	2 500	"
24	Adak Is.	S	300	Russia
25	Novaya Zemlya Is.	I	6 500	"
26	Novosibirsk Is.	I	10 000	"
27	Sakhalin Is.	D,TH	3 000	"

(modified from Williams & Heard, 1986).

[1] Subspecies: #1 *R. t. caribou*; #2 - 4 & 6 - 20 *R. t. groenlandicus*; #5 *R. t. groenlandicus/pearyi*; #21 - 23 *R. t. plathyrhynchus*; #24 - 26 *R. t. tarandus*; and #27 *R. t. fennicus.*

Methods

Data were obtained from the literature (Davis, 1980; Meldgaard, 1986; Williams & Heard, 1986; Messier *et al.,* 1988; Shtele & Pavlov, 1990) and by communicating directly with researchers listed in the Acknowledgments. The data represent estimates of herd size, population status (increasing, stable, decreasing), and temporal change in circumpolar caribou populations during the last 20 years. However, data on some populations, especially from islands in the Canadian High Arctic were not available. Each population was classified as one of four ecotypes (insular, montane, barren-ground, woodland/forest) and analysed separately.

Insular caribou ecotypes were defined as populations restricted to isolated small to medium sized islands (*i.e.* Slate Islands; Coates Island) with physical barriers limiting movement. Primary predators and potential competitors (other ungulates) are most often absent from these systems (Table 1).

Montane caribou ecotypes were defined as populations found in the alpine and boreal zones of mountainous regions with ecological barriers (valleys) often limiting movement to adjacent areas. Primary predators and potential competitors (other ungulates) are most often present in these systems (Table 2).

Barren-ground caribou ecotypes were defined as populations associated with large land areas that migrate annually over relatively long distances between boreal forest and open tundra. Primary predators and potential competitors are present in these systems (Table 3).

Woodland or forest caribou ecotypes were defined as populations associated exclusively with the boreal forest, which are relatively sedentary and often found solitary or in small groups. Primary predators and potential competitors are present in these systems (Table 4).

Ecological releases were defined as parameters that tend to promote population growth and included; large land mass (islands or continents), no or few physical or ecological barriers, opportunity for range expansion, opportunity for forage diversification (boreal and tundra), the absence of potential ungulate competitors (moose and muskoxen), absence of predators (humans, wolves, and bears), and limited human disturbance (logging, roads, urban centres etc.).

In contrast, ecological constraints were defined as parameters that tend to reduce or limit population growth and included; small land mass (small to medium sized islands), physical and ecological barriers (water and valleys), limited opportunity for range expansion, no opportunity for forage diversification, the presence of potential ungulate competitors (moose and muskoxen), the presence of primary predators (humans, wolves, and bears), and high levels of human disturbance (logging, roads, urban centres etc.).

It is recognized that different techniques were employed by researchers throughout the circumpolar region to monitor population numbers and that these data represent broad estimates. However, these data are the best available and the high quality of researchers makes these estimates highly probable. In addition, the authors feel that trends in data are the more important element and not the actual data themselves. The results are discussed in relation to current theories on caribou demography and management and the impacts of ecological releases and constraints.

Results

Insular caribou ecotypes isolated on small to medium islands characteristically experienced physical barriers to migration/dispersal, no opportunities for range expansion, no opportunity for forage diversification, no competition from other ungulates, no or limited predation, and limited human disturbance. Populations ranged in size from 75 to 10 200 animals, with 78% of the herds below 4 000 individuals. Percentage of the populations increasing, stable,

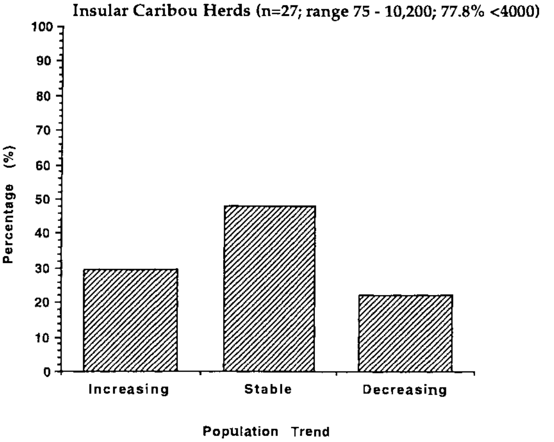


Fig. 1. Percentage of circumpolar caribou/reindeer herds designated as "insular ecotypes" that have been identified as increasing, stable, or decreasing in number.

Table 2. Circumpolar herds classified as montane caribou[1] ecotypes: I = increasing; S = stable; D = declining; TH = threatened.

No.	Name	Trend	Population Estimate	Location
1	Altin	S	500	British Columbia
2	Kaudy-Level	D	800	"
3	Spatizi-Lawyers Pass	D	1 260	"
4	Horse Ranch	I	300	"
5	Pink Mt.	S	300	"
6	Laird Plateau	S	125	"
7	Telkwa	S	40	"
8	Tweedsmuir	I	200	"
9	Itcha-Iiqachuz	I	700	"
10	Caribou Mts.	D	1 500	"
11	Selkirk Mts.	S	30	"
12	Hart River	S	1 200	Yukon
13	Little Rancheria	D,TH	450	"
14	Carcross	S	600	"
15	Aishihik	S	1 500	"
16	Burwash	S	400	"
17	Big River	D	750	Alaska
18	Delta	S	8 000	"
19	Denali	S	2 100	"
20	Kenai Lowland	S	85	"
21	Kenai Mts.	S	300	"
22	Mentasta	S	3 000	"
23	Mulchatna	I	33 000	"
24	Welchina	I	25 000	"
25	Sunshine	D	750	"
26	Setesdal Vesthei	S	2 700	Norway
27	Saudafjella	S	75	"
28	Setesdal Austhei	S	2 000	"
29	Hardangervidda	S	20 000	"
30	Blefjell	S	130	"
31	Hallingskarvet	S	2 500	"
32	Raudafjell	S	30	"
33	Fjellheimen	S	850	"
34	Brattfjell-Vindeggen	S	600	"
35	Vest-Jotunheimen	S	720	"
36	Ottadalen Sor	S	460	"
37	Ottadalen Nord	S	3 100	"
38	Fordefjella	S	100	"
39	Sunnfjord	S	600	"
40	Svartebotnen	S	130	"
41	Snohetta	S	2 800	"
42	Rondane	S	1 200	"
43	Solnkletten	S	530	"
44	Forelhogna	S	1 800	"
45	Knutsho	S	914	"
46	Tolga Ostfjell	S	200	"
47	Rendalen	S	700	"
48	Altai-Sayan Mts.	S	10 000	Russia
49	W. Okhotsk	S	16 000	"
50	Kamchatka	S,TH	4 000	"

(modified from Williams & Heard, 1986).

[1] Subspecies: #1 - 11, 13 *R. t. caribou*; #12, 14 - 25 *R. t. granti*; #26 - 47 *R. t. tarandus*; #48 - 50 *R. t. fennicus*.

Table 3. Circumpolar herds classified as barren-ground caribou[1] ecotypes: I = increasing; S = stable; D = declining; TH = threatened.

No.	Name	Trend	Population Estimate	Location	
1	Avalon	I	5 000	Newfoundland	
2	Middle Ridge	I	8 000	"	
3	Pot Hill	I	450	"	
4	Sandy Lake	I	200	"	
5	Grey River	I	4 500	"	
6	Gaff Topsails	I	1 500	"	
7	Buchans	I	2 000	"	
8	LaPoile	I	8 500	"	
9	Hampden	I	400	"	
10	Humber	I	450	"	
11	N. Peninsula	I	1 500	"	
12	Mealy Mt.	I	700	Labrador	
13	White Bear L.	D,TH	<100	"	
14	Torngat Mt.	I	7 500	"	
15	Red Wine Mt.	S	750	"	
16	George River	I	700 000	Quebec	
17	Leaf River	I	70 000	"	
18	N.E. Mainland	I	130 000	NWT	
19	Kaminuriak	450 000	"		
20	Beverley	I	420 000	"	
21	Bathurst		I	450 000	"
22	Bluenose	S	80 000	"	
23	Finlayson	I	2 500	Yukon	
24	Central Arctic	I	12 500	Alaska	
25	Fortymile	I	1 600	"	
26	Porcupine	I	150 000	"	
27	W. Arctic	I	200 000	"	
28	Alaska Peninsula	I	30 000	"	
29	Bonnet Plume	I	5 000	"	
30	W. Kola Peninsula	I, TH	230	Russia	
31	E. Kola Peninsula		I,TH	2 700"	
32	Karelia	S	11 000	"	
33	Archangel Forest	S,	14 000	"	
34	Archangel Tundra		S,TH	4 000"	
35	Komi Forest	S	4 000	"	
36	Yamal Tundra	S,TH	2 000	"	
37	Nadym-Pur River		D,TH	5 000"	
38	Taimyr	I	530 000	"	
39	Bulun	S	60 000	"	
40	Yana-Indigir River	S	100 000	"	
41	Sundrun		I	30 000	"
42	Chukotsk Tundra	S	5 500	"	
43	Chukotsk Forest	I	4 000	"	

(modified from Williams & Heard, 1986).

[1] Subspecies: #1 - 17 *R. t. caribou*; #18 - 23 *R. t. groenlandicus*; #24 - 29 *R. t.granti*; #30 - 43 *R. t. tarandus*.

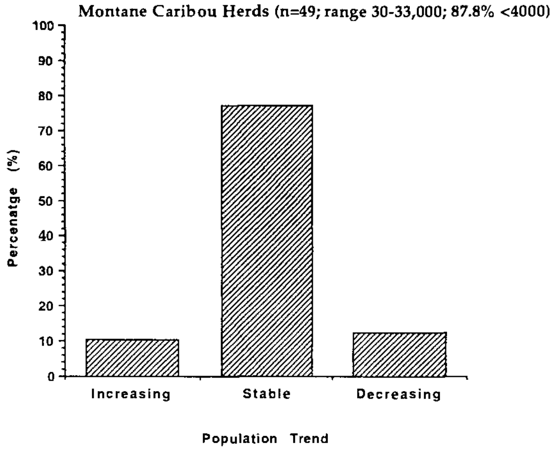


Fig. 2. Percentage of circumpolar caribou/reindeer herds designared as "montane ecotypes" that have been identified as increasing, stable, or decreasing in number.

and decreasing were 30, 48, and 22, respectively (Fig. 1).

Montane caribou ecotypes confined to the upper zones of mountains characteristically experienced ecological barriers to migration and dispersal, limited opportunities for range expansion, opportunities for forage diversification (alpine and boreal zones), potential competition from other ungulates, exposure to predators, and limited human disturbance. Populations ranged in size from 30 to 33 000 animals, with 89% of the herds below 4 000 individuals. Percentage of the populations increasing, stable, and decreasing were 10, 77, and 13, respectively (Fig. 2).

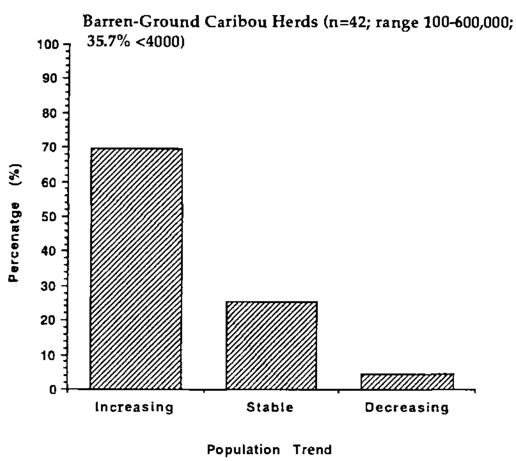


Fig. 3. Percentage of circumpolar caribou/reindeer herds designated as "barren-ground ecotypes" that have been identified as increasing, stable, or decreasing in number.

Barren-ground caribou ecotypes found on large islands or continents characteristically experienced no ecological or physical barriers, opportunities for range expansion, opportunities for forage diversification, competition from other ungulates, exposure to predators, and limited human disturbance. Populations ranged in size from 100 to over 700 000 animals, with 36% of the herds below 4 000 individuals. Percentage of populations increasing, stable, and decreasing were 70, 26, and 5, respectively (Fig. 3).

Woodland/forest caribou ecotypes limited to the boreal forest biome characteristically experienced no ecological or physical barriers, opportunities for range expansion, no opportunities for forage diversification (boreal habitat only), potential competition from other ungulates, exposure to predators, and

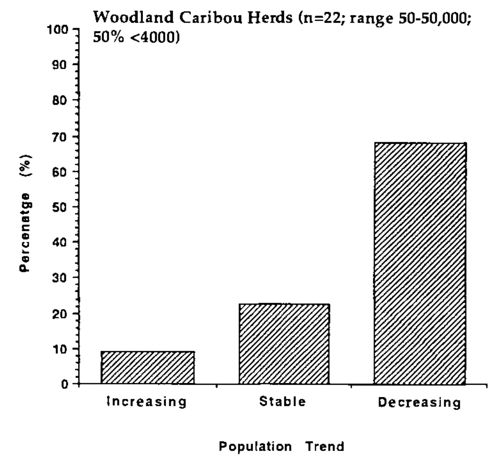


Fig. 4. Percentage of circumpolar caribou/reindeer herds designated as "woodland or forest ecotypes" that have been identified as increasing, stable, or decreasing in number.

high levels of human disturbance. Populations ranged in size from 50 to 50 000 animals, with 50% of the herds below 4 000 individuals. Percentage of the populations increasing, stable, and decreasing were 9, 23, and 68, respectively (Fig. 4).

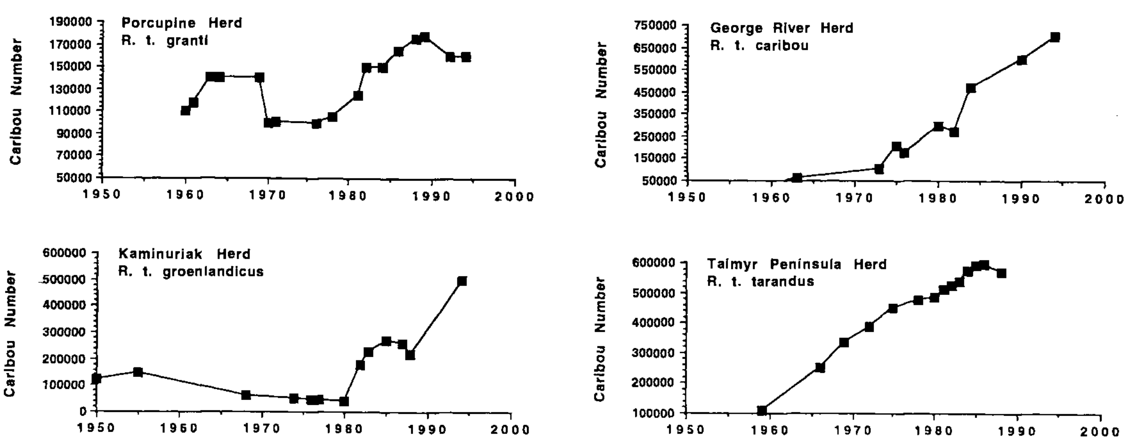
Analysis of the percentage of populations of each ecotype classified as threatened by researchers indicated that herds of the montane ecotype were least threatened and herds of the woodland or forest ecotype were most threatened (montane 8%; barren-ground 14%; insular 26%; woodland 27%). No correlation between percenatge of herds below 4 000 animals and percentage of herds classified as threatened was found (r=0.31; P>0.05).

Table 4. Circumpolar herds classified as woodland caribou[1] ecotypes: I = increasing; S = stable; D = declining; TH = threatened.

No.	Name	Trend	Population Estimate	Location
1	Lac Joseph	D,TH	<600	Quebec
2	Gaspesie Park	D	250	"
3	North Shore	D	2 000	"
4	Grand Jardins	I	67	"
5	Val d'Or	D,TH	50	"
6	James Bay	S	4 500	"
7	N.E. Ontario	D	4 500	Ontario
8	N. Lake Superior	D	<200	"
9	Manitoba	D	5 000	Manitoba
10	Saskatchewan	D,TH	2 500	Saskatchewan
11	Alberta	D,TH	2 250	Alberta
12	Finnish Forest	I	600	Finland
13	Konda-Sosva River	D	7 000	Russia
14	W. Siberia Forest	S,TH	5 000	"
15	Evenkiysk	D	50 000	"
16	Upper Angara River	D	10 000	"
17	Irkutsk	S	20 000	"
18	E. Baikal	S	8 000	"
19	Amur	D	3 000	"
20	Lena-Vilyui Rivers	D	20 000	"
21	Yukutsk Mt. Taiga	D	30 000	"
22	Taxinganling	S	980	China

(modified from Williams & Heard, 1986).

[1] Subspecies: #1 - 11 *R. t. caribou*; #12, 15, 20, 21 *R. t. fennicus/tarandus*; #13, 16, 19 *R. t. tarandus*.



Figs. 5–8. Comparison of population growth in 4 barren-ground ecotype herds during the past 5 decades.

In addition, comparison of population growth during the past 5 decades in 4 herds classified as barren-ground ecotypes (Figs. 5 - 8) indicated that herds grew synchronously throughout the circumpolar region and reached high population levels in the 1990s, although all represent different subspecies and genotypes, as defined by Banfield (1961) and Røed *et al.* (1991).

Table 5. A summary of ecological constraints (-) and releases (+) impacting the four caribou ecotypes.

Insular Caribou - confined to small and medium sized islands -
(1) experience physical barriers to migration/dispersal (-),
(2) no opportunities for range expansion (-),
(3) no opportunities for forage diversification (-),
(4) commonly no competition from other ungulates (+),
(5) limited or no predation (+),
(6) limited human disturbance (+).

Montane Caribou - confined to mountain tops -
(1) experience some ecological resistance to migration/dispersal (+/-),
(2) fewer opportunities for range expansion (+/-),
(3) opportunities for forage diversification (+),
(4) potential competition from other ungulates (-),
(5) exposure to predators (-),
(6) limited human disturbance (+)

Barren-ground Caribou - occupying large islands or continents -
(1) experience no or few barriers to migration/dispersal (+),
(2) range expansion opportunities available (+),
(3) opportunities for forage diversification (+),
(4) potential competition from other ungulates (-),
(5) exposure to predators (-),
(6) limited human disturbance (+).

Woodland/Forest Caribou - occupying large islands or continents -
(1) experience no or few barriers to migration/dispersal (+),
(2) opportunities for range expansion (+),
(3) no or few opportunities for forage diversification (-),
(4) potential competition from other ungulates (-),
(5) exposure to predators (-),
(6) high levels human disturbance (-).

Discussion

Insular ecotypes confined to isolated small and medium sized islands characteristically experience physical barriers to migration and dispersal; however, movement across ice/water barriers does occur on occasion (Euler *et al.,* 1976; R. Mulders, pers. comm.). Competition from other ungulates, such as moose or muskoxen is frequently absent and predation by primary predators is most often absent. In addition, human disturbances are most frequently absent or limited in these habitats. Typical examples of these types of ecosystems are the Slate Islands, Ontario and Coates Island, Northwest Territories, Canada. Both these sites represent one ungulate systems (caribou) with no competition or interactive impact from other ungulate species. Primary predators are or have been absent in these systems for long periods of time. Wolves have only arrived on the Slate Islands during the past few years and Inuit from Coral Harbour occasionally hunt on Coates Island. In addition, range expansion is not an option and nor is forage diversification, as island systems are usually limited to one relatively homogeneous habitat type (Coates Island-tundra/ Slate Islands -boreal forest). Evidence suggests that the primary dynamic controlling insular populations and their demographics is forage exploitation (Klein, 1968; Gates *et al.,* 1986). Forage depletion and habitat degradation have been identified as primary reasons for caribou population declines on the Slate Islands (W. J. Dalton, pers. comm.) and Coates Island, (Gates *et al.,* 1986). Populations of insular caribou ranged in size from 75 to 10 200 animals, with 78% of the herds below 4000 individuals. Percentage of the populations increasing, stable, and decreasing were 30, 48, and 22%, respectively (Fig. 1). These data indicate that approximately half of the insular populations are stable, while the other fifty percent are increasing or declining. Similar demographic characteristics have been found in island populations of many mammalian species (Bonner, 1958; Mech, 1966; Klein, 1968; Krebs & Myers, 1974; Tamarin, 1977) and this type of non-cyclic, relatively stable population pattern appears to be typical of mammal populations in isolated systems. As 78% of these populations are increasing or stable, it can be concluded that insular caribou ecotype populations are relatively healthy at this time.

Montane ecotypes confined to the upper floristic zones on mountains frequently experienced ecological barriers (valleys) to migration and dispersal and range expansion is often limited. However, movement between mountain ranges does occur and forage diversification is an option in these populations. Potential competition from other ungulates, such as moose and predation by primary predators, such as wolves and bears typically impact in these populations (Seip, 1992). Human disturbances are usually limited to more southern populations in these habitats (Davis, 1980; Seip, 1992). Typical examples of these types of populations are the Wells Gray herd in southeastern British Columbia (Seip, 1992) and the Nelchina herd in Alaska (Eberhardt & Pitcher, 1992). Both these sites represent two ungulate systems (caribou and moose) and primary predators (wolves and bears) represent significant mortalities on these herds. Range expansion is generally limited due to ecological barriers; however, forage diversification does occur, as montane systems provide both alpine and boreal habitats, which can support caribou. In contrast to insular caribou populations, the primary dynamic controlling montane populations and their demographics appears to be predation and the interactive impact of other ungulate species (Seip, 1992). Forage exploitation and habitat degradation have not been identified as reasons for caribou population decline in montane regions (Davis, 1980); however, increased human activity (ie. logging) appears to be having some influence, by increasing moose numbers and caribou susceptibility to wolf predation (Bergerud & Elliot, 1986; Seip, 1992). Populations of montane ecotypes ranged in size from 30 to 33 000 animals, with 88% of the herds below 4000 individuals. Percentage of the populations increasing, stable, and decreasing were 10, 77, and 13, respectively (Fig. 2). These data indicate that montane caribou populations are in general more stable than insular populations, although they both have similar demographic attributes, common to isolated populations. The increased stability associated with montane ecotype populations appears to be related to (1) increased forage diversity, and (2) predation by primary predators, which minimizes the chance that numbers will exceed the catrying capacity of the range. As 88% of these populations are increasing or stable, it can be concluded that montane ecotype populations are healthy, although the majority of these herds are relatively small in number.

Barren-ground ecotypes found on large islands or continents experienced long seasonal migrations from boreal forest to open tundra, have few physical or ecological barriers to movement and disperse to ranges of other populations (Messier *et al.,* 1988; D. C. Heard, pers, comm.; R. Mulders, pers. comm.). At minimum, all of these ecosystems represent two ungulate systems, with moose in the boreal forest and muskoxen in the open tundra. This results in the potential for competition and the interactive impact of other ungulate species on predation (Bergerud & Elliot, 1986; Seip, 1992). Predation by primary predators, such as humans, wolves and bears is common in these populations (Parker, 1972; Hillis & Mallory, 1989; Lamothe & Parker, 1989; Lamothe, 1991). Human disturbances, such as logging, roads, and urban centres are usually limited (F.F.M, pers. obs.). Typical examples of these types of populations are the Kaminuriak herd found along the west coast of Hudson Bay, N.W.T. (Parker, 1972) and the George River herd found in northern Quebec (Messier *et al.,* 1988). Both these locations support two ungulate systems and primary predators (humans, wolves, and bears) represent constant mortalities on these populations. Range expansion has occurred during the last 40 years in both herds and forage diversification occurs (Heard & Calef, 1986; Messier *et al.,* 1988). The fact that these herds have opportunities for ecological release through range expansion and forage diversification may explain, in part, the massive increase in numbers found throughout the circumpolar region. In contrast, populations of insular and montane ecotypes seldom attain ecological release and remain relatively stable, due to physical and ecological barriers, which limit population size. Forage exploitation and habitat degradation have been suggested as major limiting factors effecting barren-ground ecotype population decline, while predation and human activity appear to have minimal impact during periods of population increase (Messier *et al.,* 1988; R. Mulders, pers. comm.).

Populations of barren-ground caribou ecotypes ranged in size from 100 to over 700 000 animals, with 36% of the herds below 4000 individuals. Percentage of the populations increasing, stable, and decreasing were 70, 26, and 5, respectively (Fig. 3). These data indicate that most barren-ground ecotype populations are increasing synchronously throughout the circumpolar region, in contrast to the populations of other ecotypes. These changes may represent synchronous population cycles (Meldgaard, 1986), as has been found in many other mammal species (Mallory, 1987). As 95% of these populations are increasing or stable and the few declining populations have been overharvested, it can be concluded that populations of barren-ground ecotypes are very healthy, at this point in time. However, these populations will probably decline during the next decade, due to habitat exploitation and forage depletion.

Populations of woodland or forest ecotypes confined to the boreal forest, characteristically experience no limit to range expansion, no opportunities for forage diversification, potential competition from other ungulates, exposure to predators (humans, wolves, and bears), and relatively higher levels of human disturbance. Although few barriers to movement appear to exist in this habitat, woodland/forest ecotypes are relatively sedentary, commonly dispersing only short distances and returning to the same ranges annually (Edmonds, 1988; W. J. Dalton, pers. comm.). With few exceptions, these ecotypes are part of a two ungulate system, which results in potential competition and the interactive impact on predation of other ungulate species (Bergerud & Elliot, 1986; Seip, 1992). Predation by primary predators, such as humans, wolves, and bears is common in these populations (Edmonds, 1988; Seip, 1992) and fire and human disturbances, such as logging, roads, and urban development maintain large tracts of early successional forest ideal for moose, especially in the southern parts of the range (Bergerud, 1974; Jackson *et al.,* 1991).

Typical examples of these populations are the woodland caribou herds in west central Alberta (Edmonds, 1988) and the Quesnel Lake herd in southeastern British Columbia (Seip, 1992). Both these sites support two ungulate systems (caribou and moose) and primary predators (wolves and bears) represent significant mortalities on these populations (Edmonds, 1988). Range expansion is an option; however, forage diversification does not occur, as only boreal habitats are available. The primary dynamic controlling the demographics of woodland/forest populations appears to be predation and habitat loss due to human disturbance (Bergerud & Elliot, 1986; Seip, 1992). While woodland caribou have not been shown to over graze ranges in boreal habitats, habitat loss due to fire and logging appear to result in caribou population decline. Early successional boreal forest appears to increase moose numbers and caribou susceptibility to wolf predation (Bergerud & Elliot, 1986; Seip, 1992). Hunting by humans has historically impacted this ecotype significantly (Bergerud, 1974).

Populations of woodland/forest ecotypes ranged in size from 50 to 50 000 animals, with 50% of the herds below 4 000 individuals. Percentage of the populations increasing, stable, and decreasing were 9, 23, and 68, respectively (Fig. 4). As only 32% of these populations are increasing or stable, it can be concluded that populations of woodland/forest ecotypes are vulnerable and should receive intensive management effort at this time.

A summary of ecological contraints and releases impacting the four caribou ecotypes is presented in Table 5. These data illustrate that in the two ecotypes with relatively stable population patterns (insular & montane), equal numbers of positive (+) and negative (-) ecological factors are active. In barren-ground ecotype populations, 4 ecological parameters are positive (+) and 2 are negative (-) providing opportunity for ecological release and population growth until carrying capacity and new ecological contraints are reached. In contrast, in woodland/forest ecotype populations, 2 ecological parameters are positive (+) and 4 are negative (-) resulting in a general decline and loss of populations.

The data support the conclusions (1) that each ecotype is exposed to different ecological constraints and releases, which influence the demographic characteristics of their populations (2) that subspecific (genotypic) classification does not explain the demographic characteristics of caribou populations, (3) that insular and montane ecotype populations are relatively stable, (4) that barren-ground ecotype herds are currently experiencing synchronous population growth throughout the circumpolar region and may undergo population cycles, (5) that in North America, the woodland caribou subspecies (genotype) forms the largest barren-ground ecotype herd in the world and is not endangered or at risk, (6) that populations of woodland or forest ecotypes are declining and threatened throughout the circumpolar region, possibly due to the interaction of human disturbance and predation, and (7) that no relationship exists between herd size and risk of being classified as threatened by researchers.

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Development of a preliminary habitat assessment and planning tool for mountain caribou in southeast British Columbia

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Abstract: The Purcell Mountains of southeast British Columbia support a population of mountain caribou near the southernmost extension of their range. This ecotype is dependent upon late-successional forests, largely because such stands provide arboreal lichen for winter forage. Recent provincial forest practices legislation and land-use planning initiatives have provided the impetus for developing an interim caribou habitat assessment model for use as a planning tool. We applied an HSI (habitat suitability index) model developed for a nearby population as a testable hypothesis of caribou habitat selection in the southern Purcells. In a srudy area of about 6000 km^2, 512 radiolocarions were obtained for 22 animals from 1993 through 1995. Seasonal selectivity was assessed for the following model variables: elevation, slope, habitat type/current cover type, overstory size class, canopy closure, and age of dominant overstory. Caribou were most selective for stand age, which the model also defined as the greatest determinant of habitat suitability. However, we did not judge overall model output to be an adequate predictor of habitat selection by southern Purcell caribou. Seasonal ratings for each variable were therefore modified to better reflect selection patterns by animals in this study, and subjectively adjusted to ensure that potentially limiting habitat types were rated highly. An evaluation of the adjusted model established its efficacy as an interim decision-support tool. Selection analyses of spatial habitat distribution levels indicated a preference by caribou for landscapes with at least 40% suitable habitat per 250 ha and per 5000 ha. From this, it is apparent that suitable habitat is highly fragmented in this study area.

Key words: GIS, Habitat Suitability Index, HSI, Purcell Mountains, model, landscape, stand.

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Introduction

The ecotype of woodland caribou found in wet coniferous forests of southeastern British Columbia is referred to as mountain caribou (Stevenson & Hatler, 1985). This ecotype is strongly associated with late-successional forests (Simpson *et al.*, 1994; Stevenson *et al.* 1994), largely because such stands provide arboreal lichen for winter forage (Freddy, 1973; Antifeau, 1987; Simpson & Woods, 1987; Rominger & Oldemeyer, 1989; Seip, 1990; Seip, 1992). These habitats also tend to be associated with high timber value.

The southern Purcell Mountains support a remnant population of less than 100 mountain caribou (Kinley, unpubl. data) occurring near the southern limit of their range. Caribou are provincially listed as "vulnerable", and provincial forest practices legislation directs that their requirements be integrated with forest management. However, little ecological information exists for the southern Purcell population from which to develop prescriptive guidelines at strategic or operational planning levels. A long-term research program established in 1992 to improve baseline information is still underway. However, given mounting demands on this landbase and the impetus of a regional land-use planning process, an interim tool was required to integrate the best available knowledge of caribou requirements with ongoing planning initiatives in a timely fashion. In this paper we present the evaluation and adaptation of an existing mountain caribou Habitat Suitability Index (HSI) model for a nearby population (Allen-Johnson 1993), and its application at both stand and landscape levels.

Study area

The study area encompasses roughly 6000 km^2 near the southern end of the Purcell mountain range of southeastern B.C. (Fig. 1). This area is coincident with the known distribution of the southern Purcell montain caribou population, and also defines the area searched in the process of capturing study animals. Elevations range from 530 to 2850 m. Vegetation patterns are affected by elevation and a west to east gradient of decreasing precipitation. Climax communities are dominated by western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) in moist areas at lower elevations, Douglas-fir (*Pseudotsuga menziesii*) in dry areas at low elevation, and Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at mid to high elevations, although fire-successional stands of lodgepole pine (*Pinus contorta*) are common throughout. Alpine tundra occurs at the highest elevations.

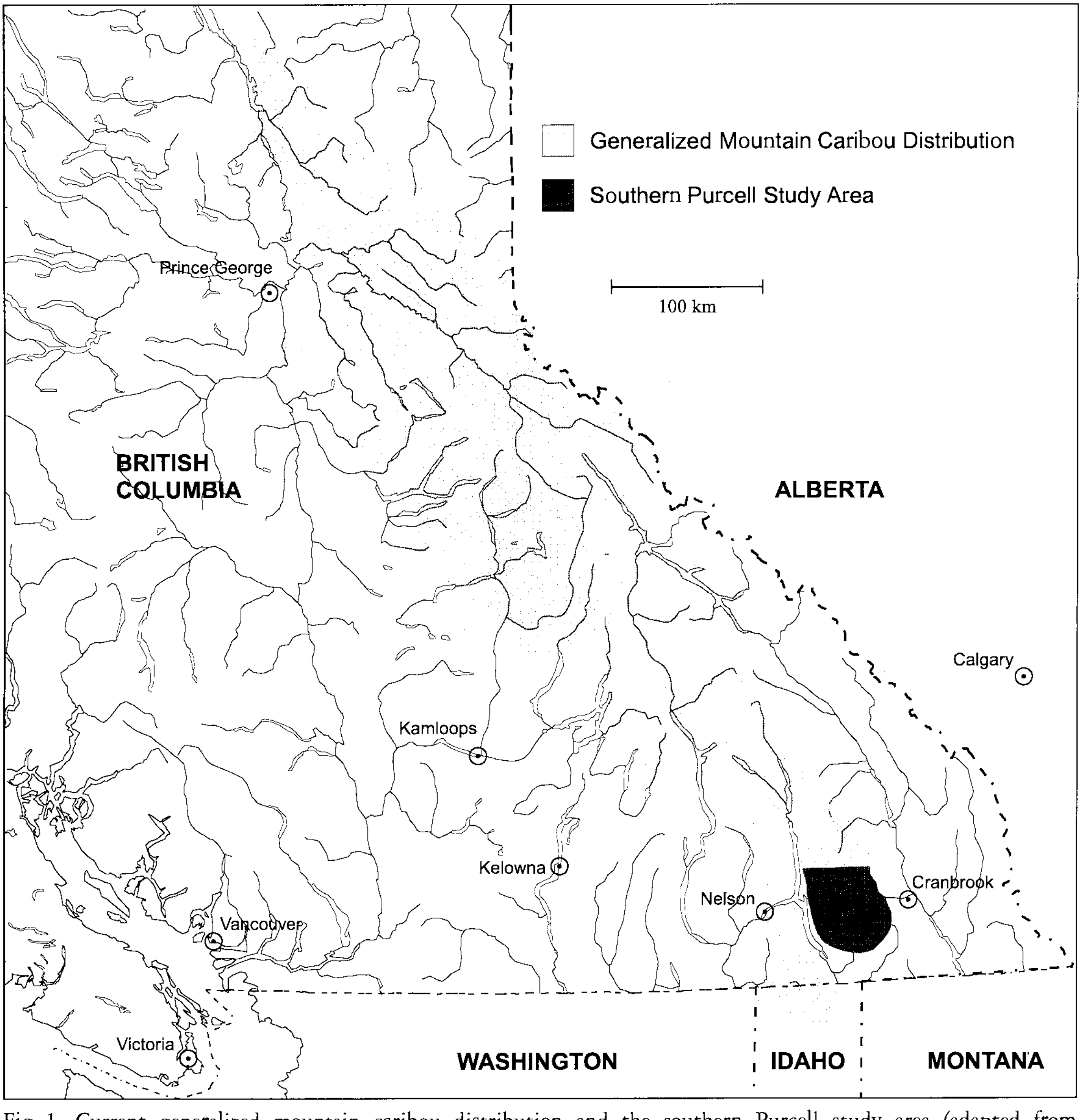


Fig. 1. Current generalized mountain caribou distribution and the southern Purcell study area (adapted from Stevenson & Hatler, 1985).

Methods

Data

Between 1993 and 1995, 22 caribou were radiocollared and monitored using standard aircraft telemetry techniques (White & Garrott, 1990). From semi-monthly sampling, 512 radiolocations were obtained and referenced to the nearest 100 m. (Because the majority of radiolocations were associated with visual sightings, they are considered acccurate to within 100 m). Data points from animals traveling together were deleted such that we could be certain that all radiolocations represented independent habitat choices.

A digital habitat database was assembled for the study area. Polygon data of forest cover attributes as well as topographic and planimetric data originally mapped at 1:20 000 scale were compiled as GIS raster coverages with a resolution of 100 m. From this, model variables were derived.

Analyses

An unvalidated HSI model was developed by Allen-Johnson (1993) for the Idaho Panhandle National Forest (Fig. 2). This area supports a herd of mountain caribou in the Selkirk Mountains, approximately 50 km from the Purcell study area. Using a GIS (Eastman, 1993), we applied this Idaho model as a testable hypothesis of habitat selection by southern Purcell mountain caribou. For each of four caribou seasons (spring, April 1 to June 15; summer, June 16 to October 22; early winter, October 23 to January 15; late winter, January 16 to March 31), model performance was evaluated by comparing observed caribou selection to four suitability classes as predicted by the Idaho model. To improve our understanding of mountain caribou habitat relationships, and to provide a basis for model improvement, we also analyzed caribou selection for each of the six model variables independently.

Data were pooled among years and individual study animals. The land area considered to be collectively available to all study animals was determined as the composite 100% minimum convex polygon of all radiolocations. For each analysis, a *G*-statistic (Sokal & Rohlf, 1981) tested the goodness of fit of habitat use versus availability for pooled radiolocations, and indicated whether selection was evident considering all habitat classes simultaneously. Habitat classes with expected use values of less than three were excluded from analysis (ibid.). Confidence intervals for "selection" or "avoidance" of each habitat class were then established using Bonferroni *Z*-statistics (Neu *et al.*, 1974; Byers *et al.*, 1984).

While retaining the original model structure, we adjusted Idaho HSI coefficients to improve model performance with respect to observed habitat selection by southern Purcell caribou. At the same time, we maintained relatively high ratings for habitats that, although were not selected according to our limited data, have been established by other research as being at least seasonally important. Thus, although our adjustments do utilize habitat selection results for each model variable, they are largely subjective.

Adjustment of model coefficients

Based on past research (Simpson *et al.*, 1994; Stevenson *et al* , 1994), we felt that the Idaho HSI model included macro-habitat variables that contribute to stand suitability for mountain caribou. We therefore restricted our analyses to only these variables. Also, because we employed univariate analysis techniques, we chose not to modify the original algebraic structure of the model.

Recognizing the limitations to direct inference of habitat requirements from selection analyses (Manly *et al* , 1993), we adopted a four-stage approach to assigning suitability coefficients. Given the potential consequences of disregarding important habitats due to a limited data set, our methods were intentionally conservative from the perspective of caribou conservation. In the first stage, we assumed that the importance of a habitat attribute is proportional to its observed degree of selection by caribou as indicated by its selection ratio (use/availability). For "avoided" habitat classes, selection ratios (0.0 - 0.99) were stratified into five groups and assigned coefficients from 0.0 to 0.4. For "selected" habitat classes, we identified the point where the array of selection ratios began to increase exponentially (>3.2), and selection ratios above this point were assigned a coefficient of 1.0. The range of remaining selection

V_1 stand elevation
V_2 stand slope
V_3 stand habitat type and current cover type
V_4 stand overstory size class
V_5 percent stand canopy closure
V_6 age of dominant stand overstory

$$\text{Stand HSI} = (V_1^2 \times V_2 \times V_3 \times V_4 \times V_5)^{1/6} \times V_6$$

Fig. 2. HSI model variables and equarion structure.

ratios (1.01 - 3.2) was stratified and assigned coefficients from 0.6 to 1.0. In the second stage, we assigned additional suitability coefficients based on the level of significance at which each variable class was either "selected" or "avoided". This allowed for the effect of sample size and the number of habitat classes within each variable to be accounted for in the interpretation of selection ratios. Selected habitats were rated as 1.0, 0.9, 0.8, 0.7 or 0.6 depending on whether selection occurred at the 95, 75, 50, 25 or 5% confidence levels respectively. Following these same confidence levels, avoided habitats were assigned ratings from 0.0 to 0.4. In both cases, confidence levels of < 5% were assigned ratings of 0.5. In the third stage, we compared these two suitability ratings for each habitat class and, where discrepancies occurred, adopted that which was closest to 0.5. To ensure that trends in suitability coefficients for each model variable were biologically meaningful, we reviewed the assigned ratings for each variable as the fourth stage. Given the limited time over which our data were collected and the variability in habitat use that may occur among years, we applied subjective adjustments to ensure that coefficients of certain habitat elements, found by other studies to be important and potentially limiting, were not underrated.

To evaluate the overall veracity of the adjusted model, HSI output was stratified into four suitability classes in the GIS, and caribou selection was assessed using the above described univariate techniques.

Landscape-level habitat distribution analysis
Mountain caribou populations appear to be influenced by the availability of suitable habitat over large areas, which may be a function of predator avoidance (Stevenson *et al.*, 1994). We therefore assessed caribou selection for habitat distributions at two broad scales. Because it is a scale commonly used in local wildlife habitat management guidelines, we initially assessed caribou selection for the proportion of suitable habitat distributed per 250 ha. We also analyzed caribou selection for the proportion of habitat distributed per 5000 ha, roughly corresponding to the average area of a core caribou home range in this study area. (Mean 75% harmonic contour home range size for 12 study animals (4M, 8F) with a minimum 24 locations sampled over at least one year = 4869 ha (Kinley & Apps, unpubl. data)).

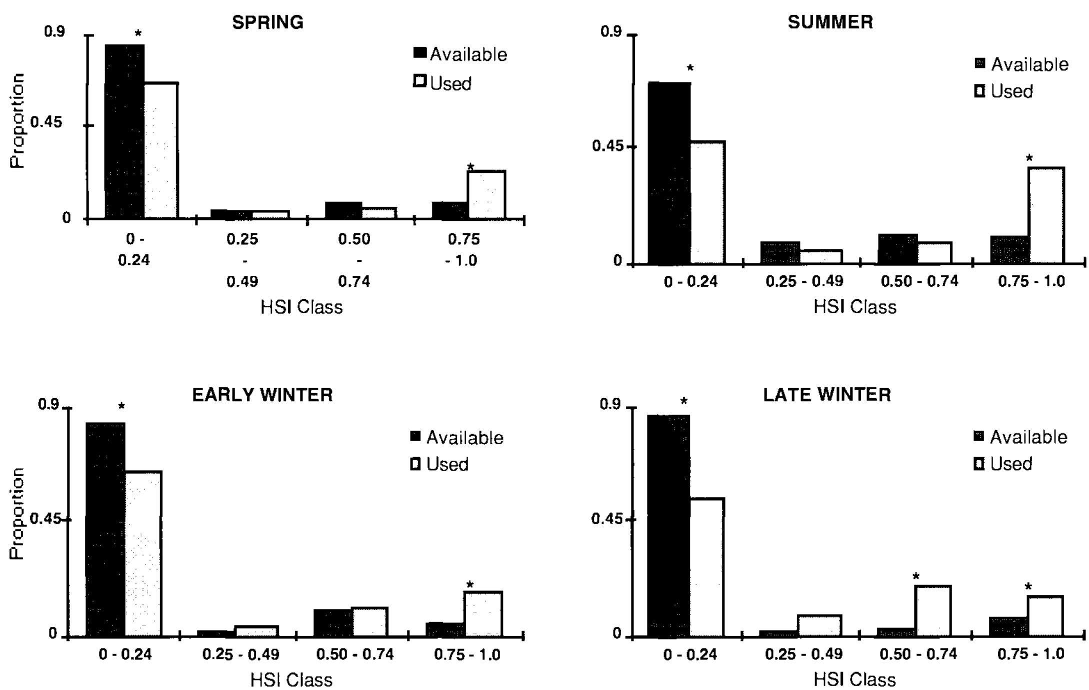


Fig. 3. Caribou selection for habitat suitability classes as defined by the Idaho HSI model. * indicates significance ($P < 0.05$) based on Bonferroni Z-statistics.

Table 1. *G*-test results for each model variable by season. Selection is evident at the probability levels indicated.

Season	Var.	G-Stat.	d.f.	*P*<
Spring	V_1	79.4	9	0.001
	V_2	14.8	3	0.005
	V_3	74.9	7	0.001
	V_4	99.0	4	0.001
	V_5	78.0	4	0.001
	V_6	168.6	2	0.001
Summer	V_1	79.7	9	0.001
	V_2	20.3	3	0.001
	V_3	69.3	7	0.001
	V_4	90.0	4	0.001
	V_5	49.6	4	0.001
	V_6	103.7	2	0.001
E. Winter	V_1	13.7	9	0.25
	V_2	7.4	3	0.10
	V_3	40.9	6	0.001
	V_4	27.5	3	0.001
	V_5	18.0	4	0.001
	V_6	22.4	2	0.001
L. Winter	V_1	50.5	9	0.001
	V_2	8.8	3	0.05
	V_3	38.1	7	0.001
	V_4	85.0	4	0.001
	V_5	40.5	4	0.001
	V_6	33.8	2	0.001

This may also approximate the broadest level at which individual caribou perceive the larger landscape.

For this landscape-level analysis, "suitable habitat" was defined as those HSI classes selected by caribou. A GIS "moving window" procedure was then carried out to determine habitat distribution per 250 ha and per 5000 ha. That is, a value indicating the proportion of suitable habitat in the surrounding landscape (either 250 ha or 5000 ha) was assigned to each 100 m-pixel. The resulting maps were then stratified into six habitat distribution classes and use/availability analyses carried out as described above.

Results

Stand-level suitability

Based on results of caribou selection for associated HSI classes (Fig. 3), we judged the original Idaho model to be inadequate as a useful planning tool for our study area. Thus, we assessed caribou selection for each model variable independently. Within each season, results indicate that caribou are selective for model variables and habitat classes within each (Table 1 & Fig. 4), with the greatest selectivity being associated with age class. New suitability coefficients determined for each model variable are presented in Table 2. Evaluation of the modified HSI model confirms its improved performance relative to our data (Fig. 5). Selection is evident for HSI ratings greater than 0.25, which are therefore considered to provide "suitable" habitat.

Landscape-level suitability

Caribou appeared to be selective for both 250 ha and 5000 ha habitat distribution classes (Fig. 6). In both cases, selection began to occur where the distribution of suitable habitat in the surrounding landscape achieved 30 - 50%.

Discussion

Results of analysing HSI variables were generally consistent with our understanding of mountain caribou ecology, as indicated by research carried out on other populations (Simpson *et al.*, 1994; Stevenson *et al.*, 1994). This was particularly true with respect to caribou selection for subalpine fir and Engelmann spruce stands dominated by old, large-diameter trees. However, we did observe several anomalies. Our data indicated an avoidance of moist, low-elevation forests of western redcedar and western hemlock on gentle slopes, even in early winter and spring when such habitats are often heavily used by other mountain caribou populations. Conversely, there was general selection for lodgepole pine-dominated stands, particularly in early winter, which has not been previously reported for this ecotype. These differences may relate to the location of this study area at the extreme southeast corner of mountain caribou distribution, an area with a drier climate than elsewhere in mountain caribou range. Thus, there may have historically been less western redcedar and western hemlock, and more fire-successional lodgepole pine available than elsewhere in mountain caribou range, causing animals in the southern Purcells to adapt to slightly different habitats. Alternatively, the observed pattern may occur in years with near-normal winter weather, but in years of more inclement weather conditions, habitat use may be similar to patterns found elsewhere in their range. A third possibility is that habitat disturbances, such as wildfires, logging, road construc-

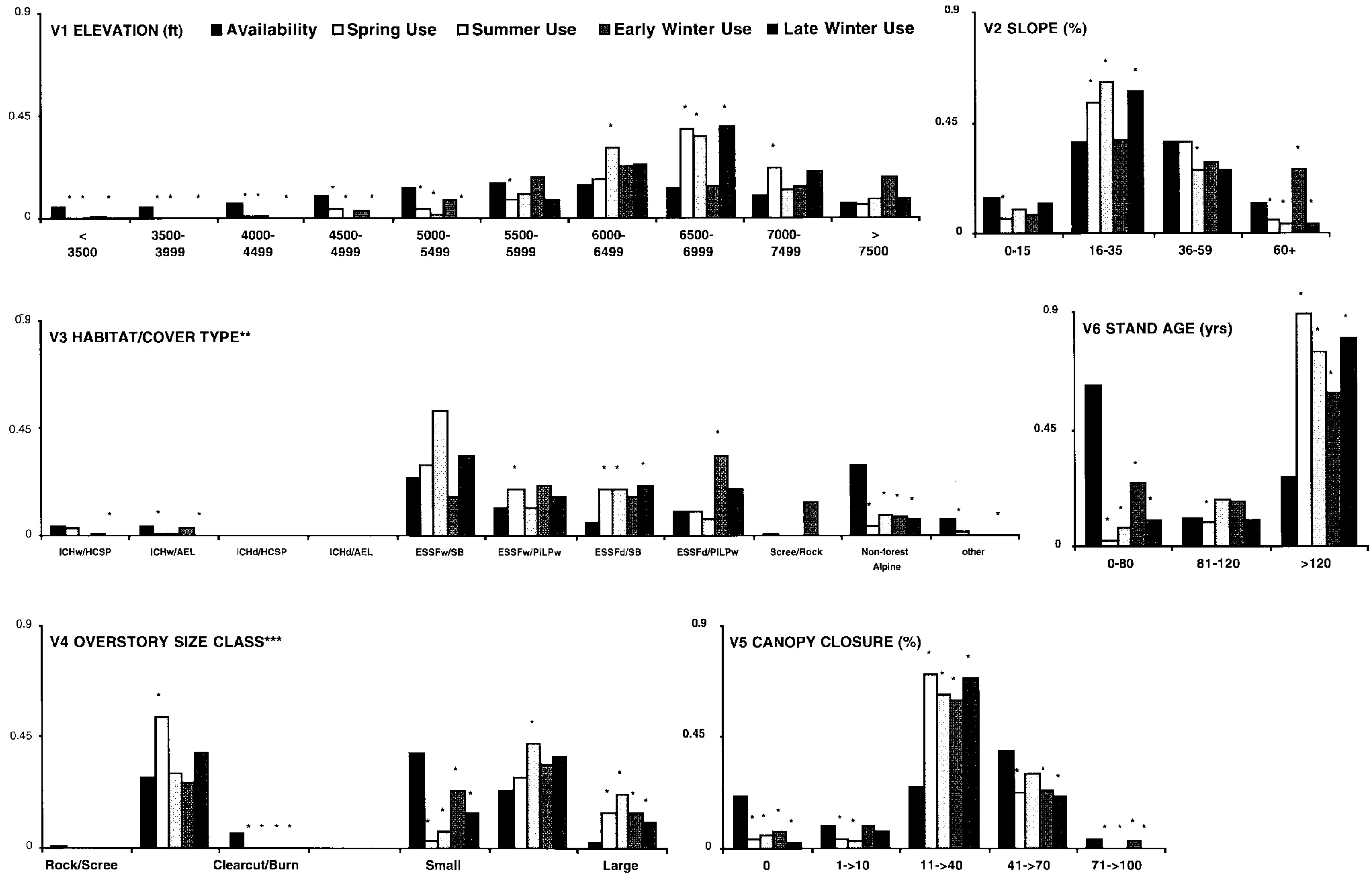


Fig. 4. Results of caribou selection for individual variable classes by season. * indicates significance ($P < 0.05$) based on Bonferroni Z-statistics. ** ICH=Interior Cedar Hemlock zone (Meidinger & Pojar, 1991)); ESSF=Engelmann Spruce/Subalpine Fir zone (ibid.); d=dry variants; w=wet variants; H=hemlock; C=cedar; S=spruce; B=balsam fir; A=aspen; E=birch; L=larch; Pl=lodgepole pine; Pw=whitebark pine. *** sapling=dbh 0.3–12.7 cm; small=dbh 12.7–22.9 cm; medium=dbh 22.9–35.6 cm; large=dbh>35.6 cm.

Table 2. Adjusted habitat suitability coefficients.

V_1 Elevation (ft)	Spring	Summer	Early Winter	Late Winter
<3500	0.0	0.0	0.1	0.0
3500-3999	0.0	0.0	0.1	0.0
4000-4499	0.0	0.0	0.7	0.0
4500-4999	0.5	0.0	0.7	0.0
5000-5499	0.7	0.0	0.7	0.0
5500-5999	0.7	0.3	0.7	0.2
6000-6499	0.7	0.8	0.7	0.7
6500-6999	1.0	0.9	0.5	1.0
7000-7499	0.8	0.5	0.5	0.6
>7500	0.5	0.5	0.9	0.5
V_2 Slope (%)				
0 - 15	0.7	0.7	0.7	0.7
16 - 35	0.7	0.7	0.7	0.7
36 - 59	0.5	0.3	0.3	0.3
60 +	0.2	0.1	0.8	0.1
V_3 Habitat/Cover Type*				
ICH wet / H, C, S, B	0.5	0.1	0.5	0.
1ICH wet / A, E, L	0.0	0.0	0.5	0.1
ICH dry / H, C, S, B	0.2	0.2	1.0	0.0
ICH dry / A, E, L	0.0	0.0	0.0	0.0
ESSF wet / S, B	0.6	0.8	0.3	0.6
ESSF wet / PI, L, Pw	0.7	0.5	0.7	0.5
ESSF dry / S, B	1.0	1.0	0.9	1.0
ESSF dry / PI, L, Pw	0.6	0.3	1.0	0.8
Scree/Rock	0.0	0.2	0.0	0.2
Non-forested Alpine	0.0	0.1	0.1	0.1
All other habitat types	0.1	0.0	0.0	0.0
V_4 Overstory Size Class				
Rock/Scree0.0	0.1	0.0	0.1	
Non-forest (A,M,NP,NC)	0.7	0.5	0.5	0.6
Clearcut/Burn	0.0	0.0	0.1	0.1
Sapling (dbh 0.3-12.7 cm)	0.2	0.1	0.0	0.1
mall (dbh 12.7-22.9 cm)	0.0	0.1	0.2	0.1
Medium (dbh 22.9-35.6 cm)	0.7	0.8	0.7	0.6
Large (dbh >35.6 cm)	1.0	1.0	1.0	1.0
V_5 Canopy Closure (%)				
0	0.0	0.5	0.1	0.0
1 - 10	0.1	0.1	0.5	0.3
11 - 40	0.9	0.9	0.9	0.9
41 - 70	0.2	0.3	0.9	0.2
71 - 100	0.1	0.0	0.9	0.1
V_6 Overstory Stand Age				
0 - 80	0.1	0.1	0.1	0.1
81 - 120	0.7	0.7	0.7	0.7
> 120	1.0	1.0	1.0	1.0

*ICH=Interior Cedar Hemlock zone (Meidinger & Pojar, 1991); ESSF = Engelmann Spruce/Subalpine Fir zone (ibid.); d = dry variants; w = wet variants; H = hemlock; C = cedar; S = spruce; B = balsam fir; A = aspen; E = birch; L = larch; Pl = lodgepole pine; Pw = whitebark pine.

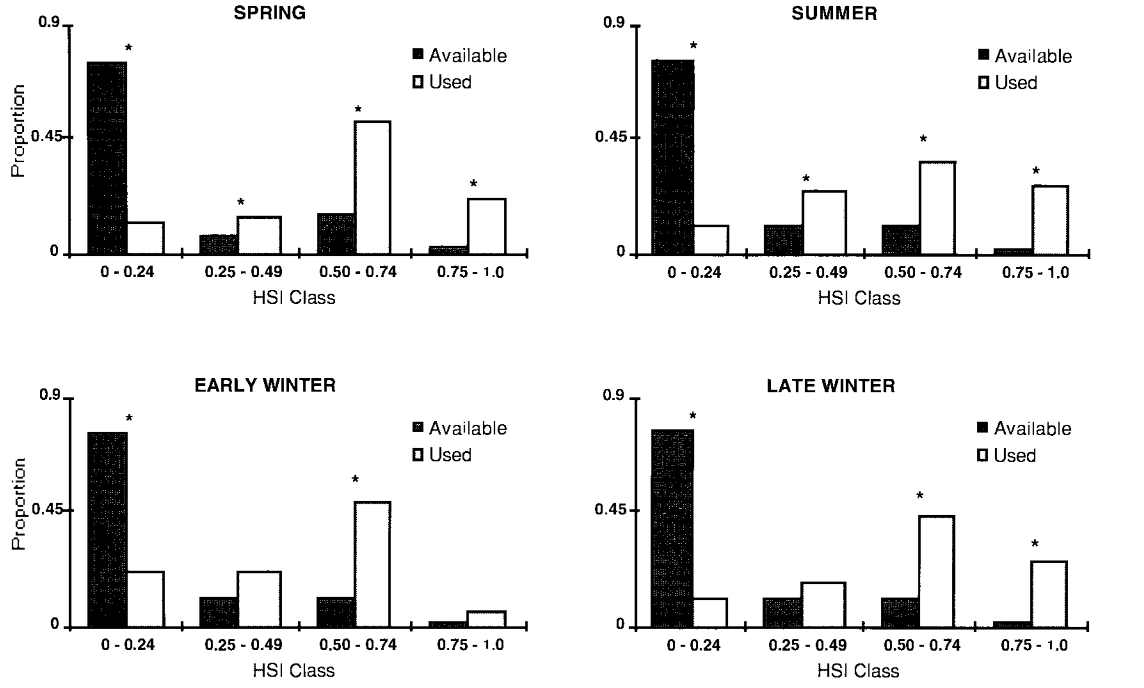


Fig. 5. Caribou selection for habirat suitable classed as definded by the adjusted HSI model. * indicates significance ($P < 0.05$) based on Bonferroni Z-statistics.

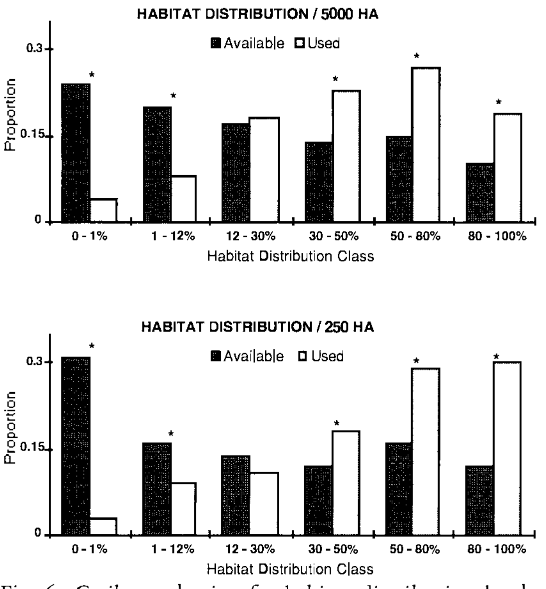
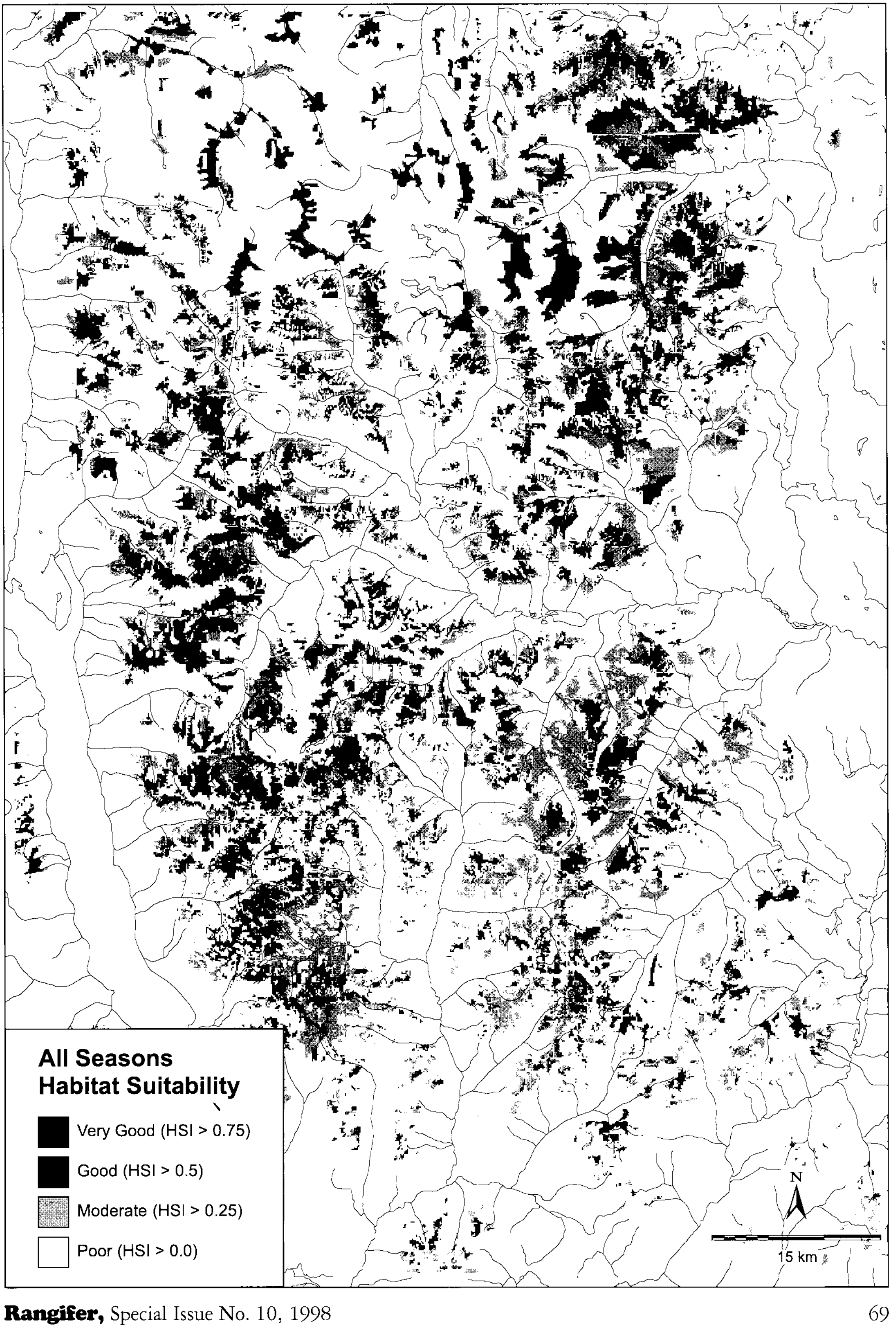


Fig. 6. Caribou selection for habitat distribution levels. Distribution classed reflect the proportion of suitable habitat (HSI>0.25) at two landscape scales. * indicates significance ($P < 0.05$) based on Bonferroni Z-statistics.

tion and human habitation, that have occurred disproportionately at lower elevations, may have caused mountain caribou in the Purcells to make much less use of low-elevation cedar and hemlock forests than in the past, such that the observed pattern may represent a recent shift. The correct explanation is far from clear, but having suitable low-elevation habitats into which caribou may move in early winter and spring is potentially critical and limiting, even if such habitats are used only occasionally or for short periods. It is by this rationale that we subjectively increased model coefficients for lower elevation classes, cedar and hemlock cover types, higher canopy closures and gentle slopes, to parallel those of the Idaho model.

Linked to a GIS database of habitat attributes at the appropriate scale and resolution, we consider the performance of the adjusted HSI model to be adequate as an interim habitat assessment and planning tool (e.g. Fig. 7). From the consistent observed selection against the lowest (0 - 0.24) HSI class, we infer a relative lack of importance of these habitats to southern Purcell caribou. The lack of significant selection for the next HSI class (0.25 - 0.49) suggests that these habitats may be "suitable" but are

Fig. 7. Combined habirat suitability for the southern Purcell study area. The maximum suitability value over each of four caribou seasons is indicated.



All Seasons
Habitat Suitability
Very Good (HSI > 0.75)
Good (HSI > 0.5)
Moderate (HSI > 0.25)
Poor (HSI > 0.0)
N
15 km

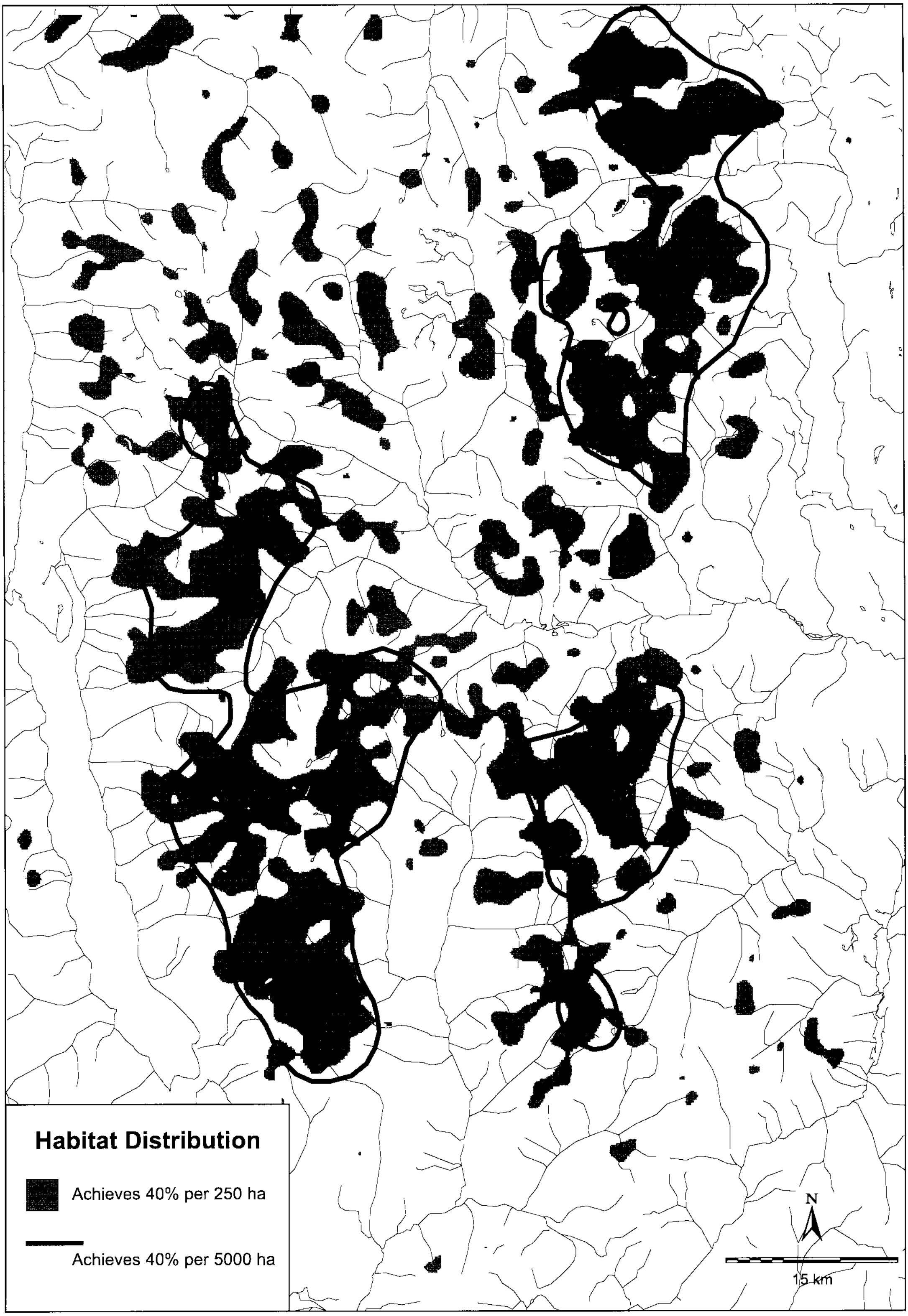


Fig. 8. Lands within the southern Purcell Montains that achieve at least 40 % suitable habitat distributed per 5000 ha and 250 ha.

not of exceptionally high quality. Consistent selection across all seasons for HSI class 0.5 - 0.74 illustrates the relative importance of these habitats, while we consider the strong selection for HSI class 0.74 - 1.0 during every season except early winter as indicative of exceptional importance to caribou. The lack of apparent selection for the highest HSI class during early winter reflects subjective adjustments to early winter suitability ratings.

Based on results of these analyses, it is apparent that landscape attributes need to be considered in habitat planning, particularly because suitably-distributed habitats appear to be highly fragmented. From our analysis, we consider the mid-point of our selected habitat distribution range (40%) as a minimum target in the maintenance of southern Purcell mountain caribou habitat (Fig. 8). Considering the large home ranges typically used by mountain caribou, lands which achieve 40% suitable habitat distributed per 5000 ha may approximate core habitat areas in which long-term use by caribou may be possible. Lands that fall much below the limits of this distribution may receive periodic use, but are unlikely to be used consistently unless they provide seasonally important attributes. Two qualifications to this are that the model does not account for the influence of apparently "unsuitable" but barrier-free movement routes, such as alpine tundra, nor does it account for habitat that is not within a suitably distributed matrix but is contiguous with one. Conversely, there are lands within the 5000 ha contour that do not meet the minimum distribution requirements at the 250 ha level and thus may not contribute to core habitat.

We recognize that numerous assumptions are at play in our approach to the adaptation of this model. Our intent was to provide an interim tool to integrate our best understanding of caribou-habitat relationships with ongoing forest planning until further information comes available. As long-term research continues, a strictly empirical, multivariate approach will be taken in model development at the stand level. Similarly, we cannot yet be certain that our identified core habitat areas represent habitat distribution levels required to maintain a viable population over the long term, but this may also change as data comes available and our understanding of the relationship between habitat distribution, road access, and mortality risk improves. However, the exercise of HSI evaluation and adaptation: 1) illustrates the potentially large differences in habitat use between adjacent populations of a single ecotype, 2) indicates that there may be important seasonal differences within the population, 3) highlights the need to manage for habitat values at a landscape level, and 4) demonstrates that interim management tools can be developed and put into use with relatively limited data. Obviously, a conservative approach to forest management is desired where our understanding of habitat relationships is uncertain. In ecosystems that are being rapidly altered through primary management for timber values, interim models based on limited data and informed conjecture may provide essential tools for maintaining habitat integrity until more complete data becomes available.

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Protostrongylid nematodes in caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*) of Newfoundland

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Abstract: Two species of protostrongylid nemarodes with dorsal-spined, first-stage larvae, are present in caribou and moose of Newfoundland. *Elaphostrongylus rangiferi* Mitskevich, 1958, a parasite introduced from Scandinavia, causes periodic epizootics of a severe neurological disease in caribou. Sick animals exhibiting signs of cerebrospinal elaphostrongylosis (CSE) were particularly noticeable in central Newfoundland each winter between 1981 and 1985. Those collected for examination were mostly male calves. The disease again became prominent in caribou on the Avalon Peninsula in the winters of 1996 and 1997; it may have spread to that isolated part of the province as recently as 1990. *E. rangiferi* was also found in moose but no cases of neurologic disease have been reported in this host. *Parelaphostrongylus andersoni* Prestwood, 1972, was found in caribou, both in central Newfoundland and on the Avalon Peninsula. Moose may also be infected. Of 1407 terrestrial gastropod intermediate hosts examined, 9 (0.6%) contained infective, third-stage, protostrongylid larvae resembling those of *E. rangiferi* and *P. andersoni* which are indistinguishable. The small dark slug, *Deroceras laeve*, dominared gastropod collections and was the only species infected.

Key words: cerebrospinal elaphostrongylosis, muscle worms, lungworms, cervidae, gastropod intermediate hosts.

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Introduction

Elaphostrongylus rangiferi has been known for some time from caribou (*Rangifer tarandus caribou*) in Newfoundland (Lankester, 1976; 1977; Lankester & Northcott, 1979) and was probably introduced with reindeer (*R. t. tarandus*) brought from Norway in 1908 (Lankester & Fong, 1989). In earlier publications, we followed European authors who recommended that this nematode found in the central nervous system and musculature of *Rangifer* be considered a synonym of *E. cervi* (see Kutzer & Prosol, 1975) or be referred to as *E. cervi rangiferi* (Pryadko & Boev, 1971; Kontrimavichus *et al.*, 1976). However, we now defer to Scandinavian workers (Stéen *et al.*, 1989; Halvorsen *et al.*, 1989; Gibbons *et al.*, 1991) who have provided new biological and morphological data supporting distinct species status for *E. rangiferi.*

In Scandinavia and northern Russia, the parasite causes a disease called cerebrospinal elaphostrongylosis (CSE) which is characterized by a lack of fear, ataxia, and posterior paralysis (Polyanskaya, 1965; Bakken & Sparboe, 1973; Handeland & Norberg, 1992). Heavy losses of young animals less than one year old periodically occur in late winter. Domestic sheep and goats that share range with infected reindeer may also succumb to the disease (Handeland, 1991; Handeland & Sparboe, 1991). In Newfoundland, *E. rangiferi* was prevalent in caribou of the Middle Ridge area in the mid 1970s when the first case of CSE was diagnosed (Lankester & Northcott, 1979). There have been opportunities for *E. rangiferi* to spread with translocated reindeer and caribou from Newfoundland to mainland Canada but there is as yet no conclusive evidence that it has become established anywhere outside of Newfoundland (Lankester & Fong, 1989).

Parelaphostrongylus andersoni, another protostrongylid nematode, is widely distributed in woodland and barrenground caribou of mainland Canada

(Lankester & Hauta, 1989). This slender nematode is easily overlooked because of its location deep within muscles of the back and hind limbs. If, as Lankester & Hauta (1989) suggested, caribou are the original host of *P. andersoni*, rather than white-tailed deer (the type host, see Prestwood, 1972), we predict that it should also occur in caribou of Newfoundland along with *E. rangiferi*. Because *P. andersoni* probably is not neurotropic (Pybus & Samuel, 1984), it is not thought to cause neurologic disease in wild cervids. However, its eggs and larvae, like those of *E. rangiferi*, develop in the lungs where an intense granulomatous inflammatory reaction contributes to verminous pneumonia (Lankester & Northcott, 1979, Anderson & Prestwood, 1981).

The first indication that caribou in Newfoundland might have both *E. rangiferi* and *P. andersoni* was provided by Lankester *et al.* (1990) following experimental infection of fallow deer (*Dama dama*) with larvae collected off Newfoundland caribou range. First-stage larvae were first passed 69 days after infection which is consistent with the shorter prepatent period of *P. andersoni*, and fragments of worms resembling both species were recovered at necropsy. Lankester & Fong (1989) mentioned finding *P. andersoni* in naturally infected caribou from Newfoundland but specimens were not described.

The purpose of this paper is to document the extent of *E. rangiferi* infection in cervids and its role in an epizootic of neurologic disease seen in the early 1980s in caribou of central Newfoundland. We also provide dimensions of *E. rangiferi* collected from moose and of *P. andersoni* from caribou in Newfoundland, and investigate the role of terrestrial molluscs in the field transmission of these parasites.

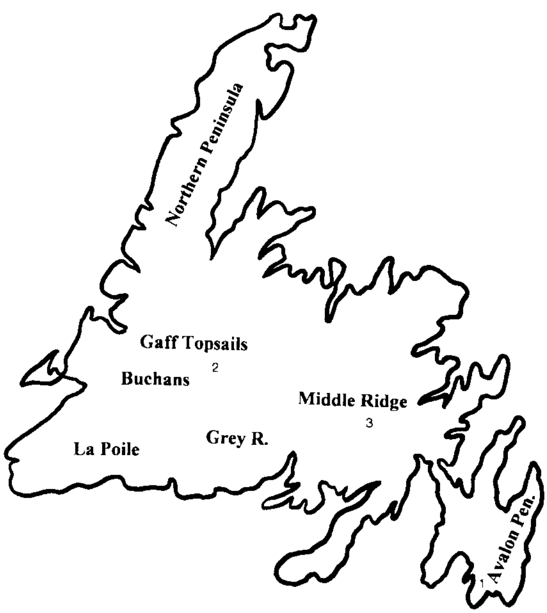

Fig. 1. Map of Newfoundland indicating the general areas occupied by major caribou herds from which sick caribou, moose, and fecal samples were collected. Locations 1- 3 are sites where terrestrial gastropods were collected: site 1 - Avalon Peninsula (Peter's River Rd., 46°47'N 54°10'W, 24 - 29 May, 1984); sites 2 & 3 - Central Newfoundland (site 2., adjacent to the Buchans Hwy #370 between Buchans and Buchans Junction, 48°37'N 57°26'W, 30 May - 3 June, 1984; and site 3., Sandy Pond, 48°05'N 55°42'W, 7 - 20 July, 1987).

Materials and methods

Examination of caribou exhibiting neurological signs

Animals behaving in an abnormal way were collected opportunistically and the body musculature of the chest and limbs was inspected visually for nematodes in the field. The head and vertebral column were removed and frozen along with a fecal sample, until examined later in the laboratory. The tops of the cranium and vertebrae were removed using a Stryker surgical saw. The brain and spinal cord were removed, and the surface and surrounding meninges checked for nematodes using a ring-lamp magnifier. Feces were examined for nematode larvae using the Baermann funnel technique.

Herd infection levels determined by fecal examination

Caribou feces were periodically collected off snow over several years (1982-90) from the traditional wintering areas of 7 major caribou herds in Newfoundland (Fig. 1). Samples were kept frozen at -15 °C until examined using the Baermann funnel technique. Pellets were floated over Kimwipe tissue (Kimberly-Clarke, Mississauga, Ontario) in stoppered, water-filled funnels (15 cm top diameter) for 24 hr, after which time 20 ml were drained into a Syracuse watch glass and examined for protostrongylid larvae at 20X using a stereoscopic microscope. First-stage larvae were pippetted onto a slide, heat relaxed on a hot-plate, covered with a cover slip and drawn and measured using a Wild drawing tube at 400-1000X.

Fig. 2. Male caribou calf with posterior paresis caused by *Elaphostrongylus rangiferi* appeared unafraid of humans and could be easily approached and restrained.

Examination of wild moose

Eight moose were shot and field examined, May 7-10, 1990; 7 (2-10 yr old) in the area occupied by the Middle Ridge caribou herd and a male calf (11.5 mo) in the area of the Gaff Topsails herd (Fig. 1). The fascia and surface of muscles beneath the shoulders were examined for nematodes. Representative nematode specimens were fixed in glycerin-alcohol and later drawn and measured. Fecal samples (22-30 pellets) taken from the rectum were frozen and later examined for larvae. Additional moose feces were collected off range in the Gaff Topsails area, March 15, 1989, frozen, and examined later for nematode larvae using the Baermann funnel technique.

Searching for P. andersoni

Two caribou were shot on the Avalon Peninsula and 2 in the Gaff Topsails area, June 23-30, 1987. Eight more were examined from the Avalon Peninsula in the vicinity of Peter's River Road, December 9-13, 1989. The cranium and shoulder muscles were examined in the laboratory for *E. rangiferi* according to Lankester & Northcott (1979) and the longissimus dorsi muscles of the back for *P. andersoni* according to Lankester & Hauta (1989). Feces were collected from the rectum of each animal.

Detecting infections in intermediate hosts

Terrestrial gastropods were collected from beneath cardboard sheets and off vegetation at one location on the Avalon Peninsula (Peter's River Rd., 46°47'N 54°10'W, 24-29 May, 1984), and at 2 sites in central Newfoundland (adjacent to the Buchans Hwy #370 between Buchans and Buchans Junction, 48°37'N 57°26'W, 30 May-3 June, 1984; and Sandy Pond, 48°05'N 55°42'W, 7-20 July, 1987) (Fig. 1). Snails and slugs were identified with the aid of Pilsbury (1939-1948), Burch (1962), and Maunder (1985), digested in artificial pepsin solution, and examined for protostrongylid nematode larvae (Lankester & Peterson, 1995). Larvae were heat-relaxed, stored in 10% glycerin in 70% alcohol, and later drawn and measured.

Differences in larval dimensions were tested using ANOVA and Duncan's Multiple Range test according to the Statistical Package for the Social Sciences (SPSS, Inc., Chicago, Illinois, USA).

Results

Examination of caribou exhibiting neurological signs

A total of 17 caribou exhibiting abnormal neurologic signs was examined from 1981 to 1985 (Table 1). Most were from the Buchans and Gaff Topsails areas of central Newfoundland, and were reported between January and April. All but one were calves (<1 yr) and 12 of 15 sexed animals were males. Affected animals were described as appearing "tame" or "stunned". They could be approached closely (Fig. 2). Some stood for long periods with the head held low and back arched. Others exhibited marked weakness of the hind limbs, sometimes dragging one or both legs (Fig. 3). Two animals were unable to stand when collected.

At necropsy, all animals (excluding nos. 4 and 5 for which the brain and spinal cord were not available) had adult *E. rangiferi* associated with the central nervous system (CNS) (Table 1). The majority of worms in the CNS (75%) were females. Many were free in the subdural space or were weakly attached by strands of connective tissue to the overlying dura or underlying pia-arachnoid. Six were lying partially or completely beneath the pia-arachnoid with up to 1 cm of their body length penetrating into brain tissue (in caribou nos. 7, 11, 15, and 16). The dura adhered firmly to the pia over much of the brain in caribou nos. 11, 14, and 16. Adhesions and membranes near worms were yellowish to pink in colour. Worms in the vertebral canal were all in the subdural space over the cervical or thoracic regions of the cord. Worms outside of the CNS were mostly found among the muscles of the chest, forelimbs, and hindlimbs. The number of first-stage larvae found in the feces of 9 animals showing signs ranged from 2 to 277/g of fresh feces (Table 1).

Wildlife protection officers reported a number of additional animals with signs characteristic of elaphostrongylosis. In the winter of 1981, 10 were

Table 1. *Elaphostrongylus rangiferi* in caribou exhibiting neurologic signs in Central Newfoundland, 1981-85

No.	Date	Location	Sex	Age[a]	Number of *E. rangiferi* Cranium	Vertebral[b] Canal	Muscle	Sex of worms in CNS	Larvae/g[c] feces
1.	3 Jan 81	Buchans	M	calf	2	1	?	?	?
2.	22 Jan 81	Buchans	M	calf	24	7	15	?	?
3.	27 Mar 81	Buchans	?	calf	1	1	20	?	?
4.	21 Jan 82	Buchans	M	calf	?	?	20	?	?
5.	Feb 82	Buchans	M	calf	?	?	21	?	?
6.	28 Jan 84	Gaff Topsails	M	calf	5	0	5	3F, 2M	6
7.	30 Jan 84	Gaff Topsails	F	yrlg	5	?	6	3F, 2M	8
8.	30 Jan 84	Grey River	M	calf	5	?	?	4F, 1M	277
9.	21 Feb 84	Gaff Topsails	?	calf	4	?	?	3F, 1M	?
10.	21 Mar 84	Gaff Topsails	F	calf	4	4	?	8F, 0M	35
11.	20 Mar 84	Gaff Topsails	M	calf	2	1	7	1F, 2M	2
12.	21 Mar 84	Gaff Topsails	F	calf	8	0	14	6F, 1M, 1?	104
13.	29 Mar 84	Gaff Topsails	M	calf	6	1	20	6F, 1M	?
14.	11 Apr 84	Middle Ridge	M	calf	2	?	0	2F, 0M	126
15.	24 Apr 84	Gaff Topsails	M	calf	5	0	21	4F, 1M	267
16.	Mar 85	Middle Ridge	M	calf	8	1	?	6F, 2M, 1?	?
17.	23 Apr 85	Gaff Topsails	M	calf	14	?	?	8F, 5M, 1?	58

[a] A calf is <1 yr old, assuming a birth date of 1 June.
[b] Worms in subdural space, beneath the pia-arachnoid or in nerve parenchyma.
[c] First-stage, dorsal-spined larvae.
? Not available for examination.

Table 2. Prevalence and mean intensity of first-stage protostrongylid larvae in caribou feces from Newfoundland[a]

	Prevalence					
Location	1982	1983	1984	1985	1989	1990
Northern Peninsula	---	50 (24) M[b](1 ± 1)[c]	---	---	---	---
La Poile R.	30 (60) M	---	---	---	38 (50) J (2±4)	---
Grey R.	70 (56) M	60 (42) A (19±29)	---	---	---	---
Gaff Topsails	50 (81) M	---	86 (29) A (24±37)	74 (27) J (8±9)	---	---
Middle Ridge	(40 (95) M	48 (27) M (3±4)	---	45 (49) J	50 (50) J (14±23)	---
Avalon Peninsula	---		---	33((40) M (94±150)	35 (40) J	31 (26)

[a] All samples collected January – April.
[b] Percent passing larvae, followed in brackets by sample size (*n*).
[c] Month of collection and, when aviable, mean no. larvae/g wet feces ± S.D. in brackets.

seen in the Buchans-Buchans Jct. area; 5 were seen in the winter of 1982, and 3 in 1983. In the winter of 1984, 17 of 28 cases reported from across the central part of Newfoundland were seen in the Gaff Topsails area as were 11 of 18 animals sighted in winter of 1985. We were not aware of any sick animals being seen in other parts of the Province during this period.

Two apparently healthy caribou were collected from the Gaff Topsails area in late June, 1987. The 2-3-yr-old male had a total of 16 adult *E. rangiferi* among muscles of the chest and legs and a 13-mth-old male had 22; no worms were found in the cranium of either animal. Neither showed neurologic signs but the gross pathology seen at necropsy was unusual. Considerable yellowish-red, subcutaneous edema and caseous exudate were visible over all large muscles of the chest, lateral abdomen, and lower limbs. Such extensive subcutaneous reaction was not seen in infected caribou examined during winter and early spring.

Herd infection level 1982-90

The prevalence of dorsal-spined, protostrongylid nematode larvae in caribou feces was lowest in samples from the La Poile and Avalon Peninsula herds and highest in the Grey River and Gaff Topsails herds; it varied little between years in any particular herd (Table 2). The intensity of larval output ranged from 11 larvae/g (mean S.D.) in samples from the Northern Peninsula to 94±150 larvae/g on the Avalon Peninsula (collected May, 1985). At the latter site, at least 4 animals, assumed to be calves because of their small pellets, were passing up to 580 larvae/g of fresh feces.

Protostrongylid larvae collected from caribou on the Avalon Peninsula in 1985 and 1989 were shorter (366±3, 310-385 µm, n=30; and 359±4, 320-392 µm, n=30, respectively) than those from caribou at Middle Ridge in 1985 (424±3, 385-470 µm, n=30) and the Gaff Topsails areas in 1985 (439±3, 405-457 µm, n=30) (P=0.04) but those collected from the Avalon Peninsula in 1990 were not (395±5, 352-445 µm, n=30).

Examination of wild moose

Four of the 7 adult moose from Middle Ridge had *E. rangiferi* on the surface of the latissimus dorsi muscle and associated fascia beneath the shoulder (Table 3). Dorsal-spined larvae (n=9, mean length 348±8; 295-372 µm) were present in the feces of only one of the four moose with adult *E. rangiferi.* Longissimus dorsi muscles were not examined for *P. andersoni.*

One of 28 moose fecal samples collected off snow in the Gaff Topsails area (April, 1989) contained 20 dorsal-spined larvae in 15 pellets. The larvae were 388±7 µm; 340-420 long. Although the mean length of larvae from moose feces in both the Gaff Topsails and Middle Ridge areas were shorter than

Table 3. Dimensions (μm) of *Elaphostrongylus rangiferi* on chest and shoulder muscles of moose from Middle Ridge, Newfoundland

	No. measured	Mean ± S.E.	Range
Males			
Length (mm)	6	35± 1	31– 38
Width	6	199± 7	175–220
Esophagus	6	681±14	650–740
Nerve ring	6	132±11	100–170
Excretory pore	4	153±13	115–175
Spicules	7	220± 4	205–232
Gubernaculum	7	75± 3	63– 85
Bursa (length)	7	174± 8	173–195
(width)	7	139± 5	128–157
Females			
Length (mm)	1	47	47
Width	3	223± 7	220–240
Esophagus	4	698±30	635–770
Nerve ring	4	131± 7	120–150
Excretory pore	4	145±13	118–170
Vulva	1	300	300
Anus	1	68	68

larvae from caribou at those locations (P.=0.05), it is noteworthy that some larvae in the sample from the Gaff Topsails exceeded 400 μm in length.

Searching for P. andersoni

Only 2 of 12 caribou had *P. andersoni* (Tables 4 and 5). Both were young animals (7 and 13 mo old). In one from the Gaff Topsails area of central Newfoundland, a portion of a male nematode (160 μm wide) resembling *P. andersoni* was found deep in the longissimus dorsi muscle. This animal also had numerous *E. rangiferi* in muscles of the shoulder and chest. A second, from near Peter's R. Rd., Avalon Peninsula, had 22 *P. andersoni* in the longissimus dorsi muscles of the back and 7 in the neck, rump, and thigh muscles.

All specimens of *P. andersoni* were found loosely coiled, deep within muscles. A dark red area of haemorrhage (0.5-1 cm diam.) was associated with about one-half of the specimens, and helped in locating them. Petechial haemorrhages (1-3 mm diam.) were visible across the entire surface of the lungs of the infected calf from the Avalon Peninsula.

Natural infections in intermediate hosts

Of 1407 terrestrial gastropods collected, 9 (0.6%) were infected with protostrongylid larvae (Table 6). A small, dark slug, *Deroceras laeve,* dominated collections in all 3 areas and only this slug was infected. Two slugs had 1 and 3 recently-penetrated, first-stage larvae (397-415 μm long, n=4); 7 had 1-15 third-stage larvae (800-1002 μm long, n=12). All measurements are of alcohol-fixed specimens.

Table 4. Examination of normal caribou from central Newfoundland (Gaff Topsails) and from the Avalon Peninsula for *Elaphostrongylus rangiferi* and *Parelaphostrongylus andersoni,* 1987-89.

No.	Date	Location	Age	Sex	*E. rangiferi* cranium/ muscle	*P. andersoni* long. dorsi muscle	Larvae/g feces
1.	30/06/87	Gaff Topsails	2-3 yr	♂	0/2 ♂♂ & 14 ♀♀	0	0.2
2.	30/06/87	Gaff Topsails	13 mo.	♂	0/5 ♂♂ &, 17 ♀♀	1♂[3]	0.2
3.	23/06/87	Avalon Pen.[1]	2-3 yr	♂	0/0	0	0
4.	23/06/87	Avalon Pen.	3-4 yr.	♂	0/0	0	0
5.	9/12/89	Avalon[1] Pen.	1.5 yr.	♂	0/0	0	0
6.	9/12/89	Avalon[1] Pen.	adult	♀	0/0	0	0
7.	9/12/89	Avalon[1] Pen.	adult	♂	0/0	0	0
8.	9/12/89	Avalon[1] Pen.	1.5 yr.	♀	0/0	0	0
9.	12/12/89	Avalon[2] Pen.	1.5 yr.	♂	0/0	0	0
10.	12/12/89	Avalon[2] Pen.	1.5 yr.	♂	0/0	0	0
11.	13/12/89	Avalon[1] Pen.	1.5 yr.	♂	0/0	0	0
12.	13/12/89	Avalon[1] Pen.	7 mo.	♂	0/0	15 ♂♂ & 14 ♀♀[4]	many

[1] Peter's River Road.
[2] Mt. Misery, S. Avalon.
[3] Partial worm, 160 μ wide (no spicules).
[4] 2/29 in neck, rump, and high muscles.

Table 5. Dimensions (μm) of adult *Parelaphostrongylus andersoni* in longissimus dorsi muscle of caribou from the Avalon Peninsula, Newfoundland

	No. measured	Mean ± S.E.	Range
Males			
Length (mm)	3	21± 2	18– 23
Width	6	102± 5	90– 125
Esophagus	6	853±50	680–1000
Spicules	6	118± 2	115– 128
Gubernaculum	5	64± 3	53– 72
Females			
Length (mm)	2	34± 0	34, 34
Width	6	125± 3	110– 132
Esophagus	4	895±37	830–1000
Vulva[1]	5	165± 8	140– 180
Anus[1]	5	56± 3	51– 65

[1] Position measured from posterior end.

Discussion

An outbreak of CSE involving calves such as that seen in the Buchans-Gaff Topsails areas between 1981 and 1985 has not been reported previously in Newfoundland, despite *E. rangiferi* having been introduced into the province over 70 yr ago (Lankester & Fong, 1989). Although Bergerud (1971) reported emaciated calves standing and feeding for long periods in central Newfoundland in March-April of 1959 and 1961, their condition was attributed to the difficulty in getting food during these two exceptionally severe winters. High mortality, also particularly involving male calves, was seen during several summers but lynx (*Lynx canadensis*) attack and subsequent *Pasturella* infection was proven to be the cause (Bergerud, 1971).

In Norway where *E. rangiferi* originated, epizootics of CSE involving the loss of many animals occur sporadically, principally in domesticated reindeer (Halvorsen *et al.*, 1980) but the disease has also been reported in wild reindeer (Bye & Halvorsen, 1984). The cause of epizootics has previously been attributed largely to conditions associated with reindeer domestication. But Halvorsen *et al.* (1980) demonstrated that the level of *E. rangiferi* infection in herds was correlated with summer temperatures. An epizootic in northern Norway around 1970 was preceded by a series of unusually warm summers. It subsided as summers cooled. Elevated mean summer temperatures at this subarctic location (above 70°N latitude) were thought to increase the rate at which larvae developed in gastropods, resulting in more infective larvae being available to reindeer before freeze-up in the fall. The likelihood of this being the principal cause of epizootics at a more southerly, maritime location like central Newfoundland (48°37'N) remains to be tested.

At the time of writing this manuscript, we became aware of another cluster of cases of CSE occurring in caribou on the Avalon Penininsula of Newfoundland (McBurney *et al.*, 1996; Shane Mahoney & Con Finlay, pers. comm.). Sick animals were reported from January to March of 1996 and 1997. Over 100 were seen in the vicinity of Cape Race, at the southern tip of the peninsula in 1997 (Con Finlay, pers. comm.). *E. rangiferi* was recovered from animals that separated from the herd, stay-

Table 6. Numbers of terrestrial gastropods examined for prorostrongylid nematode larvae in Newfoundland.

	Avalon Peninsula		Central Newfoundland				
	Peter's River Rd.[1]		Buchans Hwy.[2]		Sandy Pond[3]		
Species	No. exam.	No. infected	No. exam.	No. infected	No. exam.	No. infected	Total infected/ exam.
Deroceras laeve	321	2	675	2	294	5	9/1290
Zonitoides arboreus	11	0	2	0	65	0	0/78
Succinea ovalis	15	0	1	0	9	0	0/25
Arion sp.	2	0	9	0	---	---	0/11
Euconulus fulvus	1	0	---	---	2	0	0/3
Total	350	2	687	2	370	5	9/1407

[1] Collected at site 1 (Fig. 1) 24 May - 3 June, 1984.
[2] Collected at site 2 (Fig. 1) 7 - 20 July, 1987.
[3] Collected at site 3 (Fig. 1) 7 - 20 July, 1987.

ed for days in the same general location, were unafraid of humans approaching, and had mild to marked hind-limb paresis. Many of these animals were under-weight, despite appearing to spend considerable time eating . Both calves and older animals were showing clinical signs. It is probably worth noting that the Avalon Peninsula experienced milder than usual temperatures and an absence of snow during much of the winters of 1995-96 and 1996-97. As a result, the period during which infected gastropods remained accessible to grazing caribou probably was extended considerably. *D. laeve,* which is very abundant over much of the caribou range in Newfoundland, can remain active on ground vegetation at temperatures close to 0 °C (Lankester & Peterson, 1996).

Caribou showing neurological signs from central Newfoundland were almost exclusively young (< 1 yr) and male. Halvorsen (1986) made a similar observation in Norway. Although no signs of disease were apparent during his study, infection with *E. rangiferi* was most prevalent in the heaviest calves. These, in fact, were mostly males but larger female calves also were more frequently infected than smaller ones. This was attributed to the larger amount of food likely eaten by the largest individuals and the attendant increased risk of ingesting infected gastropods.

It has been suspected that animals showing signs of CSE are likely those with the most worms (Halvorsen, 1986). Yet, in our sample, neither the number of *E. rangiferi* present in the CNS, total numbers of worms recovered, nor the numbers of larvae being passed in feces, was correlated with the severity of neurologic signs observed. However, this may not be a valid test of the hypothesis since all animals were examined during winter and early spring when some worms were probably immature and difficult to find. Also, only sick animals were examined and counts of worms in muscles may have been underestimated working under field conditions. As well, the Baermann funnel technique has recently been shown to be unreliable for accurately estimating the numbers of protostrongylid larvae in ungulate feces (Forrester & Lankester, 1997) .

The preponderance of female worms found in the CNS of sick caribou may be noteworthy. Because they are longer and wider than males, they may experience more difficulty leaving the CNS and thereby play a greater role in the pathogenesis of infection. However, satisfactory interpretation of this observation requires more complete knowledge of the migration route taken by *Elaphostrongylus* spp. in the course of their normal development within cervid hosts. Although the route is not completely understood, developing worms initially migrate into the CNS to moult and grow in nerve tissue. After about 90 days, they begin to leave the CNS via cranial and spinal nerves to reach their definitive site among skeletal muscles (Lankester, 1977; Hemmingsen *et al.* 1993; Handeland, 1994). Infection in late summer and autumn would explain why most developing worms are in the CNS over winter but increasingly in muscles in spring and summer as observed here.

Among the herds in central Newfoundland, the prevalence and intensity of infection, as indicated by protostrongylid larvae in feces, were greatest in animals of the Topsails area, where sick animals were most commonly seen in 1981-85. However, caution must be exercised in comparing levels of herd infection measured in this way unless fecal samples are collected at similar times of the year and proportionately, from animals of similar age and sex. Most protostrongylid nematodes of cervids show marked seasonal variation in larval output and young animals typically produce the greatest numbers (Slomke *et al* , 1995). As well, the output of *E. rangiferi* larvae is known to vary with season of the year and with sex of the host; the greatest numbers of larvae apparently being passed by male reindeer in fall during the rut and by females in spring after parturition (Halvorsen *et al.,* 1985).

Data reported here suggests that *E. rangiferi* did not spread to caribou of the Avalon Peninsula until the late 1980s. Only *P. andersoni,* was found at necropsy of Avalon caribou in 1989. And, up to this time, all protostrongylid larvae found in caribou feces were less than 400 µm long as is characteristic of *P. andersoni* (see Lankester & Hauta, 1989). However, first-stage larvae from caribou feces collected on the Avalon in the winter of 1990 were up to 445 µm long, suggesting that some caribou had by that time become infected with *E. rangiferi.* Its presence in the Avalon caribou and its involvement in an outbreak of CSE in late winter of 1996 was confirmed by McBurney *et al.* (1996).

The Avalon Peninsula is connected to the central part of Newfoundland by a narrow isthmus of land only a few kilometres wide at its narrowest point (Fig. 1). This has probably limited the movement of caribou between the central and Avalon herds. The warble fly, *Hypoderma* (*Oedemagena*) *tarandi,* another parasite of caribou in central Newfoundland, also appeared in caribou for the first time on the Avalon Peninsula around 1990 (Shane Mahoney, pers. comm.), supporting the suggestion that caribou with *E. rangiferi* from one of the expanding herds of central Newfoundland may have crossed the isthmus and joined animals of the isolated Avalon herd at about that time. It may also be interesting to note that the Avalon herd has, in past at least, consistently shown a greater rate of increase than any of the central herds of Newfoundland (Bergerud, 1971; Bergerud *et al.*, 1983) that have long been infected with *E. rangiferi.*

Gastropods collected on the Avalon Peninsula in 1984 presumably had larvae of only *P. andersoni* while those from central Newfoundland could have had both *P. andersoni* and *E. rangiferi.* Nonetheless, the prevalence of protostrongylid larvae in gastropods from both parts of the Province was the same (0.6%). Such a low prevalence in gastropods is typical of this group of parasites. For example, in northern Minnesota where almost 80% of white-tailed deer become infected with *P. tenuis* before they are one year old (Slomke *et al.*, 1995), the highest rate of infection in snails and slugs was only 0.2% (Lankester & Peterson, 1996). A high prevalence of infection by these parasites are likely achieved in cervids, despite low levels in gastropods, because of the large volumes of food consumed. Caribou in particular take much of their food close to the ground where contamination by gastropods is impossible to avoid.

The dimensions and morphology of third-stage larvae recovered from gastropods collected in all localities in Newfoundland were similar to those of *E. rangiferi* and *P. andersoni* but larvae of this group cannot be specifically identified (Pybus & Samuel, 1981). The slug, *D. laeve,* is ubiquitous and abundant in Newfoundland (pers. observ.) and probably is the principal source of infection to caribou. The same species is widely distributed in North America (Pilsbry, 1939-1948) and, because it is highly mobile and active from early spring until late fall, is similarly important in the transmission of other protostrongylids of cervids (Lankester & Anderson, 1968; Samuel *et al.*, 1985; Lankester & Peterson, 1996).

In summary, *E. rangiferi* was introduced into Newfoundland with reindeer landed at St. Anthony, on the tip of the Northern Peninsula in 1908 (Lankester & Fong, 1989). Cerebrospinal elaphostrongylosis (CSE), primarily affecting young caribou, was first reported in the Buchans and Gaff Topsails herds of central Newfoundland in the 1970s (Lankester & Northcott, 1979); a larger than usual number of sick animals were collected in the period 1981-85 and are described here. Evidence also suggests that the parasite finally spread to the Avalon Peninsula caribou herd around 1990 with a large number of cases of CSE being seen in calves, as well as in older animals, in the latter part of winters of 1996 and 1997. Moose in central Newfoundland were also found infected with *E. rangiferi* but clinical signs of CSE have not been reported in this host. Only 6% of moose passed dorsal-spined larvae in their feces but the mean lengths of these larvae were slightly shorter than that expected of *E. rangiferi* larvae.

The presence of the muscle worm, *P. andersoni* is confirmed in caribou of both central Newfoundland and of the Avalon Peninsula but adult worms could only be found in young animals (< 1.5 yr). The muscles of moose were not examined for *P. andersoni* but the shorter, dorsal-spined larvae (mean < 400 µm) found in feces suggests that this parasite might become patent in moose.

In conclusion, this paper provides a biological and historical basis for further study of CSE, a significant disease of native caribou that is caused by an introduced parasite, *E. rangiferi.* Future work will be complicated by the presence of *P. andersoni* that does not cause neurologic signs but contributes to verminous pneumonia and produces similar dorsal-spined larvae in cervid feces.

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Simulating antler growth and energy, nitrogen, calcium and phosphorus metabolism in caribou

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Abstract: We added antler growth and mineral metabolism modules to a previously developed energetics model for ruminants to simulate energy and mineral balance of male and female caribou throughout an annual cycle. Body watet, fat, protein, and ash are monitored on a daily time step, and energy costs associated with reproduction and body mass changes are simulated. In order to simulate antler growth, we had to predict calcium and phosphorus metabolism as it is affected by antler growth, gestation, and lactation. We used data on dietary digestibility, protein, calcium and phosphorus content, and seasonal patterns in body mass to predict the energy, nitrogen, calcium, and phosphorus balances of a "generic" male and female caribou. Antler growth in males increased energy requirements during antler growth by 8 to 16%, depending on the efficiency with which energy was used for antler growth. Female energy requirements for antler growth were proportionately much smaller because of the smaller size of female antlers. Protein requirements for antler gtowth in both males and females were met by forage intake. Calcium and phosphorus must be tesorbed from bone during peak antler growth in males, when > 25 g/day of calcium and > 12 g/day of phosphorus are being deposited in antlers. Females are capable of meeting calcium needs during antler growth without bone resorption, but phosphorus was resorbed from bone during the final stages of antlet mineralization. Aftet energy, phosphorus was most likely to limit growth of antlers for both males and females in our simulations. Input parameters can be easily changed to represent caribou from specific geographic regions in which dietary nutrient content or body mass patterns differ from those in our "generic" caribou. The model can be used to quantitatively analyze the evolutionary basis for development of antlers in female caribou, and the relationship between body mass and antlet size in the Cervidae.

Key words: Cervidae, energetics, mineral nutrition, model, nutrient requirements, seasonal rhythm.

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Introduction

Antlers are among the most striking features of the Cervidae. Despite the importance of antlers to behavior and evolution of cervids, very little work has been done on the nutritional physiology of antler growth (Goss, 1995). In part, the lack of experimental work is caused by difficulties in separating metabolism for antler growth from metabolism necessary for growth and tissue anabolism in live animals (Brown, 1990). A further complication is that it would be desirable to use an experimental protocol which could monitor the status of energy, protein, and mineral metabolism simultaneously on several individuals. Such experiments quickly become technologically challenging and prohibitively expensive.

Simulation models are an alternative method to increase our understanding of the nutritional physiology of cervids. Most previous simulation models for wild ruminants have been limited to the winter months and dealt primarily with energy nutrition (Hobbs, 1989; Miquelle *et al.*, 1992). Some have been extended to other seasons (Hudson & White, 1985; Fancy, 1986) and nitrogen metabolism has been simulated (Swift, 1983). With the exception of the model developed by Swift, these models have been developed to address specific questions about the metabolism of a single species. Swift's model could simulate many ruminant species with adequate parameterization, but did not implement costs of productive functions such as lactation or antler growth. We have developed and validated a model which is similarly adaptable with respect to ruminant species, and which can simulate the energetic costs of gestation and lactation (Moen *et al.*, 1997).

Caribou are unique among cervids in that both males and females can grow antlers (Kelsall, 1968). In addition, males have among the heaviest antlers of extant cervids in relation to body mass (Geist, 1987). These features are of interest from an evolutionary perspective, both between male and female caribou and among cervids in general. Our model can be used to investigate previously unaddressable questions on mineral metabolism (Brown, 1990; Goss, 1995), and can be used to develop research hypotheses to be tested on live animals. In this paper we formally describe the equations required to simulate antler growth and composition, and present initial validation of the model with respect to calcium and phosphorus metabolism during antler growth. We then use the model to demonstrate the energy, nitrogen, calcium, and phosphorus needs of adult male and female caribou throughout an annual cycle. We would like to emphasize that the input values for parameters such as antler mass, body mass or seasonal changes in calcium and phosphorus content of forage can be easily changed to represent the characteristics of caribou in a specific area.

Methods

The foundation for our modeling work is the Energetics and Activity Simulation Environment (EASE), which simulates the energetics and metabolism of a free-ranging ruminant (Moen *et al.*, 1997). Unlike previous energetics models, the EASE model was designed to accept "plug-in" modules which simulate processes other than energy metabolism, such as a spatially-explicit foraging model (Moen *et al.*, 1997; 1998), nitrogen metabolism (Moen & DelGiudice, 1997), and the antler growth model described in this manuscript. The stochastic nature of many model parameters in the EASE model is another unique feature that simulates variability in real animals. Examples of such parameters include browse digestibility, efficiency of energy use for gestation, lactation, and maintenance, and the fat:protein catabolism ratio (Moen et al., 1997). For parameters that are stochastic, parameter values are drawn from a normal distribution with variation such that the coefficient of variation is 5% of the mean value for the parameter each day.

The EASE model operates on a daily time-step. Each day the energy balance is determined from forage intake and the energetic needs of maintenance, activity costs, gestation, lactation, and antler growth. If the simulated animal is in negative energy balance, body fat and protein are catabolized to meet the energy deficit. If the simulated animal is in positive energy balance, fat and protein are deposited. Nitrogen metabolism was added to the EASE model and it was then used to predict urinary urea nitrogen:creatinine ratios (Moen & DelGiudice, 1997).

To simulate antler growth, we were required to add functionality in the following areas: (1) calcium and phosphorus metabolism, (2) antler mass changes and (3) energetic requirements for antler growth. Model parameters are defined in equations 1-22 with parameter values we used in the validation and model experiment simulations. Most of these parameter values have been derived directly from the published literature on wild or domestic ruminants. In a few cases, where experimental results were not available, we estimated parameter values based on related physiological processes. These model parameters can be easily changed if new data should become available in the future.

Simulation of calcium and phosphorus metabolism

The EASE model simulates the calcium and phosphorus stored in and flowing through the body (Fig. 1). The major storage depot for both calcium and phosphorus is the skeleton, which contains about 99% of calcium and more than 75% of the phosphorus in the body (Agricultural Research Council, 1980). Both calcium and phosphorus can be resorbed from bone when metabolic needs can not be met by forage intake (Braithwaite, 1983; Muir *et al.*, 1987a). Less than 20% of the bone mass can be resorbed from a replete skeleton (Hillman *et al.*, 1973). Ash is 5.5% of the fat and ingesta-free body mass in an animal with a replete skeleton in the EASE model, and 4.5% in an animal which has completely depleted the available minerals in its skeleton. Calcium and phosphorus comprise 60% and 30% of the available skeleton mass which can be resorbed, respectively (*MaxBoneCa* and *MaxBonePhos*, g). *CaStatus* and *PhosStatus* (unitless

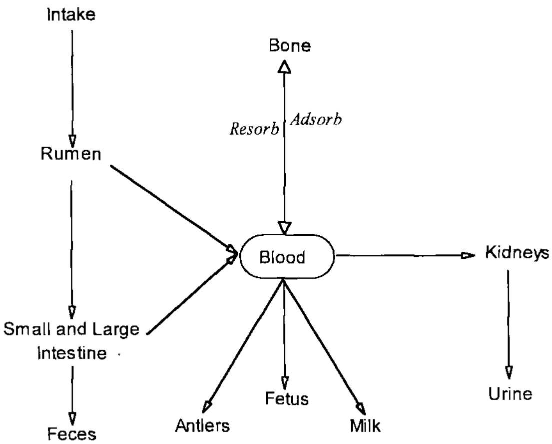

Fig. 1. Pathways calcium and phosphorus follow from ingestion to excretion as implemented in the simulation model.

fractions) range from 0.0 to 1.0 and indicate the fractional skeleton repletion for calcium and phosphorus, respectively.

Calcium and phosphorus intake is determined by the content of each of these elements in the diet. $IntakeCa_d$ (g Ca/day) is calculated from calcium content in the diet, and $IntakePhos_d$ (g P/day) is calculated from phosphorus content in the diet. Availability of ingested calcium and phosphorus depends on type of forage, mineral needs, and mineral status of the animal (Braithwaite, 1983; National Research Council, 1989). Availability increases as skeleton is resorbed, we use a base value of 35% availability when the skeleton is replete, which increases to 65% maximum availability when mineral stores in the skeleton are completely resorbed:

$$AvailFrcCa_d = 0.35 + (1.00 - CaStatus_d) \quad (1)$$
$$AvailFrcPhos_d = 0.35 + (1.00 - PhosStatus_d) \quad (2)$$

where $AvailFrcCa_d$ and $AvailFrcPhos_d$ are the available fraction of calcium and phosphorus in forage on day *d*.

Available calcium ($AvailIntakeCa_d$, g Ca / day) and phosphorus ($AvailIntakePhos_d$, g P/day) are used to meet daily requirements:

$$AvailIntakeCa_d = AvailFrcCa_d \cdot IntakeCa_d \quad (3)$$
$$AvailIntakePhos_d = AvailFrcPhos_d \cdot IntakePhos_d \quad (4)$$

The predicted daily requirements for endogenous urinary calcium ($EUCa_d$, g Ca/day) and endogenous urinary phosphorus ($EUPhos_d$, g P/day) are:

$$EUCa_d = 0.0025 \cdot weightKG_d \quad (5)$$
$$EUPhos_d = 0.0003 \cdot weightKG_d \quad (6)$$

where $weightKG_d$ is body mass in kg (Braithwaite, 1986; Muir *et al* , 1987a).

The calcium and phosphorus leaving the rumen via the intestinal tract is excreted in the feces. We partition calcium and phosphorus in feces into metabolic fecal, unavailable, and dietary surplus fractions. The predicted daily requirements for metabolic fecal calcium ($MFCa_d$, g Ca/day) and metabolic fecal phosphorus ($MFPhos_d$, g P/day) are:

$$MFCa_d = 0.0065 \cdot WeightKG_d \quad (7)$$
$$MFPhos_d = 0.025 \cdot WeightKG_d \quad (8)$$

The requirements for calcium are lower than has been shown for domestic ruminants (Agricultural Research Council, 1980), but similar requirements have been measured in wild ruminants (Muir *et al.*, 1987a; Grasman & Hellgren, 1993). Unavailable calcium ($UnAvailIntakeCa_d$, g Ca/day) and phosphorus ($UnAvailIntakePhos_d$, g P/day) are calculated from dietary intake of calcium and phosphorus and availability:

$$UnAvailIntakeCa_d = IntakeCa_d - AvailIntakeCa_d \quad (9)$$
$$UnAvailIntakePhos_d = IntakePhos_d - AvailIntakePhos_d \quad (10)$$

The dietary surplus is calculated by difference between intake and the utilization of calcium and phosphorus for metabolic needs described below.

Calcium and phosphorus are required for gestation, lactation, and antler growth. If the animal is pregnant, gestation requirements for calcium and phosphorus ($GestCa_d$, g Ca/day, $GestPhos_d$, g P/day) are predicted from the number of fetuses, weight of fetus at birth (Table 1), and the day of gestation (Robbins & Moen, 1975), assuming a calcium content in the fetus of 13 g/kg and a phosphorus content of 7 g/kg (Agricultural Research Council, 1980). Calcium and phosphorus are also required for milk production if the animal is lactating ($LactCa_d$, g Ca/day, $LactPhos_d$, g P/day). $LactCa_d$ and $LactPhos_d$ are predicted from the day of lactation, the number of young suckled, a milk production curve (Moen *et al.*, 1997), initial and peak milk production per day, and the content of calcium and phosphorus in caribou milk (Robbins *et al* , 1987; Parker *et al* , 1990). Calcium and phosphorus are incorporated into antlers ($AntlCa_d$, g Ca/day,

$AntlPhos_d$, g Ca/day) with calcium content of 36% of ash and a phosphorus content of 18% (Brown, 1990). The ratio of Ca:P does not vary during antler growth (Muir *et al*, 1987b). Prediction of antler mass and ash content is described below (Eqs. 17-22).

The net calcium and phosphorus balances ($NetCa_d$, g Ca/day, $NetPhos_d$, g P/day) on a daily basis are calculated by summation of each factor:

$$NetCa_d = AvailIntakeCa_d - (EUCa_d + MFCa_d + LactCa_d + AntlCa_d) \quad (11)$$

$$NetPhos_d = AvailIntakePhos_d - (EUPhos_d + MFPhos_d + LactPhos_d + AntlPhos_d) \quad (12)$$

Gestation, lactation, and antler growth parameters are 0 when the animal is not pregnant, not lactating, or not growing antlers, respectively. A very important implication of Eqs. 11 and 12 is that calcium and phosphorus are conserved; all sources, sinks, and storage pools of calcium and phosphorus are updated each day on the same time step to ensure conservation.

If $NetCa_d$ is < 0.0 and $CaStatus_d$ is > 0.0, or if $NetPhos_d$ is < 0.0 and $PhosStatus_d$ is > 0.0, then resorption of mineral stores to meet mineral needs occurs ($ResorbCa_d$, g Ca/day, $ResorbPhos_d$, g P/day). We currently do not limit the mineral stores available for resorption each day, i.e., $MaxBoneCa * CaStatus_d$ could be resorbed in the model. Although it is unlikely that the animal could resorb its entire calcium or phosphorus reserves in a single day, it is also unlikely, in a biologically accountable model, that an excessive amount of mineral would be resorbed on a given day.

If $NetCa_d$ is > 0.0 and $CaStatus_d$ is < 1.0, or $NetPhos_d$ is > 0.0 and $PhosStatus_d$ is < 1.0, then repletion of the mineral stores occurs ($AdsorbCa_d$, g Ca/day, $AdsorbPhos_d$, g P/day). We allow up to 5% of *MaxBoneCa* and *MaxBonePhos* to be resorbed each day. We do not currently consider the negligible amounts of calcium and phosphorus in fat and protein during anabolism and catabolism of body tissues in the model. If there is still calcium or phosphorus remaining after adsorption to the bone, it is excreted:

$$SurplusCa_d = NetCa_d - AbsorbCa_d \quad (13)$$

$$SurplusPhos_d = NetPhos_d - AbsorbPhos_d \quad (14)$$

where $SurplusCa_d$ and $SurplusPhos_d$ are the surplus of each element (g/day). Fecal calcium and phosphorus ($FecalCa_d$, g Ca/day, $FecalPhos_d$, g P/day) are calculated as:

$$FecalCa_d = UnAvailIntakeCa_d + MFCa_d + SurplusCa_d \quad (15)$$

$$FecalPhos_d = UnAvailIntakePhos_d + MFPhos_d + SurplusPhos_d \quad (16)$$

Simulation of antler mass and composition

Unlike changes in length, changes in antler mass during antler growth are extremely difficult to measure experimentally. We are aware of only 1 experiment in which antler mass was determined throughout the antler growth period (Muir *et al.*, 1987b). We used data from this experiment, corroborated by data on phenology and changes in length of antlers of caribou, moose, and red deer (Bergerud, 1976; Van Ballenberghe, 1982; Fennessy *et al*, 1992), to predict changes in mass and composition of caribou antlers.

Antlers are metabolically active until velvet is shed. For about 75% of the period when velvet is on the antler, antler length and mass is increasing. Rapid mineralization and drying of the antler occurs during the last 25% of the period. Antler mass is predicted with a logistic equation during the increasing antler mass phase in the first 75% of the antler growth period (Eq. 17), and with a linear decline in mass during the period of rapid mineralization in the last 25% of the antler growth period (Eq. 18):

$$AntKG_d = 1.25 \cdot AntKg_{AntlGrowPeriod} \div (1.0 + 30.0 \cdot e^{-10.0 \cdot 0.95 \div AntlGrowPeriod}) \quad (17)$$

$$AntKG_d = MaxAntlerKG + FrcMin_d \cdot AntMassDecline \quad (18)$$

where $AntKG_d$ is antler mass in kg on day d, *AntlGrowPeriod* is the length of the antler growth period in days, and *MaxAntKG* is antler mass at the end of velvet shedding. In Eq. 18, $FrcMin_d$ is the fraction of the mineralization period completed, and $AntMassDecline_d$ is the difference between antler mass at the start of the mineralization period and *MaxAntKG*, assuming antlers are 85% dry matter at the end of velvet shedding (Muir *et al*, 1987b). Parameters in Eq. 17 result in a peak antler mass about 20% higher than antler mass at the end of velvet shedding (Muir *et al*, 1987b).

Antler tissue is composed primarily of water, protein, and ash. Antler ash is also predicted with a logistic equation for the entire antler growth period from data of Muir *et al.*:

$$AntFrc_d = 1.07 \cdot AntFrc_{AntlGrowPeriod} \div (1.0 + 125.0 \cdot e^{-10.0 \cdot 0.95 \div AntlGrowPeriod}) \quad (19)$$

where $AshFrc_d$ is the ash fraction of the antler, and *AntlGrowPeriod* is the length of the antler growth period in days. Antler organic matter, which is essentially all protein (Brown, 1990) is predicted from data in Muir *et al.*:

$$AshToOMratio_d = 0.17 + 1.46 \cdot FrcGrowPeriod_d \quad (20)$$

where $AshToOMratio_d$ (unitless) is the ratio of ash to organic matter in the growing antler, and $FrcGrowPeriod_d$ is the fraction of the antler growth period on day *d*. The organic matter fraction of the growing antler ($OMFrc_d$, unitless), can then be calculated from the previously derived ash fraction in the growing antler:

$$OMfrc_d = \frac{AshToOMratio_d}{AshFrc_d} \quad (21)$$

Finally, water content of the growing antler is calculated by subtraction:

$$Waterfrc_d = 1.0 - (OMfrc_d + AshFrc_d) \quad (22)$$

where $WaterFrc_d$ (unitless) is fraction of water in the antler on day *d*.

Simulation of energy and protein requirements

Daily energy and protein requirements have been previously described for our model (Moen & DelGiudice, 1997; Moen *et al*, 1997). Briefly, energy needs are estimated in a factorial fashion, considering costs of basal metabolism, activity, gestation, and lactation. With the addition of antler growth, we needed to estimate the efficiency of energy use to produce antlers, a parameter which is difficult or impossible to obtain experimentally (Brown, 1990; Goss, 1995). Because most of the organic matter in antler tissue is protein, we used $OMFrc_d$ to predict the amount of protein deposition in antlers each day, and then estimated the efficiency of use of energy to be 25%, which is between the 13% efficiency of energy use for gestation and the 40% efficiency of energy use for lean tissue growth (ARC, 1980). Antler mass was considered to be a portion of body mass when antler tissue was metabolically active. Energy requirements are assumed to decline linearly to 0 during the period after the antler has stopped increasing in length until the end of velvet shedding. This may underestimate the energy requirements for mineralization of antler tissue which occurs after the antler has stopped growing and before velvet shedding.

Protein metabolism is also calculated factorially, although urea nitrogen recycling must also be accounted fot in a simulation model. The recycling rate of urea nitrogen is determined by the diet nitrogen content and the animal's energy balance (Moen & DelGiudice, 1997). In order to simulate antler growth, we modified the daily nitrogen requirements by adding an additional nitrogen sink, the antler, and assuming that antler protein was 6.25% nitrogen.

Energy balance and body mass changes are primarily determined by forage intake and digestibility input parameters. Activity budgets and energetic costs of different activities were set as in (Moen *et al.*, 1997). In year-long simulations, we set energy intake to approximately reproduce the observed annual patterns of body mass changes in free-ranging caribou (Kelsall, 1968; Adamczewski *et al.*, 1987; 1993; Huot, 1989). When simulating male caribou, we reduced intake during a rutting season of 10 days in early October to 40 kcal digestible energy/kg$^{0.75}$ body mass. We did not increase activity costs during the rut (Miquelle, 1990). All of these input parameters could be easily modified if one wished to change energy costs of the rut or body mass parameters in the future. Phenological patterns in antler growth and reproduction were from Bergerud (1976). We set annual patterns in forage mineral content and digestibility according to the published literature (Hyvarinen *et al.*, 1977; Chapin *et al*, 1980; Staaland *et al*, 1983; Staaland & Sæbø, 1993; Chase *et al.*, 1994). Diet digestibility was highest in summer at 64%, and declined in winter to 40%. Crude protein in the diet was 13.5% in summer, and declined to 6% in winter. Calcium concentrations ranged from 0.50% in winter to 0.75% in summer, and phosphorus concentrations ranged from 0.30% in summer to 0.60% in winter. Diet digestibility, crude protein, calcium, and phosphorus all followed seasonal patterns with smooth transitions between minimum and maximum values (Moen *et al*, 1997).

Model validation and simulation protocol

We validated the calcium and phosphorus components of this model by simulating independent published experiments on mineral balances and antler mass during antlerogenesis and comparing measured calcium and phosphorus mineral balances to calcium and phosphorus balances predicted by the model (Stephenson & Brown, 1984; Muir *et al.*, 1987a; Grasman & Hellgren, 1993). We also compared predicted and measured fractional and absolute contents of calcium in the antler. We have previously validated the energetics and nitrogen components (Moen & DelGiudice, 1997; Moen *et al.*, 1997). The experiments used to validate the model were not used in model development. We changed input parameters which were specific to each experiment (e.g., time of year, length of experiment, initial body mass, start of antler growth period, food intake and digestibility, dietary nitrogen, calcium, and phosphorus) for each validation simulation. The same compiled executable was used in validation simulations for both red deer and white-tailed deer, and for the initial model experiments with male and female caribou.

We also set up a model experiment to determine the effect of increased energetic costs for growing antlers. In the first experiment, we changed the efficiency of use of energy for antler growth from 0.25 to 0.133, the efficiency with which energy is used for gestation by pregnant females (Agricultural Research Council, 1980). In the second experiment, in addition to decreasing efficiency of energy use to 0.133, we increased the energy requirements of the entire antler by 10 kcals/kg$^{0.75}$ of antler mass.

We began model experiments on the first day of antler growth for male caribou, and the first day of lactation for female caribou. Male caribou began simulations weighing 150 kg with 5% body fat on Julian day 120, the first day ofiantler growth. Male and female antlers weighed 10 and 1 kg at the end of velvet shedding, respectively. The antler growth period (*AntlGrowPeriod*, eq. 17) was 125 days for both males and females. Female caribou carried a single fetus through gestation, nursed the calf for 120 days, and grew antlers weighing 1 kg at the end of velvet shedding. Females began simulations weighing 80 kg with 5% body fat on Julian day 143, the day a single 5 kg calf was born after a 220 day gestation. The first day of antler growth for females was Julian day 166. Rumen weight varied seasonally (Adamczewski *et al.*, 1987) from 10% of body mass in summer to 14% of body mass in winter. Milk production increased from 1.25 l/day at birth to 1.75 l/day at peak lactation 1 week after birth, then declined exponentially until lactation ended when the calf was 125 days old. Milk was

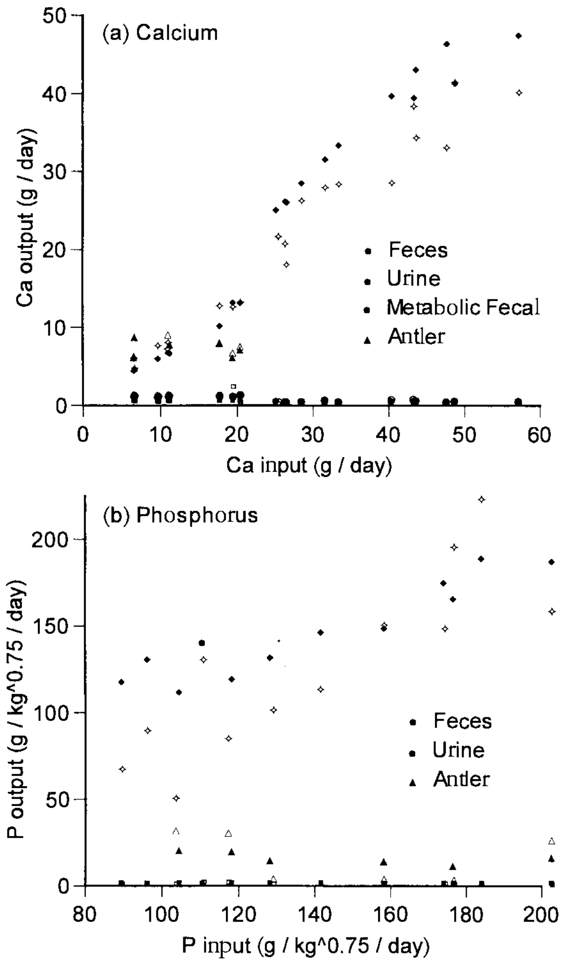

Fig. 2. Simulation of (a) calcium partitioning in adult red deer during antler growth and (b) phosphorus partitioning in adult male white-tailed deer throughout the year. Intake of each element in the model was equal to intake by experimental animals, and partitioning between urine, feces, and antlers was predicted. Solid symbols represent model output, hollow symbols of the same type are experimenral resulrs.

11% fat, 7% protein, 0.3% calcium, and 0.25% phosphorus (Robbins *et al.*, 1987; Parker *et al.*, 1990). *CaStatus* and *PhosStatus* were both set to 0.50 at the start of the simulations.

Energy costs of different activities, and activity budgets for each day are provided in Moen *et al.* (1997). The simulated activity budgets approximate activity budgets of free-ranging non-migratory ruminants and resulted in activity costs of about 20% of basal metabolic rate each day (Boertje, 1985; Fancy, 1986). Each experiment was replicated 30 times. Conditions among replications in each experiment were identical except for stochastic variation in the EASE model.

Results

Validation

Independent validation simulations were done by simulating experiments that were not used in model development. Predicted calcium partitioning of red deer and white-tailed deer and phosphorus partitioning of white-tailed deer throughout the year to urine, feces, and antlers corresponded with measured values across a wide range of calcium and phosphorus intakes (Fig. 2). Fecal production of calcium corresponded well with measured values (Fig. 2a), but the model slightly over-predicted fecal phosphorus at low dietary phosphorus intakes (Fig. 2b). We also compared measured absolute and fractional contents of calcium in growing antlers of red deer (Muir *et al.*, 1987a) to those predicted by Eqs. 17 - 22. Predicted and observed calcium fractions in the antler were not different (paired *t*-test, t_5 = 0.24, P > 0.81), nor was the absolute amount of calcium present in antlers (paired *t*-test, t_5 = 0.47, P > 0.65).

Model Experiments

Antler composition

Most of antler ash was deposited in the latter half of the antler growth period (Fig. 3). Water content peaked about midway through the antler growth period, then declined to 15% at the end of velvet shedding (Eq. 18). Antler ash, including calcium and phosphorus, increased throughout the antler growth period, and antler protein declined slightly (about 100 g in the 10 kg male antlers) during the last week of the velvet shedding period. Water comprised > 60% of antler mass until about the 80th day of growth, shortly before maximum antler mass was reached and mineralization rate increased. The high water content of developing antler is corroborated by the only published report on composition of developing antlers we are aware of (Ullrey, 1982) and follows that measured in the study used to derive eqs. 17 - 22 (Muir *et al.*, 1987b).

Energy Partitioning

Peak energy requirements for antler growth were no more than 1200 kcal/day for the male using our initial estimate efficiency of energy use for antler growth, and far lower for the female (Fig. 4a,b).

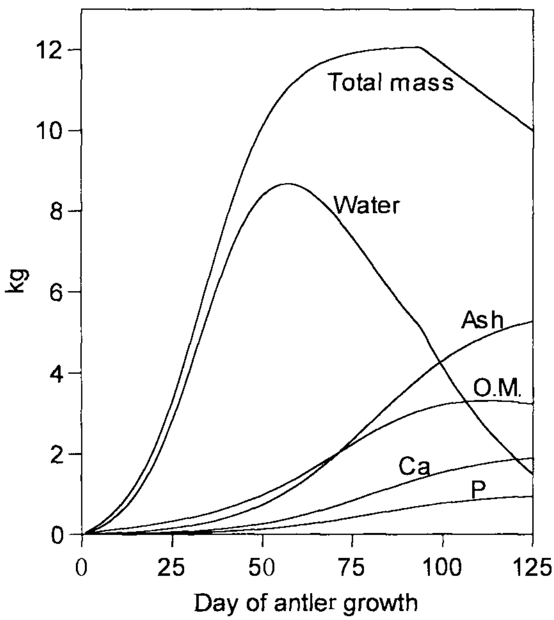

Fig. 3. Predicted antler mass and composition during the 125 day antlet growth period for a pair of 10 kg antlers from a caribou bull.

During the period when antlers were growing, about 4.5 and 25 times more energy was expended on deposition of fat and protein than on antler growth in males and females, respectively. Antler growth increased energy requirements by 8.5% and 1.5% during the antler growth period for males and females, respectively. Energy required for antler growth by females was much less than energy required for lacatation or gestation.

The low energy requirements for antler growth are due to our estimate of 25% efficiency of energy use for protein deposition in growing antlers and maintenance metabolism for the remainder of the antler. When we decreased the efficiency of energy use to 13.3% in Experiment 1, the male had to increase energy intake by 9% to maintain the same body mass, and energy required for antler growth increased to 14% of total energy requirements during the antler growth period. When we decreased the efficiency of energy use and increased the cost of maintaining antler tissue in Experiment 2, the animal had to increase energy intake by 23% to maintain a similar body mass, and energy requirements for antler growth increased to 16% of total energy requirements. In Experiment 2, the peak energy required for antler growth was about 60% of the basal metabolic rate, and energy requirements

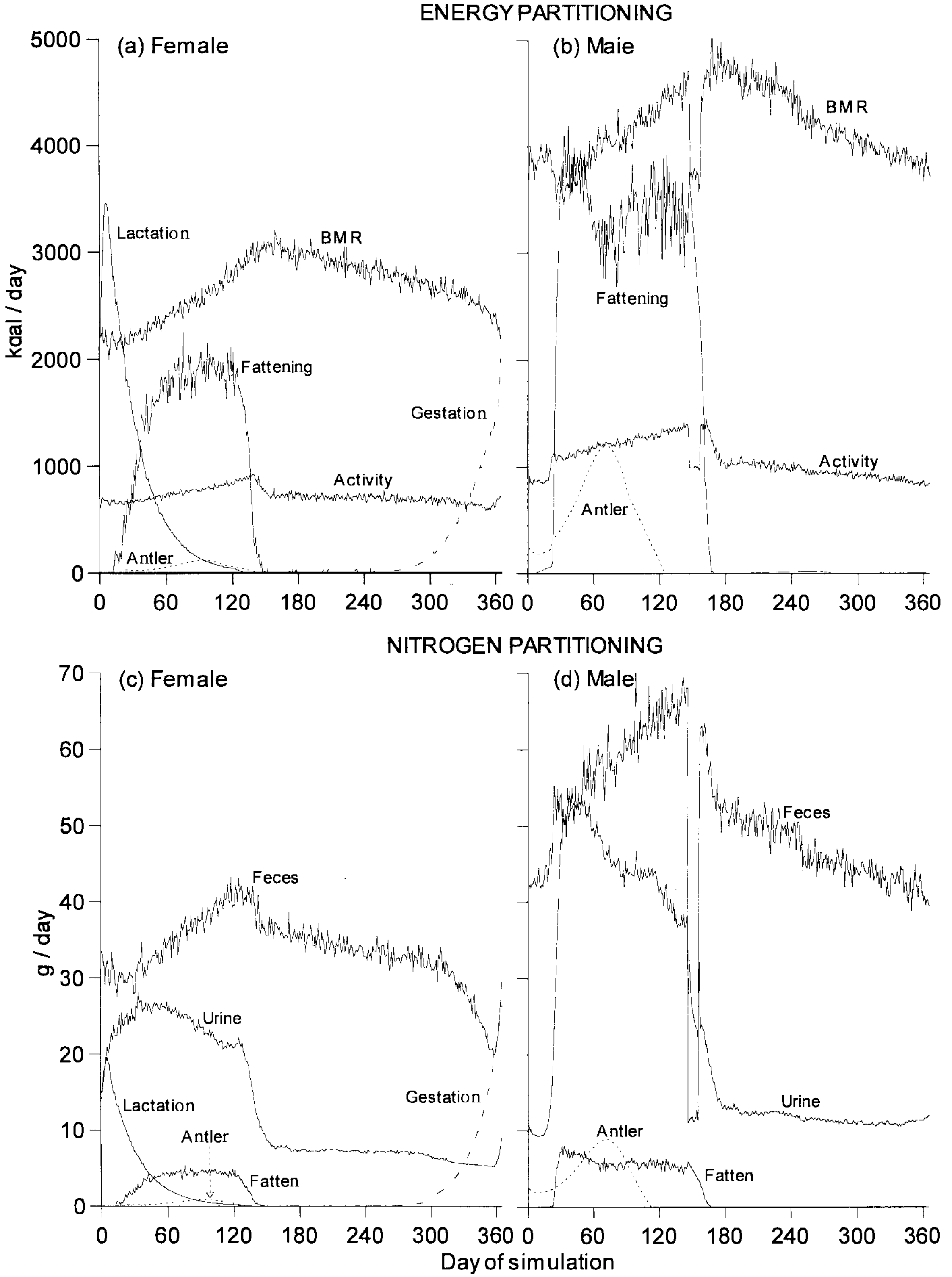

Fig. 4. Predicted annual energy partitioning for a caribou cow producing 1 calf (a) and a caribou bull (b) and predicted annual nitrogen partitioning for a caribou cow producing 1 calf (c) and a caribou bull (d).

for antler growth averaged 25% of basal metabolic rate during the period of antler growth.

Nitrogen Partitioning

Most of the ingested nitrogen from plant material is excreted in either feces or urine on a diet which is 13.5% protein in summer (Fig. 4c,d). Nitrogen is incorporated into antlers and muscle protein in the summer by males, but the total amount incorporated is < 20% of the amount of nitrogen excreted each day. Nitrogen requirements for females are higher because of requirements for gestation and lactation, but are still less than the amount excreted in summer. Nitrogen excretion declines in winter because dietary nitrogen content is low, forage intake decreases, and the nitrogen recycling rate increases.

Calcium Partitioning

Contrary to previous work with smaller antlered cervids, annual calcium requirements for male caribou are much larger than calcium requirements for gestation, lactation and antler growth in female caribou (Fig. 5a,b). For these simulations, annual calcium deposition in antlers was 1.9 kg in the male, compared to the 0.4 kg of calcium required for gestation, lactation, and antler growth in females. Calcium deposition in antlers by males was more than 25 g/day from day 66 to day 96 of antler growth. From days 55 to 96 of antler growth 0.1 kg of calcium was resorbed from the skeleton and deposited in the antler, maximum resorption was < 6 g/day. This represented about 5% of the total calcium in the antler, and > 25% of the calcium which could be resorbed from the skeleton before *CaStatus* became 0.0. These resorption rates are specific to the antler mass and calcium intake conditions of this simulation, but do demonstrate when calcium is likely to be in most demand under other conditions.

Phosphorus Partitioning

For these simulations, annual phosphorus requirements for antler growth in the male were 0.95 kg, compared to the 0.25 kg of phosphorus required for gestation, lactation, and antler growth in females (Fig. 5c,d). Phosphorus deposition in antlers by males was more than 12 g/day from day 65 to day 97 of antler growth. The male resorbed 0.1 kg of phosphorus from the skeleton and deposited it in the antler from days 47 to 101 of antler growth, with a maximum resorption rate of 4.5 g/day. This represented > 50% of the phosphorus which could be resorbed from the skeleton, and about 10% of the phosphorus in the male's antler. More resorption of phosphorus than calcium was required because of the lower concentration of phosphorus in the diet. As with calcium, these resorption rates are specific to the antler mass and phosphorus intake conditions of this simulation, but do demonstrate when phosphorus is likely to be in most demand under other conditions.

Discussion

Our results have important implications for understanding the partitioning of energy and nutrients to antler growth in caribou, and provide quantitative predictions of the daily requirements for energy, nitrogen, calcium, and phosphorus throughout the antler growth period. Energy required by males for growing antlers and increasing body mass required an intake rate up to 4.5 times the basal metabolic rate, depending on the efficiency with which energy was used for antler growth, a parameter that has not been determined experimentally. This approaches the maximum predicted energy requirements for female white-tailed deer nursing 2 fawns (Moen, 1978). Most of the energy intake of males in summer was used to meet maintenance requirements and for deposition of fat and protein. Energy requirements for antler growth in females were very low relative to other energy requirements. Strong selective pressures for growth of antlers in female caribou would exist if females can grow small antlers at a low energetic cost in summer, and then increase energy intake in winter through the behavioral dominance conferred by the presence of even small antlers.

The more negative balance for phosphorus than calcium was somewhat unexpected, given experimental work with white-tailed deer (Grasman & Hellgren, 1993). However, as those authors suggested, caribou would be the cervid species most likely to be phosphorus limited. The animal was in a more negative phosphorus balance because plant concentrations of phosphorus were lower than plant concentrations of calcium. During the period of antler growth in males, the bone Ca:P ratio increased from a normal value of about 2.0 to about 3.3 when calcium and phosphorus were uncoupled in bone resorption. This ratio may be higher than is physiologically acceptable, suggesting that some of the bone calcium should have been resorbed and excre-

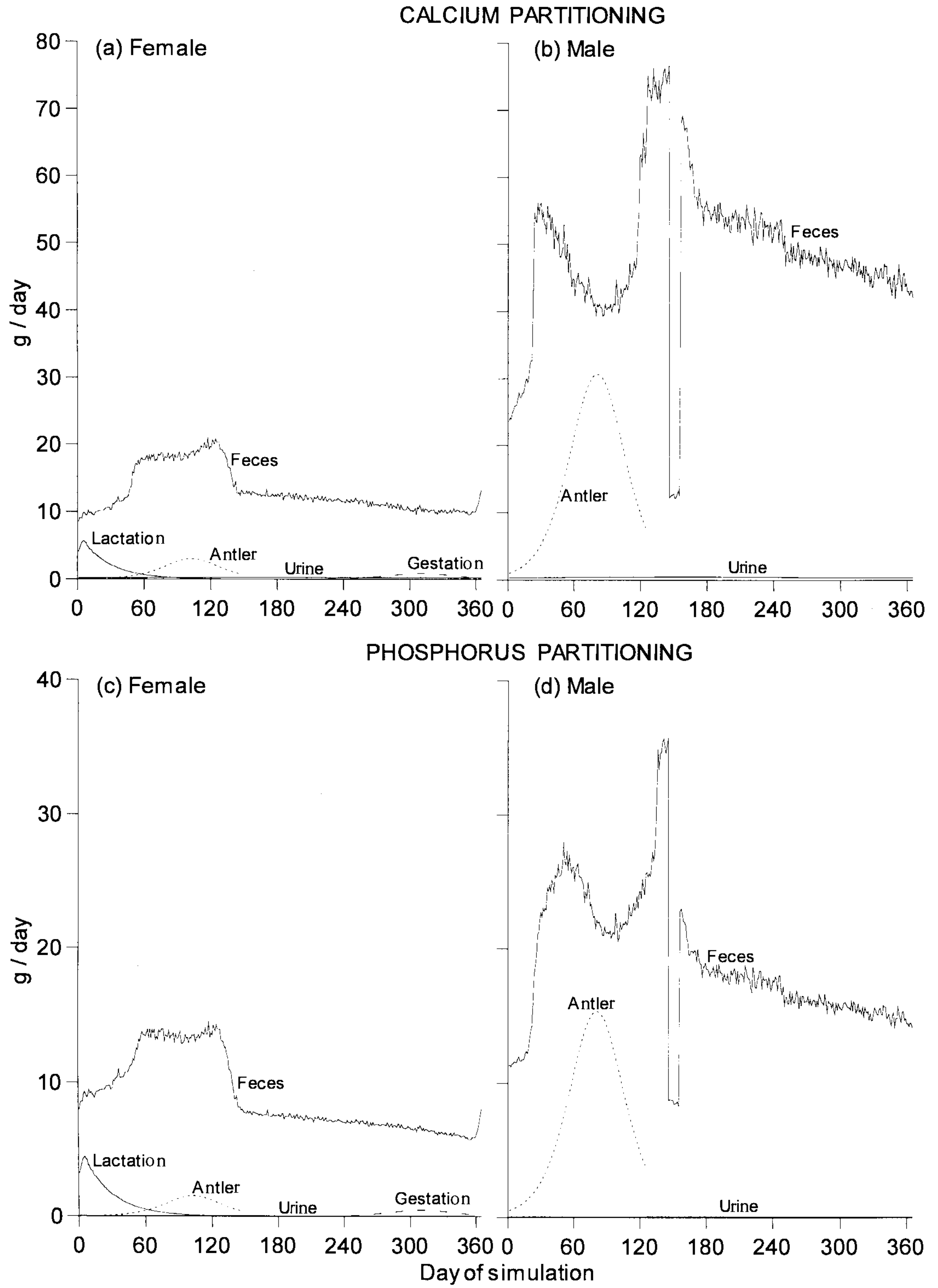

Fig. 5. Predicted annual calcium partitioning for a caribou cow producing 1 calf (a) and a caribou bull (b) and predicted annual phosphorus partitioning for a caribou cow producing 1 calf (c) and a caribou bull (d).

ted in our simulations with male caribou. An alternative mechanism to maintain a constant Ca:P ratio would be to increase the availability of phosphorus (Eq. 2, $AvailFrcPhos_d$) at a faster rate as bone phosphorus was depleted (Grasman & Hellgren, 1993). Demonstrating resorption of bone does not imply that phosphorus limitation has occurred, as resorption of bone for antler growth is a normal physiological process (Banks *et al.*, 1968a; b). Daily balance of phosphorus is less important than the seasonal balance, provided that resorption requirements on any single day of antler growth can be met.

There are some specific biological situations we do not consider in the model in its current state, and other areas where additional research would improve the model. For example, should an animal grow antlers when it is in negative energy balance in late winter and early spring, or should it just prepare antlers physiologically for growth, and begin growing as soon as spring flush of growth appears? The latter case would appear to be supported by the logistic increase in antler length observed in cervids. Antler composition during the first week of antler growth is predicted by extrapolation in the model. Experimental data from the first week of antler growth would be desirable, but given the relatively small antler mass during the first week of antler growth we feel that the extrapolation is acceptable, particularly since the alternative is to "do nothing". This is the type of data that could be collected opportunistically from caribou that are accidentally killed while antlers are growing.

The model does not currently adjust antler density. However, the model could be used to predict the effects that changes in antler density have on overall mineral requirements during antler growth. Another unresolved issue is how the animal should adjust antler growth or lactation if either phosphorus or calcium are completely depleted from bone. At the extremes of depletion, death would occur (Hyvarinen *et al.*, 1977). Prior to death, however, could the animal modify its foraging strategy so that it ate only those plants highest in available phosphorus? Results of the model suggest that peak requirements for antler growth in males would be shortly before the antler has stopped increasing in length. Selective foraging for high phosphorus plants could be tested by observation of food habits. A related issue is whether calcium and phosphorus status (*CaStatus* and *PhosStatus*) should be coupled more tightly in the model, to prevent the high Ca:P ratios in bone that we observed in the model as it is currently formulated. Coupling calcium and phosphorus status would have little effect on model results, only a small reduction in body and ash masses would occur.

Requirements for antler growth appear to be generalizable to the point that the same set of equations can be used to predict antler mass and composition for most if not all cervid species. Even though data on antler mass during growth are only available for red deer, patterns in changes of length of growing antlers are similar for red deer, moose, and caribou when scaled appropriately (R. Moen, unpubl. data). The set of 6 equations required to predict antler mass and composition (Eqs. 17-22) present the opportunity to develop many testable hypotheses on antler composition and growth for caribou, and also for cervids in general.

This simulation model represents a summary of current knowledge about cervid physiology, specifically energy, nitrogen, calcium, and phosphorus metabolism. We used it to predict the annual energy, nitrogen, calcium, and phosphorus metabolism in both male and female caribou on a daily time step. We believe that the integration of energy, nitrogen, calcium, and phosphorus metabolism within the same simulation is a strong test of the biological accountability of model predictions. The modeling effort identified several areas where research would result in an improved simulation model, and also would result in improved knowledge of caribou biology.

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Status of woodland caribou in Ontario: 1996

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Abstract: Over 20 000 woodland caribou were reported in Ontario during 1966, the highest figure ever published. Photographic counts of the Pen Islands herd, bordering Manitoba, have shown constant increases from 2300 in 1979 to 10 800 in 1994. Elsewhere in Ontario, estimates have been declining, from 13 000 in 1965 to 11 000 in 1989 to under 10 000 in 1996, a trend that may or may not be real because of differing survey methods. On the Hudson Bay Lowlands (excluding the Pen Islands caribou) 8600 were reported in 1965, 7200 in 1989, 5500 in 1996, an apparent decline. The transitional fotest populations has remained stable. Estimated caribou numbers inhabiting the ttue boreal forest have dropped from nearly 4000 in 1965 to 2700 in 1996, but this decrease was not confirmed by careful within-district breakdowns of sub-populations by habitat types and may be an artifact of classification from distticts to regions. The sharpest decrease was reported for the Central Region, north east of Lake Superior, where estimates dropped from 500 in 1965 to 475 in 1989 and to 68 in 1996. Individual caribou bands approach recognized minimum numbers for isolated populations, and even totals by sub-population remain low: over 1 300 in commercial forests, about 500 in potentially commercial forests, and 8-900 in parks. Due to small numbers in widely dispersed band-locations, the potential for human disturbance affecting these forest dwelling caribou is substantial.

Key words: *Rangifer tarandus caribou*, population, trends.

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Introduction

Extensive areas, dense forests, and small, widely-spaced bands make estimating numbers of caribou in Ontario difficult. Present methods remain imprecise, yet attempts must be made in order to determine current status. Woodland caribou once ranged south to about 46 degrees latitude in Ontario, but by 1993 their contiguous range extended southward only to about 50 degrees (Cumming & Beange, 1993). Most authors (DeVos & Peterson, 1951; Cringan, 1957; Simkin, 1965; Darby *et al.*, 1989; Cumming & Beange, 1993) have assumed related decreases in caribou numbers, and ascribed them directly or indirectly to expanded human activities in the forest. Thus the question of caribou numbers addressed in this paper has immediate implications for caribou management and conservation, and for forest management in Ontario. Overall estimates, although useful for global planning, may conceal changes within component populations that might require management response. Thus, in addition to compiling total numbers for Ontario, this paper breaks down the overall figure into estimates for individual populations, and suggests management implications.

Methods

Woodland caribou currently range over the Precambrian Shield in Ontario from Hudson Bay to Lake Superior, an area that grades from open muskeg to full boreal forest. Ahti (1967) classified this area into 7 regions and Simkin (1965) provided population estimates for 6 of these. I have used them once more in this paper so that comparisons with previous estimates would be possible. Coastal Tundra Belt and the Sub Arctic Lichen Belt (combined by Simkin, 1965) constitute the Hudson Bay Lowlands; Ahti (1967) considered the latter the best lichen range in Ontario. To the south lies an ecotone between the muskegs of the north and the true boreal forest of the south, recognized by (Ahti, 1967) as the Northwestern Region and the Eastern Swamp Region. In the boreal forest itself he identified the Western Rock Region, the Nipigon-Superior Region, and the Central Region.

Cumming & Beange (1993) showed a northern limit to commercial forests in Ontario. This line includes as commercial the three southern regions, except for the northwestern corner of the Western Rock Region; on the other hand, it includes as commercial a small southern corner of the Northwestern Region, and a belt along the southern boundary of the Eastern Swamp Region. Thus the regions cannot be assigned exactly to the non-commercial/commercial split but the included and excluded areas approximately balance so summaries proclaim the three southern regions as commercial forest.

The information for this paper was collated from estimates of caribou numbers provided for 13 districts of the Ontario Ministry of Natural Resources (OMNR) by district biologists and other management personnel. OMNR personnel in each district were asked to examine, revise, and return tables with previous estimates by district (Cumming & Beange, 1993). New tables were returned to each respondent for corrections and modifications. Finally, telephone calls and Faxes helped to sort out problem areas. Unfortunately, district boundaries have changed and personnel moved so that exact comparisons among districts are not always possible. Compilations provided estimates for larger areas with fewer boundary problems, and for the province as a whole.

Field survey methods differed widely among districts due to the diversity of habitat conditions and caribou numbers. Pen Islands caribou, living mainly in open country, were counted from aerial photographs (Abraham & Thompson, 1998), undoubtedly the most reliable method used by anyone contributing information. Elswhere in open country, transects similar to those initiated by Simkin (1965) have been continued by Thompson (1986) and others, but in forested country such methods are not possible. Direct aerial counts of caribou on randomized plots, such as those carried out for moose in Ontario since 1956 (Cumming, 1958; Bisset & McLaren, 1995) are not feasible for caribou, nor do they make sense for a species so scarce and widely distributed, but moose surveys occasionally contributed knowledge about caribou by locating randomly selected survey plots in places where aircraft otherwise would seldom fly, but where caribou were found.

Less reliable methods can provide some ideas of caribou numbers in places where preferable methods are not possible. Caribou can be counted when they move onto frozen lakes during March and April; however, because observed proportions of the bands can seldom be guessed, the counts provide only minimum estimates, perhaps supported by other information (e.g., Cumming & Beange, 1987). When tracks are few, numbers of animals can be determined, but in larger track complexes this becomes impossible.

Recently, increased efforts at determining use of forest stands by caribou for forest planning have located new caribou bands in several districts. Subsequent efforts to follow movements with the ARGOS satellite tracking system (Craighead & Craighead, 1987) have provided increasingly accurate ideas about numbers.

Results

Compiled 1996 data totaled 20 757 caribou (Table 1), the highest estimate ever published for Ontario (compared with 1300-3000 estimated by DeVos & Peterson, 1951; 7200 by Cringan, 1957; 12 555 by Simkin, 1965; and 15 682 by Darby et al., 1989). The largest component population, the Pen Islands herd estimated at 10 798 animals (Table 1), contributed over half the caribou in Ontario. Having increased steadily in numbers from 2 300 in 1979, they also represent the only Ontario population that is unquestionably growing, or immigrating (Abraham & Thompson, 1998).

Apart from these Pen Island caribou, district estimates ranged from 12 to 4500 caribou (Table 1). With this great variation, total numbers have little meaning. Even district comparisons are difficult as they may change dramatically over time for reasons that are not always clear. Some, like those for Cochrane District (32 for 1996 v.s. 373 by Darby *et al.*, 1989) may be due to movements of caribou across borders (see note Table 1). Others districts, as with Dryden (25 v.s. 7), report changed numbers due to shifts in district boundaries. Many district estimates appear to vary greatly because numbers of caribou are so few that counts change from year to year. A few estimates are identical with those of Darby *et al.* (1989) because no new estimates are available from remote areas where expense and

Table 1. Estimates of woodland caribou numbers in Ontario for 1996 by Ministry of Natural Resources districts.

District[a]	Caribou estimates by district	Bases of estimates: Flights, ground observations, photographs to count caribou	Flights for moose surveys	Reports from the public	General knowledge of OMNR personnel	Estimates reported by Darby *et al.* (1989)	Comments on current estimates and reasons for changes from Darby *et al.* (1989)
Cochrane	32	X	X			373±345	Movement between Ontario and Quebec[b]
Dryden	25	X				7 (entered as Ignace)	Also share some animals with Thunder Bay
Geraldton	950	Winter, summer			X	2709	Difference unexplained
Hearst	12				X	22	
Kapuskasing	24				X	80	
Kenora	50	X		X	X	37	Moving among Woodland Caribou Park, commercial forests, and Manitoba
Moosonee	4534	10% survey				4528±1075	Based on Thompson (1986)
(Penn Islands)	10798	Photographs				4800	Population increase
Nipigon	178	X			X	278	New boundaries
Red Lake	275					570	Movement between Ontario and Manitoba
(WPLUP)	500						Based on OMNR (1982)
Sioux Lookout	720	X			X	1750	
(WPLUP)	1750						Based on OMNR (1982)
Terrace Bay (Slate Islands)	35 375	Summer ground observations		X	X	476	Population crash, partial recovery, on Slate Islands
Thunder Bay	375	X			X	0	Discovery of new bands, changes in boundaries
Wawa	124	X	X	X	X	52	Some small bands up, some down
Total	20757					15682	

[a] District names, personnel and estimates as of August, 1996.
[b] During the winter of 1996-97, 300 additional caribou were found in Cochrane commercial forest. Since a similar number had previously been reported for adjacent Qubec, caribou may move back and forth.

logistics prohibits annual estimates. Although most differences can be explained, they are so numerous that district by district comparison is not very fruitful.

To reduce difficulties in assigning counts to districts, estimates were collated within the 6 caribou habitat regions (Table 2) used by Simkin (1965). Even in these larger units, assigning estimates proved difficult, and at least some of the apparent differences may result from mis-classification of districts into the larger regions. To further reduce classification difficulties, regions were grouped in pairs according to habitat type.

The Sub-Arctic Lichen Belt appears to have progressively decreased from 6976 in 1965 to 3273 in 1996, only half of its former size (Table 2). The Eastern Swamp Region, on the other hand, is at least holding its own. However, the decrease in the first region is such that the two regions combined also show a progressive decrease. Estimates for the Northwestern Region have increased substantially, while those for the Western Rock region have decreased. These changes raise suspicions that the differences may be due to the difficulty in assigning districts to regions. Indeed, the combined total for these two regions shows no apparent trend.

In a similar way, the Nipigon-Superior Region shows gradually increased estimates while the Central Region has shown a remarkable decrease. In this case, the overall trend for the combined regions remains downward. Furthermore, the sum for the True Boreal Forest was also slightly downward. The totals for Ontario, excluding the Pen Islands herd, have also gradually decreased over this period (Table 2).

More precise comparisons can be made over a shorter term by comparing estimates for 1990 with those for 1996 (Table 3). These data show increases in estimates of caribou numbers: from approximately 800 to 1300 in the commercial forest, 400 to 480 in the potentially commercial forest, and 600 to 800 in parks and other protected areas. The total estimate for the commercial portion of the boreal forest doubled during those 6 years, probably due to increased effort at finding caribou bands.

Discussion

Caribou near the Pen Islands may have migrated from farther north in the early 1970's (Abraham & Thompson, 1998), and they continue to move in and out of Manitoba, but they constitute the largest and fastest growing population in Ontario. Those on the Hudson Bay Lowlands, in contrast, may have been declining. For the Lowlands caribou, habitat disturbance has changed relatively little over hundreds of years, but they have been subjected to relatively heavy hunting, a possible cause for the apparent decline. Caribou in the transition zone face relatively little habitat disturbance and less hun-

Table 2. Comparisons of 3 sets of estimates (1965, 1989, 1996) in regions reported by Simkin (1965) (excluding Penn Island caribou).

Region	Simkin (1965)	Darby (1989)	Present (1996)
Sub Arctic Lichen Belt	6976	4528	3273
Eastern Swamp Region	1590	2709	1761
Total Hudson Bay Lowlands	8566	7237	5034
Northwestern Region	232	2320	2250
Western Rock Region	2857	44	1820
Total Western Transitional	3089	2364	4070
Nipigon-Superior Region	400	806	787
Central Region	500	475	68[a]
Total Eastern Boreal	900	1281	855
Total commercial forest[b]	3989	3645	2675
Totals for Ontario	12555	10882	9959

[a] See note Table 1.

[b] Including the Western Rock Region, Nipigon-Superior Region, and Central Region.

Table 3. Estimates of caribou numbers for 1996 in the commercial portion of Ontario's boreal forest compared with those reported for 1990 by Cumming & Beange (1993). Increases were believed due mainly to finding additional caribou bands.

	Reported for 1990[a]	Current 1996
In current commercial forests	828	1328
In potential commercial forests	400	481
In parks and undisturbed islands	600	839
Total estimate for boreal forest area of Ontario	1828	2648[b]

[a] Cumming & Beange, 1993.
[b] The difference from Table 2 is due to a finer breakdown among habitat categories within districts.

ting; they seem to be holding their own. In the more southerly portions of the true boreal forest, habitat disturbance has been widespread. Although changes in distribution suggested substantial declines prior to 1965 (Cumming & Beange, 1993), the evidence for continuing decline is less clear. The Central Region reported fewer caribou than previously, but in more westerly regions, discovery of new caribou bands offset any losses in numbers.

The further breakdown of Boreal Forest caribou into 3 sub-populations (Commercial, Potential Commercial, and Protected) provided similar advantages. Caribou estimates for the true boreal forest after an apparent decline from 1965 to 1989 showed an apparent increase, not only in the totals, but also for commercial forests, potentially commercial forests (i.e. may be designated commercial in the next few years) and in parks. However, most of the increase appeared to be in commercial forests where increased efforts at identifying stands supporting caribou revealed previously unknown bands. Parks continue to harbor substantial numbers (total 839-964 caribou, with over 600 of these supplied by Wabakimi and Slate Islands parks.

Implications for management

Thomas (1998) maintains that estimates of caribou (*Rangifer tarandus*) numbers contribute little toward setting management goals. This view may be true for barren-ground caribou, but for woodland caribou with their modest, widely separated bands, the importance of dispersion information (how many and where) can scarcely be doubted. Management goals for very small caribou herds, such as 25-30 Selkirk caribou shared between British Columbia and neighboring states (Freddy 1979) must differ widely from those for very large ones, e.g. the 800 000 George River herd (Couturier *et. al.*, 1996). In Ontario the question is, "Which populations should be managed toward which goals?".

The growing Pen Islands herd is probably being under-harvested; management goals might include increased hunting to approach a sustained yield. Other caribou in the Hudson Bay Lowlands show some evidence of decrease since 1965. In this situation, management must involve decisions regarding allowable surpluses, effects of snowmobiles, whether legal hunting by non-natives should be introduced, and similar concerns. Thus, management of both the Pen Island population and the remaining Hudson Bay Lowland caribou should aim at sustained yield, but from opposite directions. Caribou in the transition forests show continuing good populations and are threatened by neither hunting nor habitat disturbance. Little management is necessary at the present time.

Management of caribou in the true boreal forest faces other problems. Caribou are occasionally hunted by aboriginal people, but they prefer moose (Hamilton, 1984), and legal hunting has not been permitted since 1929. On the other hand, caribou bands have been lost along the southern limits of their distribution throughout this century, apparently due to habitat change (Cumming & Beange, 1993). There is widespread agreement that this northward retreat must be stopped to retain any caribou in the commercial forest. The currently higher estimates of caribou numbers relieve concern to some extent, but do not remove it. The 50:500 rule (50 animals for short term survival, 500 for the long term, Soulé, 1987) must be at least doubled, perhaps tripled, for a caribou population to include the many non-breeding animals. At double the estimates by Soulé (1987), there remain plenty of caribou in the boreal forest as a whole for long term survival. But these caribou are widely dispersed in bands not exceeding 500, most 150 or less. They probably always have been (Simkin, pers. comm.). In the past genetic exchange among caribou bands was assured by movement of individuals between bands. Radio telemetry has supported this idea by showing that caribou travel extensively, visiting other caribou bands with which they do not regularly associate (Cumming & Beange, 1987), and this finding has been confirmed by recent ARGOS tracking (Gollat, pers. comm.). However, if the large caribou bands, in and out of parks, become the only ones in the commercial forest, such exchange is no longer assured. To guarantee future presence of caribou in the forest, a network of small caribou bands must be retained among the larger aggregations to perpetuate genetic variety. Survival of even the larger bands and park caribou may depend on retaining these linkages. Caribou in the boreal forest must be managed with the goal of species richness: no species should be lost from the original ecosystem complex, least of all, these striking, large, and historically important woodland caribou. Managers might rely on parks for continuance of caribou presence in the commercial portions of the boreal forest of Ontario, but with Wabakimi and Slate Islands parks contributing over two thirds of the animals, numbers in the remaining parks appear too low for any confidence of survival even in the short term, and their wide spacing almost ensures island-like isolation. As for resource managers, it would be professionally unthinkable to manage the forests of northern Ontario in ways that would result in one of the most important indigenous species being lost from our forests. Every band saved by maintaining suitable habitat helps keep these caribou a step further from such a fate.

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Status of woodland caribou in Saskatchewan

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Abstract: Recent research has shown that woodland caribou in Saskatchewan exist as relatively separate populations within a metapopulation. Preliminary analyses show that individuals within all populations are selecting peatland habitat types (i.e., fens and bogs) throughout the year. Despite an absence of hunting, populations south of the Precambrian shield appear to be declining slowly, while those on the southern margin of the shield may be declining more rapidly. The apparent population decline is likely due to high tates of predation, especially on neonates. To maintain viable caribou populations in the region, forestry operations must be managed to maintain adequate amounts of preferred habitat types and connections among populations. At a coarse scale, preferred habitat is that which acts as a refuge from predators. Addirional information is required to categorize specific peatland types, as data in the existing provincial forest inventory are inadequate for both selection analysis and management purposes. Ongoing research into revisions to the forest inventory and analyses of bog and fen rypes selected by caribou are needed to focus future management strategies.

Key words: demography, forestry, habitat,management, metapopulation, peatland, population.

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Background

Woodland caribou (*Rangifer tarandus caribou*) in Saskatchewan range from the southern limits of the ranges occupied by the Beverly and Qamanirjuaq herds to the southern margin of the boreal forest (Fig. 1). Kelsall (1984) estimated the provincial population at 2500 animals (ca. 0.01 caribou·km^{-2}) and Edmonds (1991) considered all woodland caribou in the province to belong to the boreal ecotype. Furthermore, Ruttan (1960) observed few interactions among individual groups of caribou in the region, suggestive of several populations within a metapopulation (*sensu* Wells & Richmond, 1995).

Rock (1992) concluded that most human impacts on caribou habitat in Saskatchewan have been restricted to the area south of the Churchill River, particularly in the area south of the Precambrian shield that contains the province's commercial forestry operations (Fig. 1). In 1966 the province's first pulp mill was constructed, and road building began in the southern boreal forest. Logging and other habitat disturbances that favour early seral stages are thought to support higher moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) densities, leading to a subsequent increase in wolf (*Canis lupus*) density (e.g., Schwartz & Franzmann, 1989). Holleman & Stephenson (1981) documented the preference of wolves for caribou and other small ungulates when they were available. An increase in moose density can therefore facilitate predation on caribou by wolves (Bergerud & Ballard, 1988). Although wolves have been observed preying upon caribou throughout the region, moose and white-tailed deer have been thought to be more common prey (Ruttan, 1960; Trottier, 1986).

Prior to the mid 1980's, data available on caribou demography were largely limited to information on the success rates of sport hunters. The provincial licensed caribou harvest peaked in the early 1970's, and was followed by 13 years of steadily declining

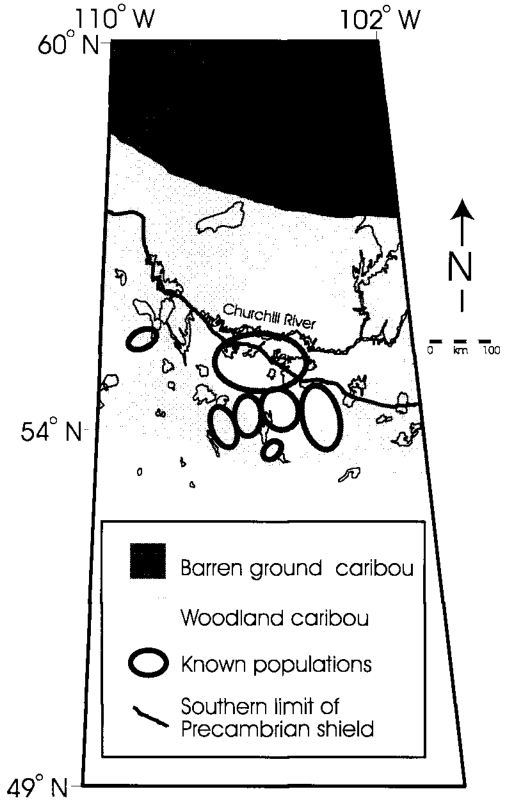

Fig. 1. Distribution of caribou in Saskatchewan showing location of identified woodland caribou populations.

hunter success rates prior to a moratorium being put in place in 1987 (Rock, 1992). Hunter success rates declined by an order of magnitude during this period. Though the use of population trend data has been characterized as unreliable in recent literature (e.g., Bradshaw & Hebert, 1996), the data used by Rock (1992) were collected in the same area by the same method over a 20 year period and they show a clear trend of decline. Rock (1992) reported that hunting was the likely proximate cause for the observed decline. Local reports indicated that increased hunting followed the increase in logging activity and road construction, and resulted in the decline or disappearance of many local caribou populations (Trottier, 1988). The pattern of decline or extirpation of woodland caribou populations following human activity has occurred across North America (Bergerud, 1974).

From the limited data available, Rock (1992) concluded that the birth rate of caribou in the region was high, but that both calf and adult survival rates were low. Minimal levels of subsistence hunting (Trottier, 1986) and the end of sport hunting should have produced an increase in the caribou population in the absence of major limiting effects of food shortage, disease, or predation. Rock (1992) speculated that the northern portion of the region was likely to contain the best remaining caribou range based on a history of limited logging activity and his assessment of the quality of the available habitat types in the area. Edmonds (1991) suggested that the required information on caribou in Saskatchewan should include a provincial caribou inventory and the acquisition of data on the size and status of various herds, as well as the delineation of caribou range.

Recent research

The first major study of woodland caribou in Saskatchewan was conducted between 1992 and 1996 with the objectives of assessing habitat selection and demographic performance of caribou south of the Churchill River (Fig. 1).

Demography

Caribou in central Saskatchewan are segregated into several populations with few interactions among individuals from different populations (Rettie & Messier, in press). This finding supports the observations reported in Ruttan's (1960) work, as well as more recent results in Alberta (Stuart-Smith *et al.*, 1997).

Rettie & Messier (in press) discussed demography of the woodland caribou metapopulation in central Saskatchewan and their findings are summarised in Table 1. Adult mortality of caribou in the region was similar to that reported for other populations thought to be in decline (e.g., Fuller & Keith, 1981; Stuart-Smith *et al.*, 1997). Rettie & Messier (in press) suggested that the metapopulation was not food limited based on their observations of early reproductive maturity, a high pregnancy rate, and a high parturition rate. They calculated the rate of increase from 1993-1996 survival and recruitment data and attributed the low rate of increase to high rates of predation on neonates and adult animals. Although Rock (1992) speculated that the more northerly portions of the study area would contain the best caribou habitat owing to lower levels of human disturbance, Rettie & Messier (in press) found the poorest demographic performance (r = -0.16) among animals in this region. The metapopulation does not appear to be increasing despite

Table 1. Demographic performance of woodland caribou in central Saskatchewan based on data from 1993-1996 (from Rettie & Messier (in press)).

Parameter	Value*
Adult survival rate (*n* = 63.6 caribou radio-tracking years)	0.84 ± 0.05
Conception rate of females at 16 months (*n* = 5 cows)	1.00 ± 0.00
Pregnancy rate (*n* = 51 cows)	0.94 ± 0.03
Minimum parturition rate (*n* = 28 cows)	0.86 ± 0.07
Calf:cow ratio (March) (*n* = 223 cows)	0.28 ± 0.03
Metapopulation rate of increase	-0.05 ± 0.06

* All rates and ratios presented as mean annual values ± 1 SD.

a ban on sport hunting and reportedly low levels of subsistence hunting. Rettie & Messier (in press) suggested that high levels of ptedation arising from (1) higher densities of black bear (*Ursus americanus*) and (2) an increase in wolf numbers in response to expanding moose and deer densities, were the proximate causes of the lack of population growth. Increased predation, especially on caribou neonates may be independent of caribou density and may ultimately be linked to habitat changes following logging.

Habitat selection

The distribution of woodland caribou populations is heterogeneous in response to habitat characteristics that may isolate them from wolves as reported by Cumming *et al.* (1996). Rettie and Messier (in press) speculated that such behaviour may place calving caribou in areas with higher densities of black bears. Preliminary analyses (Rettie - unpublished data) suggested that caribou in central Saskatchewan preferentially select peatland habitat throughout the year. Areas on the Precambrian shield may be inherently different in the quantity, quality, or distribution of peatland habitats secure from predators and may be more sensitive to human disturbance than areas further south. The provincial forest inventory maintained by the Forestry Branch of Saskatchewan Environment and Resource Management places the numerous distinct bog and fen communities into two coarse peatland (or "muskeg") categories. The lack of detailed information in the forest inventory has precluded the identification of specific bog and fen communities that woodland caribou may be selecting. Researchers at the University of Alberta have recently completed a detailed classification of bogs and fens in a 5000 km^2 portion of central Saskatchewan to provide the data against which to measure selective use by woodland caribou.

Current status of woodland caribou in Saskatchewan

Information currently available does not permit a revision of Kelsall's (1984) estimate of woodland caribou in Saskatchewan. Population trends suggest that the caribou metapopulation south of the Churchill River is fragmented and likely declining. The effect of logging activity in the area has included the production of habitat well suited to black bears, moose, elk (*Cervus elaphus*), and white-tailed deer, and hence to wolves. Viable caribou populations inhabit the remaining patches of habitat that are extensive enough to provide refuge from predators. Continued resource exploration and extraction in central Saskatchewan will further limit the amount of caribou habitat available and will result in the decline, and possibly the disappearance, of local caribou populations.

Research and management recommendations

If caribou are to remain viable in the region south of the Churchill River, the persistence of small local populations should be the key management objective as there appears to be little movement among populations. Furthermore, movements among populations are likely to become more restricted as the region becomes increasingly fragmented by roads and logged areas, an outcome that may prevent recolonization following local extinctions. Providing habitat to preserve the areas with low densities of predators used by local caribou populations, as well as to preserve corridors among them, should represent a management priority. Recent research activities have identified some of the remaining caribou populations, and will ultimately provide information on selective use of various habitat types. In this regard, it is likely that more data will be required to quantify the availability of the various types of peatlands in the region. These data are required to assess the relative preferences of caribou for different types of bogs and fens.

In contrast to the predictions of Rock (1992) we do not expect current research to support the idea that the best woodland caribou habitat in the region is in the areas on, or immediately adjacent to, the Precambrian shield. Despite higher levels of disturbance, the caribou populations which are stable or possibly even increasing are to be found further south. Though the more southerly populations are closer to active logging operations, they may still have access to larger or higher quality predator-free areas. The proximity of logging operations to remaining caribou populations increases the need for prompt action.

In summary, we agree with Edmonds (1991) that some local caribou populations may not be viable, and support the recommendation of Rock (1992) that parts of the boreal forest will need to be managed for caribou in order to ensure their persistence. Long-term monitoring of the distribution and demography of caribou in the region will be required to assess the success of any management strategies. Effective management will require cooperation from the forest industry, government, and aboriginal groups as suggested by Thomas & Armbruster (1996).

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Status of woodland caribou in Alberta

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Abstract: A recent teview of woodland caribou (*Rangifer tarandus caribou*) status in Alberta estimated that there are between 3600 and 6700 caribou occupying 113 000 km² of habitat. There are two ecotypes of caribou in Alberta; the mountain ecotype in the west central region and the boreal ecotype primarily in the norrh. Mountain caribou populations are stable or declining and boreal populations, where data are available, appear ro be stable or declining slowly. A major iniriative in caribou management in Alberta has been the development of the Woodland Caribou Conservation Strategy. This document was developed over two and a half years by a committee of multi-stakeholdet representatives. The past five years has seen an increase in baseline inventory and applied research jointly funded by government, industry and universities, addressing a wide range of management issues from caribou response to logging to interactions of moose, wolves and caribou in the boreal ecosystem. Land use conflicrs on caribou range remain high with timber harvesting, oil and gas development, peat moss extraction, coal mining, agricultural expansion and increasing road access overlapping. Cumulative effects of these disturbances are poorly understood and have received little attention to date.

Key words: population size, distribution, current research and management programs.

Rangifer, Special Issue No. 10, 111–115

Current status

Woodland caribou and their habitat are threatened in Alberta and the *Wildlife Act* lists them as an endangered species. This means that caribou are likely to become endangered in Alberta if the factors causing their reduction in numbers are not reversed. Since 1900, caribou distribution and numbers have declined along the southern edge of their range where human encroachment has been greatest. Alberta has two ecotypes of woodland caribou; a mountain ecotype in west central Alberta and a boreal ecotype primarily in northern Alberta. There are few data on past and current population sizes, and the decline in caribou numbers and distribution documented by Edmonds (1986) has been challenged (Bradshaw & Hebert, 1996). A recent assessment estimates that 3600 to 6700 caribou inhabit about 113 000 km² of northern and west central Alberta (Alberta's Woodland Caribou Conservation Strategy, 1996) (Fig. 1).

Mountain herds are estimated to total 600 to 750 animals with growth trends varying from stable to declining sharply (Brown *et al.*, 1994; Alberta Environmental Protection, unpubl. data). Densities and population trends estimated in two studies of boreal herds were 0.05 caribou/km² and stable (Alberta Environmental Protection, unpublished data) and 0.08 caribou/km² and stable or declining slowly (Stuart-Smith *et al.*, 1997). Most of the boreal herds of Alberta have not been adequately inventoried. However, baseline inventory and research studies of Alberta's woodland caribou populations have increased substantially in the past five years so the knowledge base has improved for understanding population numbers, trends, and limiting factors (Edmonds & Smith, 1991; Bradshaw, 1994; Brown *et al.*, 1994; Hornbeck & Moyles, 1995; Bradshaw *et al* , 1995; Stuart-Smith *et al.*, 1997).

Limiting Factors

In Alberta, scientists and managers agree that predation by wolves (*Canis lupus*) is the major cause of death of caribou that inhabit undisturbed habitat (Brown *et al* , 1994; Stuart-Smith *et al* , 1997; Alberta's Woodland Caribou Conservation Strategy,

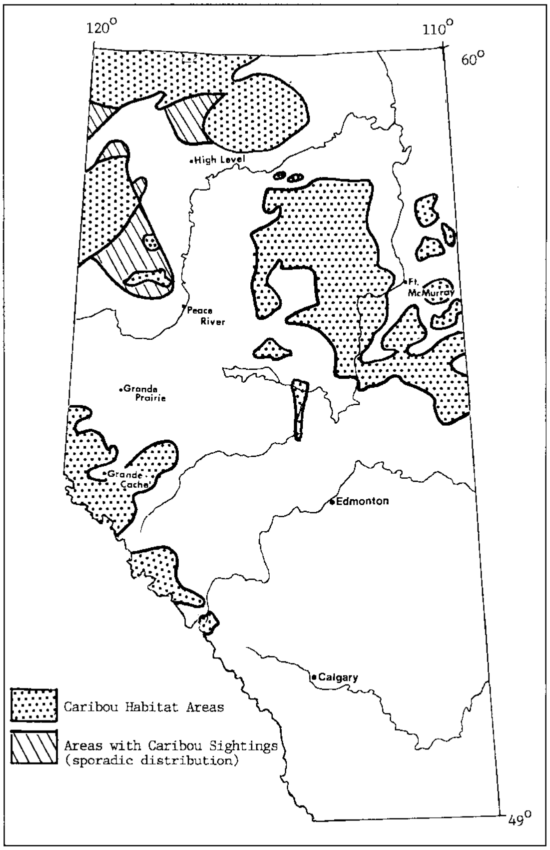

Fig. 1. The present distribution of caribou habitat in Alberta.

1996). Grizzly bear (*Ursus arctos*) predation is also an important factor in the mountain caribou herds (Edmonds, 1988; Brown *et al.*, 1994; Alberta Environmental Protection, unpubl. data).

Direct mortality from humans results from illegal hunting (recreational sport hunting was closed in 1981), mistaken identity (caribou shot in mistake for moose, deer or elk) and native subsistence harvest. Generally, data on human harvest is poor. In west central Alberta where monitoring has been longer and more successful, and road access within caribou range is abundant, at least five to ten caribou a year are shot (about 1% of the population) (Alberta Environmental Protection, unpubl. data). One study in northeast Alberta determined that three of 16 radio- collared caribou (18%) that died during the four year study were shot (Stuart-Smith *et al.*, 1997). Vehicle collisions are a serious problem with one mountain caribou herd where as many as 17 caribou (about 10% of the herd) have been killed in one winter on a highway that bisects their winter range (Alberta Fish & Wildlife, unpubl. data).

An adequate amount of suitable habitat is a key factor in maintaining viable caribou populations in Alberta. Timber harvesting, oil and gas exploration and development, coal mining, peat moss extraction, agricultural expansion and the proliferation of access routes have and will continue to result in loss, fragmentation or alteration of important habitat elements such as winter ranges, calving areas or migration routes. All caribou range in west central Alberta outside of provincial and national parks, and most range in northern Alberta has been committed to timber harvesting through Forest Management Agreements or Quota Licences. Conflict between timber harvest and caribou range in west central Alberta is high. In northern Alberta this conflict may not be as significant, particularly for the herds that remain for much of the year in large fens and peatlands. Expansion of coal mining in west central Alberta will remove alpine winter range and possibly disrupt seasonal movements of a mountain caribou herd. Oil and gas exploration and development generally does not result in much direct loss of habitat but the associated access can be a significant disturbance Incremental increases in the abundance and quality of roads, pipelines, seismic lines, etc. will result in increased mortality from hunting and vehicle collisions. Predator efficiency and seasonal movements may also be affected. Proliferation of access is one of the primary factors degrading the effectiveness of caribou habitat in Alberta.

Management

In 1994, the Natural Resources Service, Wildlife Branch convened a committee to develop a Provincial Woodland Caribou Conservation Strategy. This committee consisted of representatives from a variety of industries, conservation groups, aboriginal groups, academic and government agencies. They produced a document that identified and assessed the various factors (biological, social and economic) that may affect the overall vision of a healthy caribou population in Alberta; developed solutions to deal with those factors; recommended specific actions to make the strategy effective; and outlined the consequences of those actions. Maintaining the effective partnerships, cooperation, and lines of communication that were developed among the stakeholders will be key to achieving the caribou population and habitat goals that the committee endorsed.

The Caribou Conservation Strategy is provincial in scope and a more specific level of management is required. Presently three regional caribou management committees exist to develop management plans for caribou in northern and central Alberta. These committees are comprised of government, industry, university and aboriginal representatives. They; develop guidelines for how industrial activity will be conducted on caribou range and how adequate amounts of caribou habitat will be maintained in the short and long term; determine what further research or inventory is required in order to assess the effectiveness of the guidelines and habitat supply analysis; and develop a cost sharing agreement for the management of caribou and their habitat (Rippin *et al.*, 1996).

There are two main challenges in caribou management in the next decade:

1. to resolve and better define the conflict between timber harvesting (wood supply for the mills) and caribou habitat needs in both the short and long term;
2. to resolve and better define the conflict between caribou habitat and oil and gas development, which generally requires high quality access to extract and move their product to markets.

Resolution of these conflicts require a commitment from industry to try new approaches and to accept the increasing cost of operating in a fashion that maintains the sustainability of all resources on public land. The majority of industries in Alberta are meeting this challenge and along with government agencies and concerned public groups, are willing to try the concept of adaptive management as a way to ensure the long term survival of current caribou populations.

Current research

There are presently six research and inventory studies of woodland caribou being conducted in Alberta. Table 1 outlines the type of study, location, duration, primary investigator or contact person, and progress reports, if any.

Research needs

A relatively accurate and cost effective method of caribou herd inventory is needed. Woodland caribou herds are sparsely distributed often in forested habitat making sightability low. For the mountain caribou ecotype a large sample of marked animals is required, and the time of year when caribou are most visible must be determined. There are other methods that show some promise to assess population trends of the boreal ecotype such as annual March surveys to obtain cow;calf ratios and stratified track density surveys (Farnell & Gauthier, 1988). The technique of using faecal pellet counts and DNA sequencing for a 'mark/capture' estimation of population size also deserves investigation. Assessment of population status is of considerable importance to industries working within caribou range where operational guidelines can be costly. Industry and the public are concerned about our ability to manage viable caribou populations in the face of increasing human and natural impacts.

Future studies are needed to assess the effectiveness of mitigation guidelines applied to industrial and recreational activity on caribou range. New guidelines for operating in caribou range should be implemented on an experimental basis, monitored for population response and then if justified applied more broadly, i.e implement adaptive management. Changes in population trends; herd distribution and movements in response to disturbance (particularly the extensive linear developments of the petroleum industry); and recovery of lichens and other habitat attributes after logging are a few of the factors needing study. In northern Alberta, further information on the extent of human harvest is needed, and cooperative approaches with aboriginal communities are essential and are being developed.

Cumulative impacts are poorly understood. Several industrial developments can occur on caribou range simultaneously, complicating our understanding of individual limiting factors. Government regulation of human impacts on the land are dealt with individually. There is no requirement of an applicant to assess their impact within the context of other land use activities unless the type of project requires an environmental impact assessment. In Alberta, this is not required for land based forestry operations or oil and gas exploration. The regional management committees have recognized the presence and impact of multiple users on the land and are trying to co-ordinate and mitigate their accumulated activities. The field of cumulative impact assessment is a young discipline in Alberta, but models for elk and grizzly bears are being developed. The development of GIS (Geographical Information Systems) greatly increases

Table 1. Current studies of woodland caribou being conducted in Alberta.

Type	Location	Duration	Primary Investigator/Contact	Progress Reports in preparation
Woodland caribou response to clearcut logging on winter range	Grande Cache – west central Alberta	1993-1997	K. Smith Alberta Environmental Protection, Edson, Alberta T7E 1T2 ksmith@env.gov.ab.ca	(goal for distribution December 1997)
Woodland caribou and wolf distribution relative to linear corridors	Wabasca and Winefred Lakes – northeastern Alberta	1994-1997	K. Stuart-Smith Dept. of Forest Science, Oregon State University, Corvallis, OR, 97331-7501, USA stuartK@fsl.orst.edu	poster published – these proceedings
Spatial relationships dynamics of wolves, moose and caribou.	Northeastern Alberta	1994-1997	A. James Alberta Environmental Protection, Natural Resources Service. Grande Prairie, Alberta. T8V 6J4 ajames@env.gov.ab.ca	Ph.D. Thesis in prep. Dept. of Biological Sciences, University of Alberta T6G 2E9
Woodland caribou population, distribution and habitat use in northwestern Alberta predator-prey and	Caribou Mountains and Red Earth	1995-1999	B. Wynes Diashowa-Marubeni International Ltd., Peace River, Alberta T8S 1Y4 bwynes@telusplanet.net	none
Response of caribou to a long-term heavy oil development project	Wabasca	1996-199?	Elston Dzus Nova Gas Transmission Ltd. 158-10114 Ave. Edmonton, AB T5M 2Z4 elston.dzus@pipe.nova.ca	none
Movements and survival of caribou in relation to linear corridors	Red Earth, Wabasca and Caribou Mtns	1995-1998	Elston Dzus (see above)	none

Web Sites	Woodland Caribou Research and Management in Alberta http://129.128.55.125/profs/lmorgant/caribx/carib1.htm
	North American Caribou Resources http://www.ualberta.ca/~ajames/Caribou.html

our ability to do cumulative effects analysis. The next decade will require the application of such a management tool if caribou are to survive on some of the more heavily impacted ranges.

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Caribou in British Columbia: A 1996 status report

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Abstract: Caribou (*Rangifer tarandus*) in British Columbia are classified inro mountain, northern and boreal ecotypes based on behavioural and ecological characteristics. We recognized 12 mountain caribou herds, 27 norrhern caribou herds, and an area occupied by low density boreal caribou dispersed in the boreal forests of the northeast portion of the province. Abundance estimates were usually based on attempts at total counts made from rhe air. Trends were based on repeated population estimates or the difference between recruitment and mortality rares for each herd. In 1996 there were approximately 18 000 caribou in British Columbia; 2300 mountain and 15 600 northetn and boreal. These estimates suggest a slight increase in the numbers of both ecotypes over the last 18 years. Fifteen percent of the herds were reporredly increasing, 10% were decreasing, 31% were srable, but for 44% of the herds the trend was unknown. Historically caribou were found throughout 8 of the 14 biogeoclimatic zones in B.C. Catibou are now rarely found in the Sub-Boreal Spruce zone, likely due ro increased predation from wolves that increased in response to increasing moose numbers. Ranges of several herds in the Engelmann Spruce – Subalpine Fir and Alpine Tundra zones of south-eastern British Columbia are also reduced relative to historic conditions, probably because of habitat loss, habitat fragmentation, ptedation and hunting. Forest harvesting represents the greatest threat to caribou habitat and current research focuses on the mitigation of forest harvesring impacts.

Key words: *Rangifer tarandus*, caribou, demography, forestry impacts, distribution, habitat, biogeoclimatic zones.

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Introduction

Caribou (*Rangifer tarandus*) in British Columbia are classified into mountain, northern and boreal ecotypes (Bergerud, 1978; Edmonds, 1991; Stevenson, 1991) based on behavioural and ecological differences. Mountain caribou are found in the rugged mountains in the south-eastern portion of the province (Fig. 1). They winter at high elevations and rely almost exclusively on arboreal lichens because the deep snowpack restricts access to terrestrial foods (Stevenson & Hatler, 1985). Mountain caribou have been designated as a blue-listed species by the British Columbia Conservation Data Centre because of past declines in distribution and abundance. As a blue-listed species, these caribou are considered vulnerable or sensitive, and need special management to ensure their survival.

Northern caribou, on the other hand, occur in the mountainous western and northern parts of the province where snowfall is low, relative to mountain caribou habitat (Bergerud, 1978). They winter in either mature low elevation lodgepole pine or black spruce forests where they feed primarily on terrestrial lichen and to some extent on arboreal lichen, or also on high wind-swept slopes where there is access to terrestrial lichens (Bergerud, 1978; Stevenson & Hatler, 1985).

The boreal ecotype occurs in the relatively flat boreal forests of the northeastern portion of the province. They do not appear to occur in discrete herds, but live in small, dispersed, relatively sedentary bands throughout the year (Edmonds, 1991; Stevenson, 1991). The boreal ecotype is sometimes lumped with northern caribou (e.g., Seip & Cichowski, 1996) and because neither are considered vulnerable or sensitive, are yellow-listed.

The status of caribou in the province has been reviewed in whole or in part by Bergerud (1978),

Table 1. Status of British Colombia caribou herds in 1996.

Herd number	Herd name	Estimate	Trend	Other names	Source
	Monntain Caribou Herds				
1	South Selkirk*	50	stable	Kootenay Pass; Salmo-Creston	Simpson *et al.*, 1997
2	South Purcell	100	declining		Simpson *et al.*, 1997
3	Central Sclkirk	220	declining		Simpson *et al.*, 1997
4	Monashee	20	declining		Simpson *et al.*, 1997
5	Revelstoke*	400	stable		Simpson *et al.*, 1997
6	Central Rockies	50	stable		Simpson *et al.*, 1997
7	Wells Gray*	350	stable	North Thompson; Wells Gray North and Wells Gray South	B. Shear, pers. comm.
8	Quesnel Lake*	125	increasing	Cariboo Mountains	J. Young, pers. comm.
9	Barkerville	40	declining		J. Young, pers. comm.
10	George Mountain*	50	unknown		G. Watts, pers. comm.
11	Narrow Lake*	20	increasing		G. Watts, pers. comm.
12	Yellowhead*	875	increasing	McGregor; Hagen; Sugar Bowl; Hart Ranges	D. Heard, nnpubl. data
	TOTAL	2,300			
	Northern Caribou Herds				
13	Charlotte Lake	50–100	stable		J. Young, pers. comm.
14	Itcha-Ilgachuz-Rainbow*	1700	stable		D. Cichowski, pers. comm.
15	Tweedsmuir-Entiako*	500	stable		D. Cichowski, pers. comm.
16	Telkwa*	9	declining		R. Marshall, pers. comm.
17	Quintette*	200	unknown	includes Tumbler Ridge	J. Elliott, pers. comm.
18	Kennedy Siding*	100	unknown		D. Heard. unpubl. data
19	Moberly	200-400	unknown		J. Elliott, pers. comm.
20	Wolverine*	300–500	unknown	Omineca Mts; Germansen Lake	M. Wood, pers. comm.
21	Takla*	100	unknown		D. Heard, unpubl. data
22	Chase*	500–900	unknown	Omineca Mts; Axelgold-Sikanni	Wood, 1996
23	Graham*	800	unknown	Halfway-Prophet	J. Elliott, pers. comm.
24	Pink Mountain*	1300	stable	Sikanni Chief; Cypress River; Prophet River; Cameron-Chowade; Beatton-Blueberry	J. Elliott, pers. comm.
25	Finlay	200–400	unknown		J. Elliott, pers. comm.
26	Spatsizi*	2200	stable	Lawyer's Pass; Edozadelly; Tomias; Caribou Mt.; Pitman River	D. Cichowski, pers. comm.
27	Edziza	<200	unknown		R. Marshall, pers. comm.
28	Level-Kawdy	1400	unknown		R. Marshall, pers. comm.

29	Cry Lake*	>150	unknown		R. Marshall, pers. comm.
30	Frog	150	unknown		J. Elliott, pers. comm.
31	Gataga	250	unknown		J. Elliott, pers. comm.
32	Muskwa	1250	unknown	Mt. Dell; Crest; Toad; MacDonald-Racing	J. Elliott, pers. comm.
33	Rabbit	800	unknown	Kechika	J. Elliott, pers. comm.
34	Liard Plateau	150	stable		J. Elliott, pers. comm.
35	Horse Ranch	300	increasing	Deadwood	J. Elliott, pers. comm.
36	Little Rancheria*	450	declining	Blue-Rancheria	R. Marshall, pers. comm.
37	Jenning	200	unknown		R. Marshall, pers. comm.
38	Atlin East	500	unknown		R. Marshall, pers. comm.
39	Atlin West	300–400	stable	Carcross	R. Marshall, pers. comm.
40	Boreal caribou	725	unknown	Northeast	J. Elliott, pers. comm.
	TOTAL	15,559			

* Herd ranges shown in Fig. 1 were based primarily on the movement of radio-collared caribou.

Stevenson & Hatler (1985), Williams & Heard (1986), Edmonds (1991), Seip & Cichowski (1996) and Simpson *et al.* (1997). This paper maps the distribution of all caribou herds in the province and summarizes recent estimates of herd sizes and trends.

Methods

We asked biol gists in the province to supply us with their most recent population estimates and range boundaries. Mapped ranges include the year-round distribution of all animals and for 22 of the herds, boundaries were based primarily on the movements of radio-collared caribou (Table 1). Abundance estimates included calves and were usually based on attempts at total counts made from the air. Trends were based on repeated population estimates or the difference between recruitment and mortality rates.

Results and discussion

Distribution

Two systems of classification have been used to describe the major ecosystems of British Columbia. The Biogeoclimatic Ecosystem Classification system (BEC) classifies areas by climate and vegetation, whereas the Ecoregion Classification system (EC) defines major climate and physiographic regions (Meidinger & Pojar, 1991). There was no correlation between caribou distribution and ecoregions possibly because the EC classifies the landscape into contiguous geographic units that circumscribe all elevations. The historical and current distribution of caribou is closely related to biogeoclimatic zones, probably because the BEC delineates altitudinal belts within geographic units (Meidinger & Pojar, 1991), which are important components of caribou foraging and anti-predator strategies (Bergerud *et al.*, 1984).

Historically, caribou were found in 7 forested biogeoclimatic zones: Sub-Boreal Spruce (SBS), Engelmann Spruce-Subalpine Fir (ESSF), Interior Cedar-Hemlock (ICH), Montane Spruce (MS), Sub-Boreal Pine Spruce (SBPS), Spruce-Willow-Birch (SWB) and Boreal White and Black Spruce (BWBS) and the adjacent Alpine Tundra (AT) (Fig. 2). Caribou no longer occupy about 15% of their historic ranges (Seip & Cichowski, 1996). Caribou are now rarely found in the Sub-Boreal Spruce zone, likely due to increased predation from wolves that

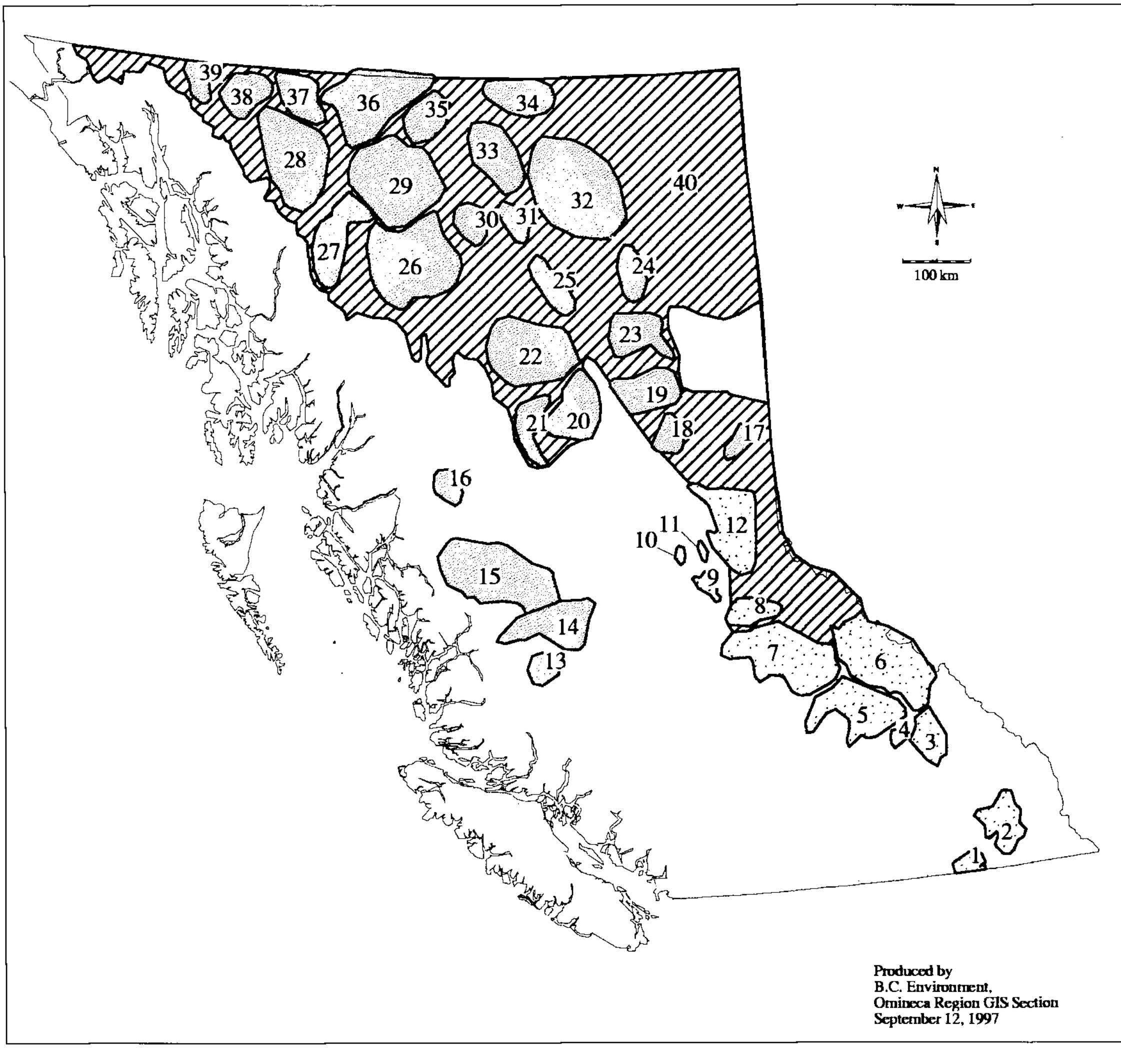

Fig. 1. Distribution and range boundaries of mountain, northern and boreal caribou ecotypes in Brirish Columbia. Stippling represents the mountain caribou herds, shading the northern caribou herds, and diagonal lines the areas of low caribou density and, in the northeast, where caribou do not appear to occur in defined herds (i.e., the boreal caribou).

increased in response to increasing moose numbers. Caribou are absent from the alpine and adjacent forested areas south of the Spatsizi and Edziza herds, and their range has shrunk, relative to historic conditions, within the other previously occupied biogeoclimatic zones in the southern half of the province (Figs. 1 and 2), probably because of habitat loss, habitat fragmentation, predation and hunting. Caribou have never occurred in the Interior Douglas-fir (IDF), Bunchgrass (BG), Ponderosa Pine (PP), Coastal Douglas-fir (CDF), Coastal Western Hemlock (CWH) or Mountain Hemlock (MH) biogeoclimatic zones to any great extent.

We recognized 39 discrete herds; 12 mountain and 27 northern caribou herds (Fig. 1, Table1). Where herd boundaries were based on the movements of radio-collared animals, there was little interchange between adjacent herds. The boreal caribou in the northeast do not appear to occur in discrete herds (represented by the number 40 on Fig. 1).

Abundance

In 1996 there were about 18 000 caribou in British Columbia; approximately 2300 mountain caribou and 16 000 northern and boreal caribou (Table 1).

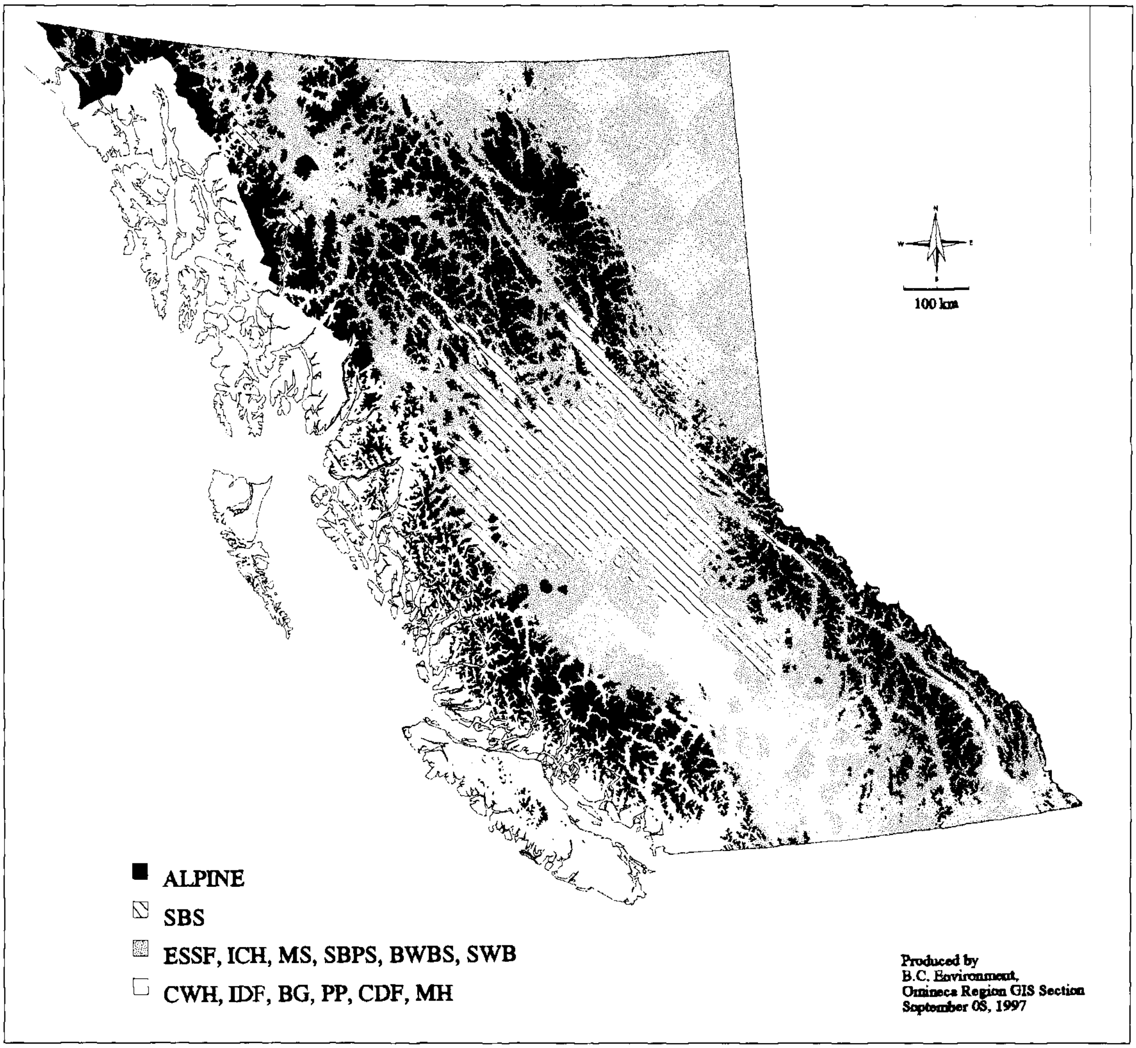

Fig. 2. Groupings of biogeoclimatic zones by relative importance as caribou habitat. Caribou occupy most of the ESSF, ICH, MS, SBPS BWBS SWB and the adjacent Alpine Tundta and, formerly, also occupied rhe SBS. See the text for names of the biogeoclimatic zones.

This provincial total is slightly higher than the 1991 estimate of 13 800 to 17 000 animals, of which 1900 - 2000 were mountain caribou (Edmonds, 1991), and substantially higher than Bergerud's provincial estimate of 10 500 - 13 000 (Bergerud, 1978). Both Bergerud (1978) and Stevenson & Hatler (1985) estimated the number of mountain caribou to be about 1500. There appears to have been an increase in the number of both mountain and northern ecotypes over the last 18 years based on those reports. More intensive survey effort may have contributed to the apparent increase in numbers of the northern ecotype.

Of the 39 herds, 15% (6) are increasing, 10% (4) are decreasing, 31% (12) are stable, and the trend for the remaining 44% (17) of the herds is unknown (Table 1). The trend for boreal caribou is unknown.

Population Dynamics

The status of the following herds has changed relative to previous reports. In 1996, a total of 19 caribou was translocated from the Yellowhead and Wells Gray herds to the range of the South Selkirk herd that extends into Washington State. Those animals may make a substantial contribution to a herd of only 50 individuals.

Simpson *et al.* (1997) concluded that caribou numbers were stable in the Wells Gray and Quesnel Lake herds in 1996, but both of those herds now appear to be increasing based on recent counts and Seip & Cichowski's (1996) analysis of birth and death rates.

Even though Simpson *et al.* (1997) considered the George Mountain herd part of the increasing Yellowhead herd, we considered it a separate herd because no radio-collared animals have left the mountain and conversely no radio-collared animals from the Yellowhead or Narrow Lake herds have traveled there. The trend for the George Mountain herd is unknown.

The Yellowhead and Itcha-Ilgachuz-Rainbow Mountains herds have increased as expected based on analysis of birth and death rates (Seip & Cichowski, 1996). But contrary to their prediction of a decline, the Tweedsmuir-Entiako herd population estimates have not changed.

The Telkwa herd has continued its long decline and with only 9 individuals remaining, is clearly in danger of extinction.

The abundance of most caribou populations appears to be primarily a function of their ability to avoid wolf predation (Bergerud, 1978; Bergerud *et al.*, 1984; Seip & Cichowski, 1996). Caribou numbers declined, following the range expansion by moose in the early 1990's into central BC. Because moose provide alternative prey for wolves, this leads to a wolf population that is not only larger, but shows no negative feedback to declining numbers of caribou.

The expansion of moose range may not only explain the decline in caribou abundance, but may also explain changes in their distribution. Increased predation was likely responsible for the elimination of caribou from their former range in the Sub-Boreal Spruce biogeoclimatic zone because caribou were too far from the relative safety of alpine and subalpine refugia.

Increased moose and wolf numbers are most pronounced where moose take advantage of the early seral habitats created by logging. Industrial development (primarily logging, but also mining and oil development, and associated road building for all three) also contributes to population declines and reduced home ranges. Logging eliminates old growth forest stands which bear arboreal lichens. Roads provide access for people, which increases the potential for disturbance from increased recreational activities such as snowmobiling and hunting (Stevenson & Hatler, 1985; Simpson, 1988). The resulting reduced foraging options force caribou to seek food elsewhere which may make them more vulnerable to wolf predation. Plowed roads, skidoo trails and snowshoe trails also increase access by wolves to caribou winter ranges with concomitant increase in predation. Development may also isolate and fragment small herds which then become more susceptible to extirpation from random variation in population processes.

Current Research

Many landscapes in the province are currently being managed at a variety of spatial scales which may mitigate the adverse effects on caribou habitat. Forest companies have had to avoid some areas, plan for extended rotations, change the size and shape of cut-blocks and retain movement corridors (Seip, 1998). An interconnecting mosaic of temporary and permanent reserves and integrated management areas are recommended to maintain the long-term viability of this species (Simpson *et al.*, 1997).

Most current research is designed to increase our understanding of caribou ecology in order to mitigate the impacts of forest development. Specific studies are being carried out to determine habitat selection at various scales (landscape, forest stand and feeding site) and for various behavioural purposes (feeding, migration and calving), relationships between predators and prey, the impact of logging practices on the growth of arboreal and terrestrial lichen and calf and adult mortality.

Several projects across the province continue to use radiotelemetry or trailing studies to review caribou behaviour, ecology, and habitat relationships in order to assist in setting management recommendations for land use. Future research should test those operational recommendations.

Acknowledgments

We thank Debbie Cichowski, John Elliott, Dave King, Rick Marshall, Dale Seip, Bob Shear, Sue Stevenson, Glen Watts, Mark Williams, Mari Wood and Jim Young for providing information on caribou populations and for their stimulating discussions. Sarge Bhatti and Jordan Kirk, BC Environment GIS Section, Prince George, produced the maps.

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Herd size, distribution, harvest, management issues, and research priorities relevant to caribou herds in Alaska

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Abstract: There are presently about 960 000 caribou in 32 herds in Alaska, including 4 herds shared with Yukon and Northwest Territories. Since complete population data were lasr published in the mid-1980s, Alaska's caribou population has doubled in size, largely from increases in the Western Arctic and Mulchatna herds. The number of recognized herds has increased by 6, largely because of increased use of radiotelemetry to inventory small caribou herds in inaccessible areas, and transplanting caribou to unoccupied ranges. About 33 000 caribou are harvesred annually in Alaska, mostly from the Western Arctic, Mulchatna, and Nelchina herds. The primary wildlife management problem in Alaska for caribou and othet species is the lack of clear management authority among state and federal agencies. Research priorities include work on the influence of short-term and long-term weather trends on nutritional ecology of caribou, and predation mitigation including sterilization, translocation, and diversionary feeding of wolves during the catibou calving petiod.

Key words: *Rangifer,* population size.

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Population Size and Distribution

Since the last published status report on caribou in Alaska (Williams & Heard, 1986), the number of recognized herds has increased from 26 to 32 (Fig. 1, Table 1). Increased use of radiocollars, a greater effort to inventory wildlife resources in remote areas of the state, and transplanting caribou to unoccupied ranges are primary factors resulting in the increase in recognized herds. The herd definition based on use of discrete calving areas, originally proposed by Skoog (1968), continues to be useful and appropriate for management. All major caribou herds (those larger than 5 000) are censused with aerial photography of postcalving aggregations every 1 to 3 years, and minor herds are censused (total count method) during the postcalving period or during the rut as frequently as needed for management.

As of the 1995 census season, there were about 960 000 caribou in Alaska including 4 herds shared with Yukon (Porcupine, Chisana, Nelchina, and Mentasta), and 1 shared with Yukon and Northwest Territories (Porcupine) (Fig. 1, Table 1). Over 800 000 of these caribou are in the 2 largest arctic herds (Western Arctic and Porcupine), and the Mulchatna Herd (Table 1). The Mulchatna Herd has been increasing at about 17% per year since the mid-1970s and shows no signs of slowing (Van Daele, pers. comm.). The Western Arctic Herd grew at about 13% per year from 1977 to 1990 and then began to stabilize due to decreased calf production and recruitment and increased adult mortality. Many smaller Interior Alaska caribou herds declined from 1989 to 1994 due to warmer summers, severe winters, increased predation of calves, and increased vulnerability of adults to wolf predation (Boertje *et al.*, 1996; Valkenburg *et al.*, 1996a). Population size of most caribou herds in Alaska is no longer significantly influenced by harvest. However, the Fottymile Herd which was once one of Alaska's most important herds, has not recovered from a population low exacerbated by overhunting in the early 1970s (Davis *et al.*, 1978; Valkenburg *et al.,* 1994).

The distribution of most caribou herds in Alaska has remained virtually unchanged during the last 25 years. However, the prolonged increase of the

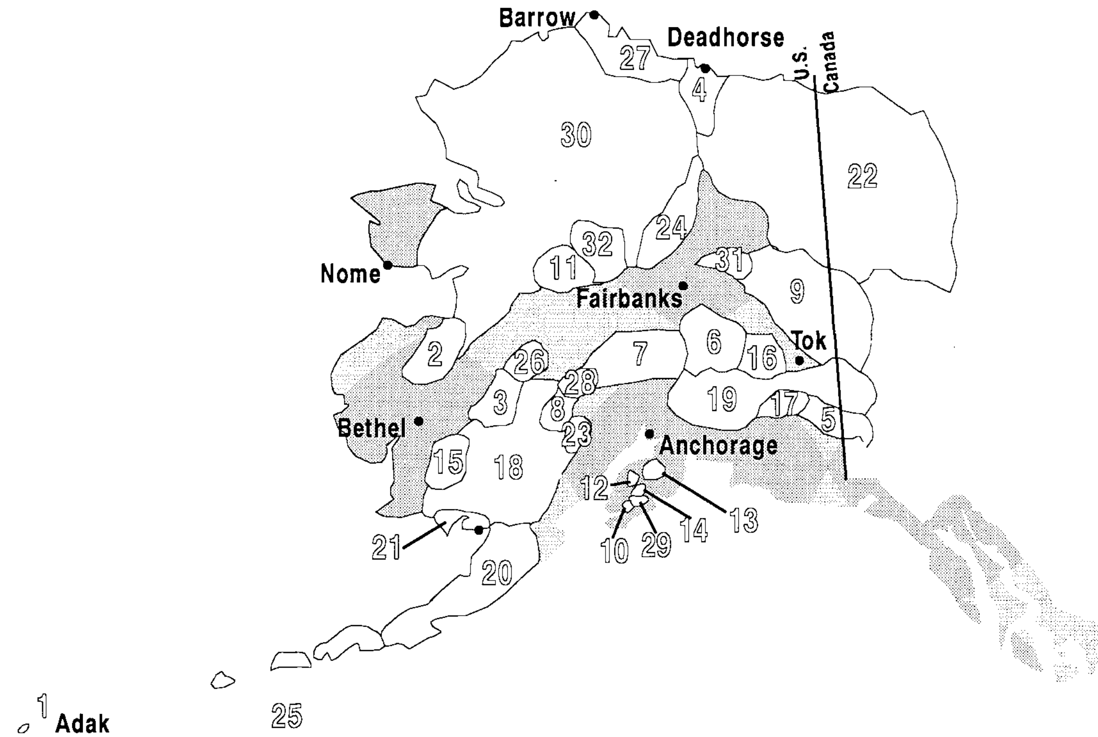

Fig. 1. Location of Alaskan caribou herds.

Mulchatna Herd in southwestern Alaska has resulted in a doubling of range size and reoccupation of ranges, especially winter ranges, that have not been used by caribou for over a hundred years. The Western Arctic Herd has also expanded its winter range southward in the area between the Yukon River and Norton Sound.

Harvest

About 33 000 caribou are being harvested annually in Alaska. An additional 2 500 caribou are taken each year from the Porcupine Herd and about 100 are taken from the Nelchina Herd in Canada. About half of the caribou taken in Alaska are harvested by about 25 000 local residents in the range of the Western Arctic Herd. Alaskan caribou herds presently could support a much larger harvest, especially the Western Arctic and Mulchatna herds, but these areas are largely inaccessible to most hunters because they are roadless, aircraft landing sites are limited, and native-owned lands have been closed to access by nonlocals in northwestern Alaska.

Along the road system in Interior Alaska caribou hunting opportunities have been limited in recent years because many of the more accessible herds have declined from natural factors (Boertje *et al.*, 1996; Valkenburg *et al.*, 1996a), and recruitment continues to be low. The Nelchina Herd will continue to provide most of the road-accessible caribou hunting opportunity for the next several years, but it has been closed to all nonresident hunters because of state and federal subsistence priority laws.

Management Issues

Management authority

The primary wildlife management problem in Alaska for caribou and other species is conflicting management authority between state and federal agencies. In the United States, the states have traditionally been responsible for managing resident wildlife. However, in 1980 Congress provided for a federal takeover of management of subsistence hunting on federal public lands in Alaska if the state did not provide a priority for "rural residents." Because of the "equal opportunity clause" in the state constitution the state cannot provide a "rural preference," and, consequently, the federal law and state constitution are in conflict. Because wildlife management for subsistence uses on federal lands is

Table 1. Date of most recent census, 1995 population estimate and 1994–1995 harvest estimates for Alaskan caribou herds.

Herd no.[a]	Herd name	Year of census	Census count	1995 Estimate	1994–1995 Harvest estimate	Population trend since previous census
1	Adak	1993	661	1 500?	77	up
2	Andreafsky	1991	0	0	0	extirpated
3	Beaver Mountains	1993	429	200?	2	down
4	Central Arctic	1995	18 093	18 100	341	down
5	Chisana	1995	723	775	0[b]	down
6	Delta	1995	4 646	4 700	0[b]	stable
7	Denali	1995	931	2 300	0[b]	stable
8	Farewell-Big River	1984	700	750?	46	down?
9	Fortymile	1995	22 558	22 600	338	stable
10	Fox River	1995	83	85	0[b]	up
11	Galena Mountain	1993	259	400	2	unknown
12	Kenai Lowlands	1995	84	90	0[b]	stable?
13	Kenai Mountains	1996	425	425	28	stable
14	Killey River	1995	261	290	11	up
15	Kilbuck	1993	3 682	4 216[c]	47	down
16	Macomb	1995	477	500	0[b]	down
17	Mentasta	1995	739	852	0[b]	down
18	Mulchatna	1994	168 351	200 000	6 129	up
19	Nelchina	1995	49 808	50 281	3 579	up
20	Northern Peninsula	1995	11 500	12 000	1 273	down
21	Nushagak Peninsula	1993	1 007	1 519	35	up
22	Porcupine	1994	146 808	152 000	3 266[d]	stable
23	Rainy Pass	1990	231	500?	57	unknown
24	Ray Mountains	1995	1 727	1 750	12	up
25	Southern Peninsula	1995	1 434	1 550	0[b]	stable
26	Sunshine Mountains	1993	553	600?	0	unknown
27	Teshekpuk	1993	27 630	28 000	0[e]	up
28	Tonzona	1991	1 101	800?	25	down
29	Twin Lakes	1995	48	50	0[b]	up
30	Western Arctic	1993	451 067	450 000	20 000	up
31	White Mountains	1992	832	1,200	21	stable?
32	Wolf Mountain	1992	595	625?	2	unknown

[a] Numbet corresponds with number on Fig 1.
[b] No open season.
[c] Merging with Mulchatna.
[d] Includes Canadian harvest.
[e] Included with Western Arctic harvest.

not separable from other management on other lands, the state and federal agencies are in conflict. Courts have issued contradictory rulings supporting opposing viewpoints, and the US Supreme Court has, so far, been unwilling or unable to address the issue. Congress must act in order to settle the issue, but state and federal politicians are caught between major constituencies and are reluctant to take the lead. In response to perceived conflicts among hunters, large areas of federal land have been closed by federal regulation to caribou hunting by "nonrural" residents even though, in most cases, data do not support allegations of conflict. Problems with management decision-making mean that caribou hunting opportunities have been eliminated or are restricted to well below biological limitations. Decision-making is also becoming inefficient and costly, and management planning is impossible amid the chaos.

Herd management issues

For the first time the Alaska Department of Fish and Game is proposing to control the size of a major caribou herd to prevent a long-term decline. The Nelchina Herd, which numbers 50 000 to 60 000, will be reduced to below 40 000 beginning in fall 1996. Body condition and body size have been declining and peak calving time has become relatively late (Eberhardt & Pitcher, 1992; Valkenburg *et al.*, 1996b). The 1996 harvest goal is 10 000 cows and up to 5 000 bulls. Under an experimental harvest regime, most hunters will be required to shoot a caribou with "6 antler points or less on 1 side" to prevent an overharvest of large bulls and promote harvest of cows. Road corridor closures will be used to avoid hunter crowding and allow caribou to cross roads relatively undisturbed.

The Adak caribou herd, was introduced to a predator-free island in the late 1950s to provide emergency food and recreational hunting for the US Navy. The herd was kept at a relatively stable size for almost 30 years by harvest, but since the base was decommissioned the herd is increasing rapidly and will soon overgraze the island. ADF&G worked with federal agencies, native groups, and environmental organizations to remove caribou from the island. However, fear of adverse publicity is preventing allocation of money by the US Congress, and the dilemma remains unresolved.

Research Priorities

After major caribou herds declined in the early 1970s, using refined survey methods ADF&G intensified ecological research on caribou in cooperation with the University of Alaska and other agencies. We intensively studied several caribou herds for 15 to 20 years, including periods of population increase and decline (c.f. Adams *et al.*, 1995; Gerhart *et al.*, 1996; Valkenburg *et al.*, 1996a,b; Whitten, 1996). Recent declines in Interior caribou herds were caused by increased vulnerability to wolf predation. New research priorities include: 1) determining how short- and long-term weather patterns affect caribou nutrition and vulnerability to predation; 2) developing nonlethal methods of predation management; and 3) monitoring caribou body condition. Three graduate student projects are nearing completion: 1) the influence of insects on feeding and other caribou behaviors, 2) the influence of moisture and sunlight regimes on plant nutrition and productivity, and 3) the influence of microclimate on selection of calving areas. Beginning in 1998, dominant wolves in the range of the Fortymile Herd will be neutered and subordinate wolves will be translocated to increase caribou calf survival in that herd. We will also continue experiments with diversionary feeding in the Delta Herd to keep key wolf packs from feeding on caribou calves during the critical 3-week period after calving (Valkenburg, 1997).

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The status of *Rangifer tarandus caribou* in Yukon, Canada

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Abstract: This paper summarizes the population trends as well as research and management programs for woodland caribou (*Rangifer tarandus caribou*) in Yukon. Most herds are stable although not all are counted regularly and systematic monitoring of herds remains an essential need. Ovet the past decade the Southern Lakes, Aishihik, and Finlayson herds have been well studied and provide valuable models for guiding Yukon management programs. Over harvest and the spread of agriculrure, forestry and mining are ongoing human activities ate of concern to caribou managers.

Key words: woodland caribou, North America.

Rangifer, Special Issue No. 10, 131–137

Introduction

This paper summarizes the most recent population trends and research and management programs for woodland caribou (*Rangifer tarandus caribou*) in Yukon. Woodland caribou in Yukon are classified as the mountain/terrestrial ecotype based on their winter foraging behavior (Edmonds, 1991) and relative to barrenground caribou occur at lower densities, form smaller aggregations, make less extensive seasonal movements and disperse rather than concentrate at calving. Studies indicate that the likelihood of population change due to inter-herd movement is low, at least for present densities.

First Nation harvesting rights are assured under the Yukon Act and thus unrestricted by law necessitating voluntary restraint by First Nation hunters where restrictions are required. As well, under the Yukon Land Claim Agreement indigenous and scientific information are evaluated within a co-management framework comprised of 14 local Renewable Resource Councils and a Yukon-wide Fish and Wildlife Management Board. Further, because Yukon is a Territory of Canada the Federal Government retain jurisdiction over land, water and timber resources, limiting the ability of Yukon to manage caribou habitats. These factors greatly influence harvest management of caribou within Yukon.

Caribou inventory and research

Woodland caribou studies essentially began in Yukon in 1980 when the first systematic inventory of herds was established. The primary objectives of this program were to identify distinct seasonal movements and distribution of herds, secure reliable population estimates, monitor population trends through annual or periodic winter census and assess herd composition through fall breeding season surveys.

Caribou studies have increased markedly over the last 3 years (Fig. 2) in response to public concern for the welfare of wildlife exposed to expanding human settlement and industrial activity. A total of 236 animals have been captured, radio-collared and monitored since 1993 and an additional 90 have been collected to provide data on caribou physical condition and the presence of contaminants (Gamberg & Scheuhammer 1994; Gamberg 1993; Florkiewicz, 1993). A total of 128 relocation surveys were flown since 1993 providing 2200 contacts with radio-collared caribou. As well, 77 census and sex/age composition surveys have been flown.

Status of caribou

Woodland caribou are estimated to number approximately 28 000-35 000 in Yukon, within 22

Table 1. Status of caribou in Yukon.

Herd	Population Estimate	Survey Technique	Last Survey	Status	Comments
Woodland Caribou					
1. Hart River	1 200	Estimate[1]	1978	Unknown	Lightly hunted due to inaccessibility.
2. Bonnet Plume	5 000	Guess	1982	Unknown	Increased mineral exploration in summer of 1995.
3. Mayo	Unknown			Unknown	Anecdotal information only.
4. Ethel Lake	300	Estimate[2]	1995	Stable	Vulnerable to over-hunting.
5. Moose Lake	200	Estimate[2]	1991	Stable	Small herd with limited access.
6. Tay River	4 000	Estimate[2]	1991	Stable	Naturally regulated herd with limited access.
7. Redstone	5-10 000	Guess	1982	Unknown	Ranges Largely in N.W.T., heavy hunting pressure.
8. Finlayson	4 000	Estimate[2]	1996	Decreased/ Stable	Experienced dramatic population flux following wolf control in the 1980's. Record high mining exploration activity on summer range.
9. Nahanni	2 000	Guess	1996	Unknown	Presently under intesive study by Nahanni National Park.
10. La Biche	400	Estimate[3]	1993	Unknown	Presently a remote and undisturbed population.
11. Smith River	200	Guess		Unknown	Remote and unhunted population shared with B.C.
12. Little Rancheria	700	Estimate[2]	1988	Stable	Under study to mitigate concern from planned forestry development. Highly accessible to winter hunting by First Nations.
13. Wolf Lake	1 200	Estimate[2]	1995	Stable	Naturally regulated herd with limited access.
14. Atlin	500-1 000	Estimate[3]	1995	Unknown	Ranges mostly in B.C., closed to hunting in Yukon.
15. Ibex	340	Estimate[1]	1995	Increasing	Increasing rapidly following prohibition of harvest. Closed to hunting.
16. Carcross	450	Estimate[1]	1997	Increasing	Ranges near large urban center and provides excellent viewing opportunity. closed to hunting.
17. Pelly Herds	1 000	Guess		Unknown	As yet no study but significant population based on incidental sightings.
18. Tatchun	300	Estimate[1]	1995	Stable	Vulnerable to over-hunting and presently under study.
19. Klaza	430	Estimate[2]	1996	Stable	Intense mineral exploration in the area. Permit hunt.
20. Aishihik	750	Estimate[1]	1996	Increasing	Harvest prohibition and wolf control used to restore herd to 2 000.
21. Kluane	180	Estimate[1]	1996	Increasing	Protected population ranging partly in Kluane Game Sanctuary. closed to hunting.
22. Chisana	700	Estimate[1]	1996	Decreasing	Experiencing rapid decline due to poor forage/nutrition and heavy predation. Closed to hunting.
Barrenground Caribou					
23. Nelchina	49 000	Estimate[4]	1995	Increasing	Has migrated into Yukon since 1991. Winter registration permit hunt.
24. Fortymile	22 000	Estimate[4]	1995	Stable	Recent plan to increase herd size to 50 000. Closed to hunting in Yukon.
25. Porcupine	160 000	Estimate[4]	1995	Increasing	Potential for oil and gas development on calving grounds.

[1] Total Count. [2] Stratified Random Quadrate. [3] Extrapolation. [4] Direct Photocount.

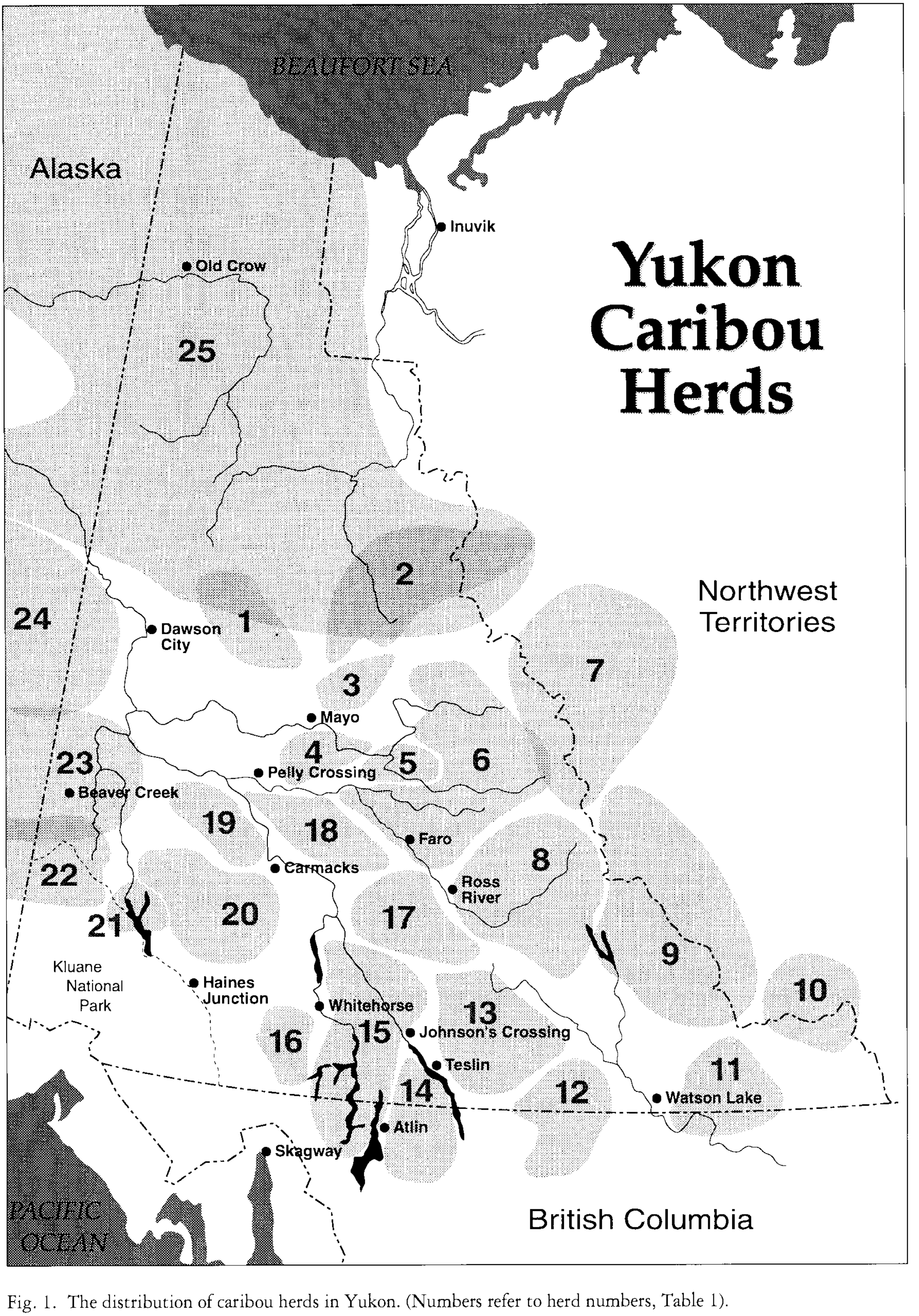

Fig. 1. The distribution of caribou herds in Yukon. (Numbers refer to herd numbers, Table 1).

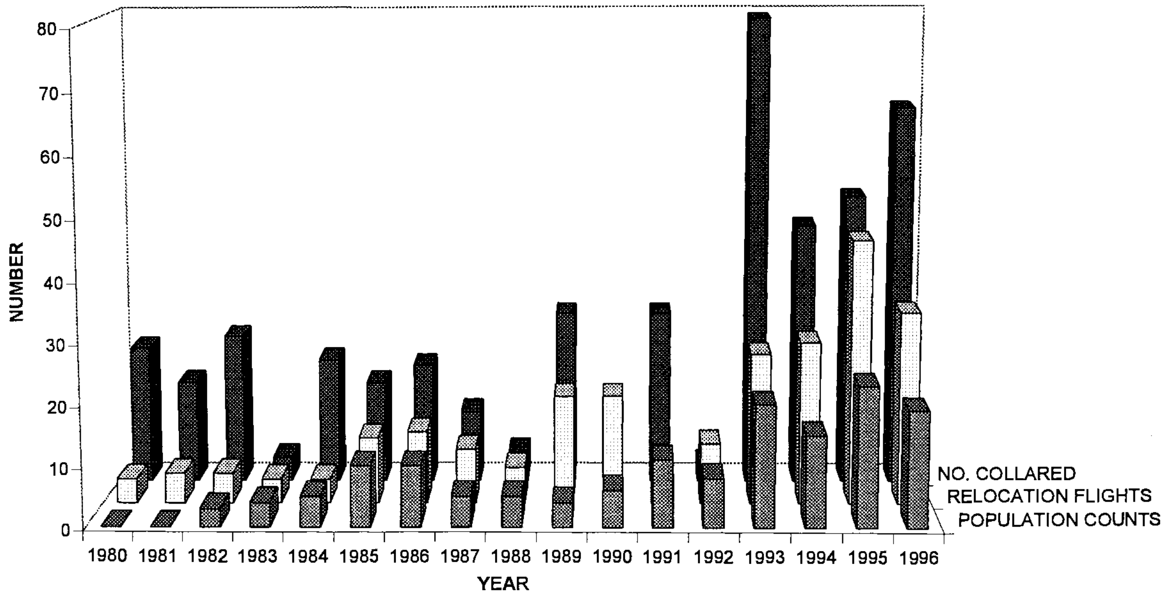

Fig. 2. Number of caribou radio-collared, relocation flights, and population counts conducted to inventory Yukon woodland caribou between 1980 and 1996.

recognized herds ranging from 180 to perhaps 10,000 individuals (Fig. 1, Table 1). Fifteen herds have been surveyed during the 1990s and of these 4 are increasing, 7 are stable, 1 is decreasing, and 3 are of uncertain status. For the other seven herds only crude estimates of population size and trend are available. The latter are populations in remote localities and their distributions are conjectured from superficial survey activity and/or anecdotal information from people with long term local knowledge of the area.

Annual licensed harvest of caribou has declined and become more erratic in the last 5 years and has averaged 271 (SD = 47) animals compared to 336 (SD = 28) in the 1980s (Fig. 3). Much of this change is due to increased restriction on caribou harvest. Harvest has been restricted to males only since 1984, and more recently, six herds have been closed to hunting (Table 1). Presently quotas are being formulated for licensed outfitters who guide non-resident hunters. The average annual harvest by residents (n=162) is greater than non-resident hunters (n=154). First Nations harvest is unknown but is suspected to equal that of licensed hunters harvest. Enforcement of compulsory reporting by all licensed hunters began in 1994.

Research and management programs

A number of herd ranges are known to overlap with adjacent jurisdictions and joint management efforts are underway with Alaska (Chisana herd), British Columbia (Carcross, Atlin, and Little Rancheria herds) and with the N.W.T. (Nahanni herd - Nahanni National Park). However, there are no formal management agreements in place at present. While these informal management arrangements appear adequate at this time, more formal management plans may be required where harvest and land use issues persist between neighboring jurisdictions. The Redstone herd remains a potential management problem with moderate to high levels of harvest and minimal population information available.

There are presently 3 programs directed at recovery and maintenance of woodland caribou herds in the Yukon (Fig. 4).

Southern Lakes Caribou Recovery Program

The Southern Lakes caribou program is aimed at rebuilding what may be called the 'urban caribou herds' (Ibex, Carcross, Atlin) that exist near Whitehorse, Yukon (O'Donohue, 1996) (Fig. 4a). Southern Lakes caribou had declined in both numbers and distribution since historic times and their biological viability had come into question. A management plan to restore the herds was developed in 1992 which entails co-management with 6 First Nations whose traditional territory boundaries include the herd ranges. Hunting was prohibited (including First Nation hunting by voluntary com-

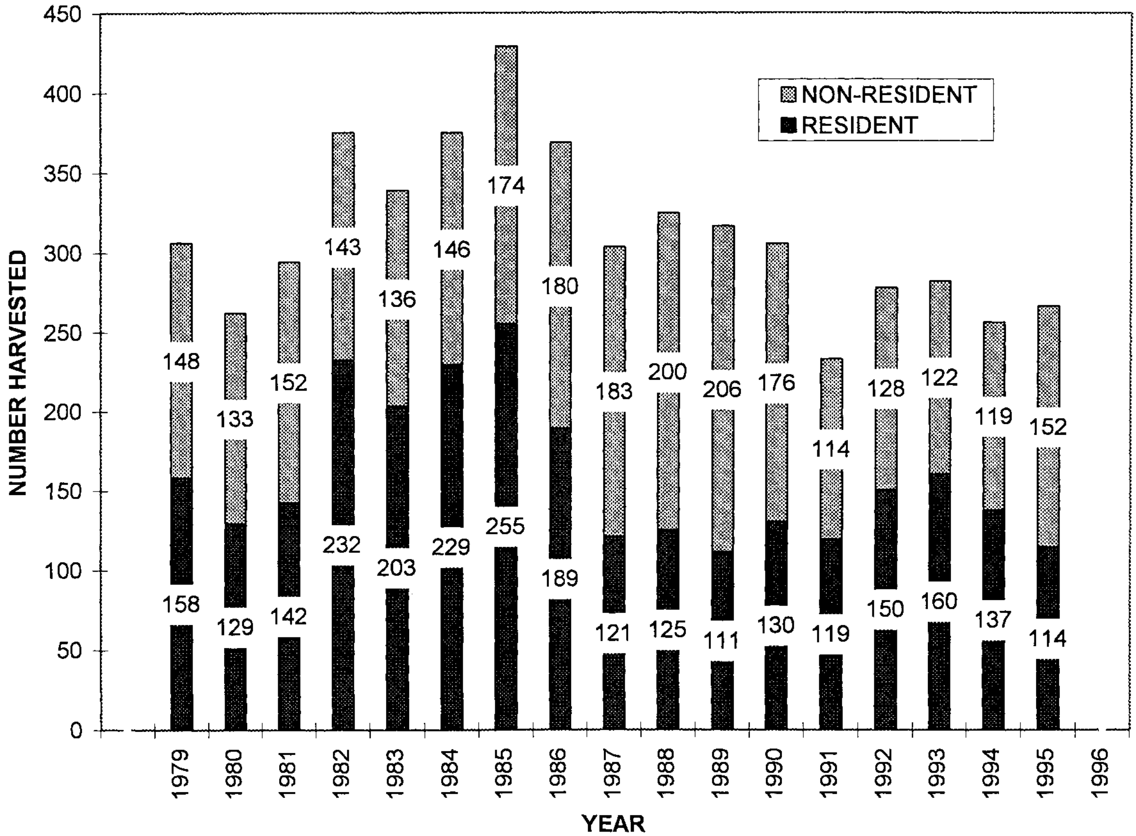

Fig. 3. Number of woodland caribou harvesred in Yukon 1979 - 1995.

pliance) and meaningful input made to logging and agricultural land use practices. Initial indicators suggest that at least the Ibex and Carcross herds are now experiencing population growth as a result ofi this program. It is recognized that local harvest demand can never be satisfied by these herds and will one day be allowed for cultural and traditional consumptive uses only. Nevertheless, the Southern Lakes caribou herds offer enormous wildlife viewing benefit for tourists and people who reside in the area.

Aishihik Recovery Program

The Aishihik Recovery Program began in 1993 in response to both scientific and traditional information indicating that the herd had drastically declined, and was showing poor calf recruitment and an imbalanced sex ratio (Hayes, 1992) (Fig. 4b). An intensive research and management plan was developed to attempt herd recovery using harvest prohibition (including First Nation harvest) and wolfi control following the provisions and guidelines set out in the publicly developed Yukon Wolf Conservation and Management Plan (Yukon Wolf Management Planning Team, 1992). An initial 2 year evaluation found significant increase in calfi survival following an 80% reduction in wolves compared to untreated (no wolf control) caribou herds (Wolf Lake, Ibex, Klaza, and Chisana, Fig.1) (Yukon Fish and Wildlife Branch, 1994). Surveys have further documented improved adult survival, based on reduced mortality of radio-collared caribou, normalization of sex ratio and population increase. While providing valuable research on predator-prey relationships, the Aishihik project has nevertheless been controversial nationally and internationally because it entails lethal control of wolves. Locally the herd is recognized as an important resource for subsistence hunters and as an integral component of one ofi Yukon's most diverse large mammal ecosystems.

Finlayson Herd Management Program

Management ofi the Finlayson herd is the most advanced of all Yukon's woodland caribou programs (Fig. 4c). Harvest reduction and wolf control were

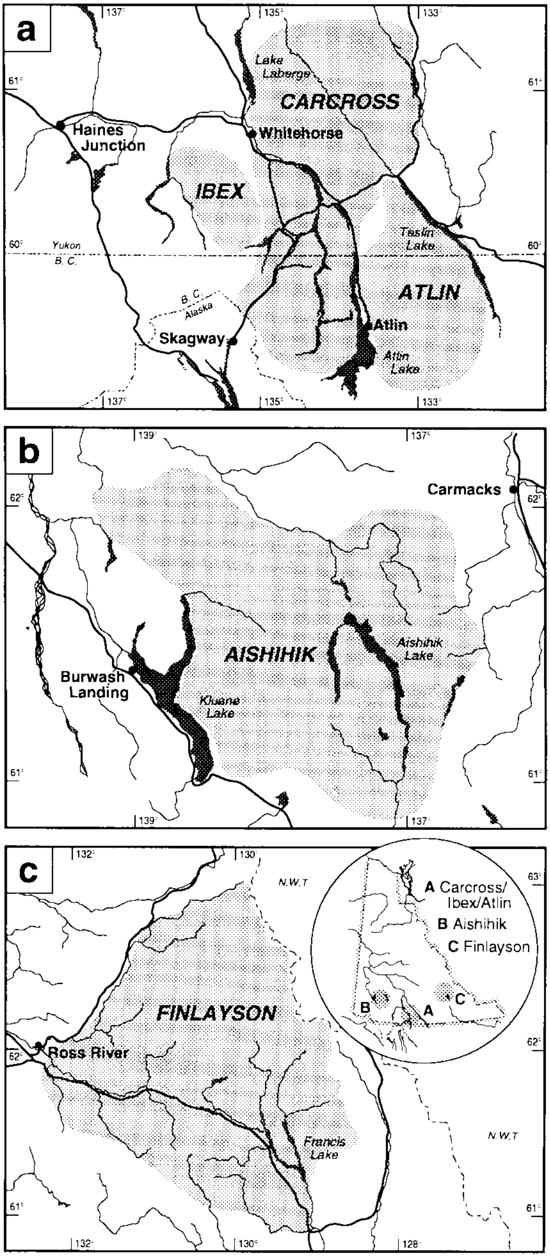

Fig. 4. Distribution of the Southern Lakes[a], Aishihik[b], and Finlayson[c] caribou herds.

used to restore this population in the 1980's (Farnell *et al.*, in prep.). The herd increased from approximately 1800 to 4500 adults in the span of 7 years (1983-1990) following an 80% reduction in wolves. This was accompanied by an increase in the region's moose population from 3000 to 10 000. Wolves subsequently rebounded and stabilized at 250, higher than the pre-reduction population size of 215. Meanwhile the caribou herd appears to have presently stabilized at 4000 adults. Efforts are now directed at sustainable harvest management and assessment of potential disturbance impacts from recent large scale mining exploration activity. The range of the Finlayson herd experienced a record 16 000 new quartz claims registered in 1995-96 following discovery of massive sulfide ore deposits with high metal values on the herd's summer range (Dept. of Northern and Indian Affairs, 1996). This development presents a new challenge to herd management. Findings from disturbance assessment work presently being carried out cooperatively with mining companies may shed new light on how industrial developments can be mitigated to lessen or avoid serious impacts to caribou.

Research priorities and management needs

Predation, primarily by wolves, has been considered limiting for Yukon's Kluane (Gauthier & Theberge, 1986), Aishihik (Hayes *et al.*, 1994), and Finlayson herds (Farnell *et al.*, in prep.). Wolves occur at natural densities in Yukon and therefore play an important role in the interaction with factors such as human caused mortality, climate, and forage/nutrition relationships.

Yukon has conducted wolf control and found it unacceptable to much of the Canadian public. Research focused on development of more humane non-lethal control methods may provide a publicly acceptable alternative to the trapping or shooting of wolves. Experimental fertility control is presently being applied to slow the recovery of 6 selected wolf packs in the range of the Aishihik caribou herd (Bubela, 1995). This involves artificially reducing birth rates by sterilizing wolves whose territories occur in the control area. The objective is to reduce wolf numbers but also wolf immigration from outside the control area. If successful, this technique could be applied in exceptional circumstances where predation must be addressed to sustain caribou herds.

Problems associated with logging and agricultural development (increased access, direct loss of habitat, changing predator/prey relationships) are rapidly spreading northward into Yukon. Following experience in British Columbia and Alberta, it is expected that these activities could precipitate declines in Yukon caribou if management actions are not taken to maintain population levels. It is therefore essential that baseline inventory data be used to develop specific timber harvesting quotas and guidelines, and to direct allocation of agriculture land in a way which minimizes threats to caribou. Yukon's caribou inventory effort should proceed in all cases before caribou ranges are designated for logging and agricultural development. Long-term monitoring of specific herds should also continue to provide baseline assessment of changes over time.

Increased mining exploration activity in central Yukon is cause for some concern. Behavioral responses to disturbance associated with mining activity could result in range abandonment and subsequently compromise caribou antipredation tactics and/or foraging strategies. Moreover, post exploration development and production activity may result in direct losses of caribou where such activity traverses winter range concentration areas. Because of the normally high adult mortality rates in these caribou herds, any increased mortality could result in lost human harvest opportunities. While perhaps acceptable to the resident hunting fraternity, this would be unacceptable to local First Nations.

Preliminary caribou disturbance assessment is underway in cooperation with mining proponents. Caribou distribution, peak of calving date, annual calf recruitment levels, and population size are being monitored to assess potential behavioral and demographic responses to advanced exploration activity. Input to the long-term access and seasonal activity plans of mining companies is absolutely essential to avoid population decline.

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Fractal measures of female caribou movements

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Abstract: Understanding caribou movement during short-term searches for specific habitats, potential mates, and refugia against predarors can help resolve ecological questions on how individual caribou perceive their environment. We used measures of fractal dimension and standardized pathlength to compare the movement pathways of female caribou. Satellite telemetry locarions were collected over a 2-year study, March 1994 to mid-May 1996, for a caribou popularion in central Saskatchewan living in the southern boreal forest. Female caribou displayed more random searching behaviour during winter and more regular dispersal movements during early winrer/spring and autumn periods. Females wirh a calf showed no difference in movement pattern (fractal dimension) telative to females without a calf but their standardized path length was shortet. We discuss the advantages of using fractal dimension as a measure of the tortuosity of movement pathways and how changes in fractal dimension over a range of scales can define domains of consistent ecological processes.

Key words: fractal dimension, hierarchy, landscape, movement pathway, scale, space use, *Rangifer tarandus*.

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Introduction

An understanding of animal movement behaviour is central to the basic questions of distribution and abundance (Swingland & Greenwood, 1984). Social and ecological factors interact to create spatio-temporal patterns of space-use by animals (e.g., search behaviour; Bell, 1991), and long-term dispersal movements (Stenseth & Lidicker, 1992). Animal movements are influenced by factors intrinsic to the animal, such as timing of their reproductive cycle and physiological condition, as well as by factors extrinsic to the animal, such as predation and the spatial characteristics of their habitat. These factors affect the spatial dynamics of populations, metapopulation structure, and trophic dynamics of the ecosystem within a hierarchy of space-time.

As patterns of animal movements correlate with time (Dicke & Burrough, 1988), space (Wiens & Milne, 1989), and body size (Swihart *et al.*, 1988), ecologists need to use scale-independent measures of movement patterns. Fractal dimension of a movement pathway is scale-independent and provides a useful measure to compare different taxa as well as to make intraspecific comparisons among populations or among sex-age-reproductive classes. We expect measures of movement patterns to differ with animal size, community structure, and phylogeny (Wiens *et al.*, 1995). Also, movement patterns are influenced by the spatial structure of the environment and how animals perceive habitat heterogeneity (With, 1994).

The term 'fractal' describes temporal and spatial patterns that show details at all scales (Mandelbrot, 1983; Burrough, 1988). Fractal geometry is an alternative mathematics to Euclidean geometry and uses the concepts of self-similarity and power laws to calculate fractal dimension (Hastings & Sugihara, 1993). Animal movements qualify as fractal because they are continuous and difficult to differentiate. A continuous line is differentiable if it can be split into an infinite number of straight lines. In contrast, a continuous, but non-differentiable line, such as an animal movement pathway, cannot be split because the smaller parts continue to show 'wiggliness' (see Dicke & Burrough, 1988). The fractal dimension, D, of a movement pathway is a quantifi-

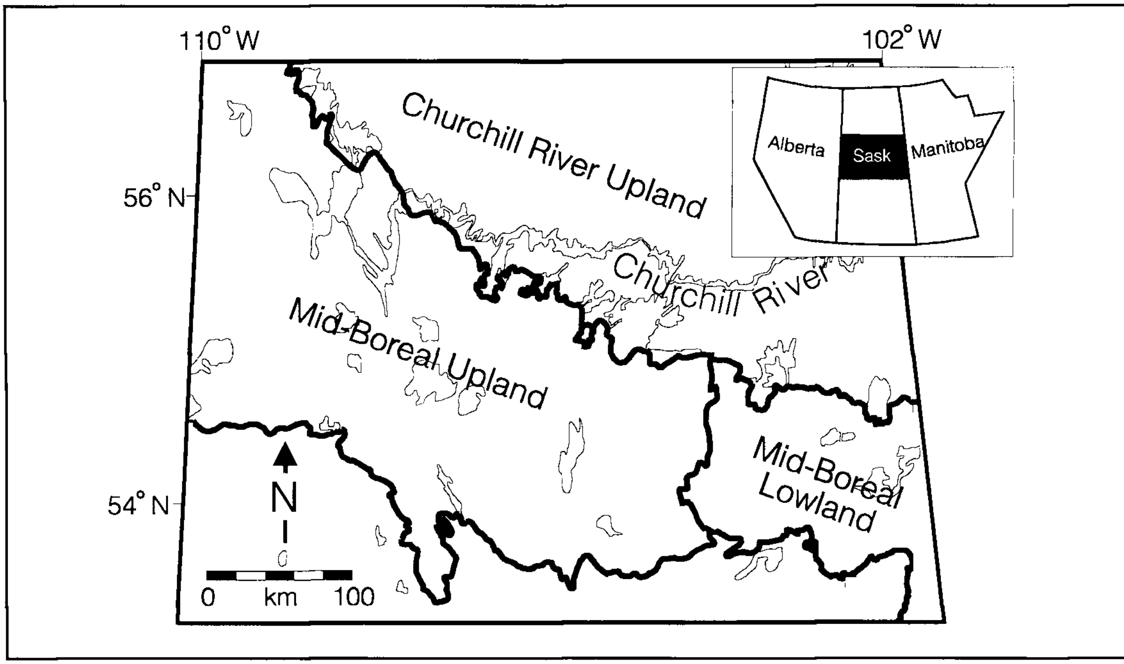

Fig. 1. Location of study area in central Saskatchewan, Canada.

able measure of roughness or irregularity and varies between 1 and 2 (Dicke & Burrough, 1988; Ferguson & Messier, 1996). As D increases, the irregularity of the trail increases so that a value of D approaching 2 represents a wiggly trail that frequently intersects itself.

Here, we use fractal measures to compare movement patterns of female caribou (*Rangifer tarandus caribou*) with and without calves over five seasons and 2.2 years. We expect differences in movement patterns to reflect differences in reproductive cycle over seasons, and differences in the risk of predation to a female and her calf versus a barren female. This is part of a study of caribou-forestry relations in the southern boreal forest of central Saskatchewan.

Methods

Study Area

The study area (Fig. 1) lies between approximately 53°30'N and 56°00'N and 104°00'W to 110°00'W (see Rettie *et al.*, 1997) and is largely within the Mid-Boreal Upland Ecoregion (Ecological Stratification Working Group 1995). Topography is mainly undulating to rolling plains (Harris *et al.*, 1989). The climate is cool and subhumid with mean January and July temperatures of -19 °C and +16 °C, respectively. Mean annual precipitation is 45.6 cm, including a mean snowfall of 147 cm (Atmospheric Environment Service, 1993). Vegetation in the area is subject to frequent fires, and dominant tree species are white spruce (*Picea glauca*), black spruce (*P. mariana*), jack pine (*Pinus banksiana*), and aspen (*Populus tremuloides*; Rowe & Scotter, 1973). Other ungulates in the region include moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and wapiti (*Cervus elaphus*). In addition to wolves (*Canis lupus*), large carnivores include coyotes (*Canis latrans*), black bears (*Ursus americanus*), and lynx (*Lynx canadensis*).

Capture and Radio-Collaring

Over four winters of radio collar deployment (5 in 1992, 10 in 1992-93, 24 in 1993-94, and 13 in 1995), a total of 40 female caribou were radio-collared (Telonics, Inc., Mesa, Arizona, USA), including the replacement of 12 collars. The number of radio-collars functioning at the end of each winter were 27 in 1994, and 31 in 1995. Individuals were tracked continually on a 2-day cycle during the post-calving season and on a 4-day cycle for the remainder of the year. Only caribou with almost continual observations were used (16-23 locations per season). Seasons were defined as follows: post-calving (16 May to June 30), summer (1 July to 15 September), autumn (16 September to 30 November), early winter (1 December to 28 February), late winter/spring (1 March to 15 May). If during a season more than 2 locations were of poor quality (< class 1; Keating *et*

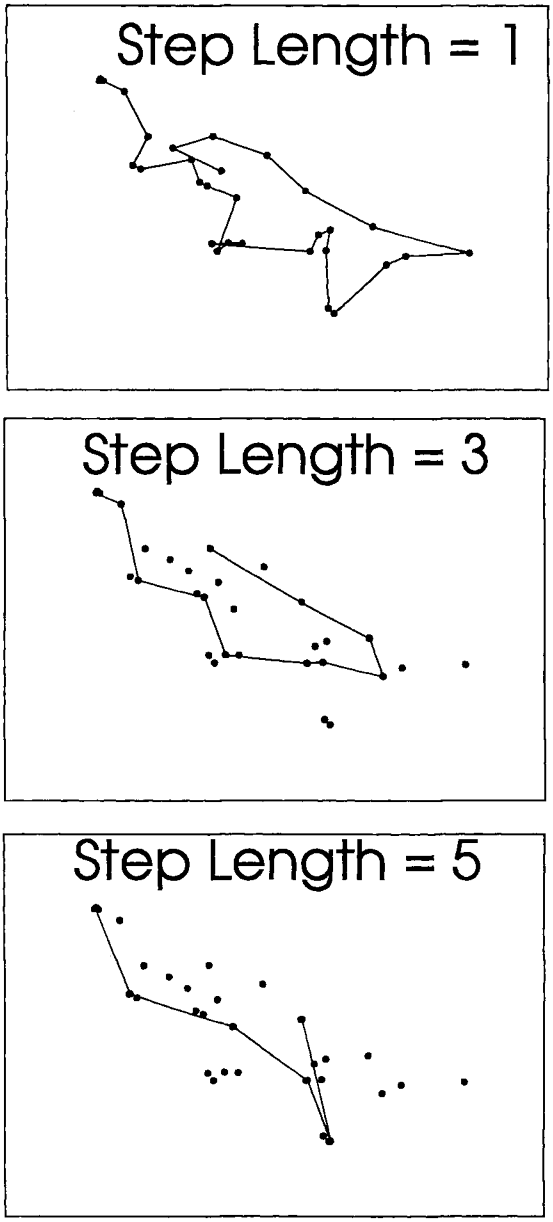

Fig. 2. Example showing changes in caribou movement pathway (locations every 4th day) according to changes in step length. For step length = 1, all locations are used; for step length = 3, locations are recorded every 12th day; and for step length = 5, locations are recorded every 20th day. For each step lengths the distances are summed to calculate total length of pathway.

al, 1991) then we did not calculate the fractal dimension of the movement pathway for that season. A total of 38 female caribou were used over 11 continuous seasons that resulted in 221 estimates of fractal dimension.

The pregnancy rate for collared females caribou (>16 months old) was 94% (unpubl. data). For the following comparisons we assumed all collared females gave birth to a calf. During March surveys, if a female was seen without a calf then we assumed she had lost her calf soon after giving birth and she was designated "female without a calf" for the entire reproductive year.

Calculation of Fractal Dimension of Caribou Movements

Our focus was on coarse-scale movement of female caribou over seasons. At this scale we expected the fractal dimension to reflect weekly foraging as well as seasonal migration. Most measures of animal pathways, such as straight-line distance from beginning to end of a pathway, are scale-dependent. In comparison, fractal dimension is a scale-independent measure of the complexity or tortuosity of a pathway (Wiens *et al.*, 1995). We measured total length (m) of a pathway over six different step lengths. For example (Fig. 2), for a step length of three, and a 4-day duty cycle, we summed the length between every 3rd location, or every 12 days. Note that on step length of three there are three possible starting points. We used total length measurements for all three, starting on location one, location two, and on location three. We then took the mean total pathlength using all three distances. This same process was repeated for each step length. For example (Fig. 2), for a step length of five, we measured by starting on location one, location two, location three, location four, and location five, and then we took the mean of the five distances. We ignored the "remainder" of the total distance moved when the step length did not divide evenly into the total number of locations (see Carr & Benzer, 1991 or Hastings & Sugihara, 1993 for options for dealing with the remainder).

The measured length of a pathway (L) decreases as the measurement scale (δ) increases according to the following power-law function:

$$L(\delta) = K \cdot \delta^{1-D} \quad (1)$$

where D is the fractal dimension (Mandelbrot, 1983). D is derived by regressing log L on log δ (Fig. 3), where δ represents a measurement scale (see Dicke & Burrough, 1988; Milne, 1991). Due to our small sample sizes (16-23 locations per season) and highly irregular pathways of caribou (mean D = 1.88), some log-log regressions estimated fractal dimension as greater than 2.0 (70 of 221).

Another scale-independent measure of caribou

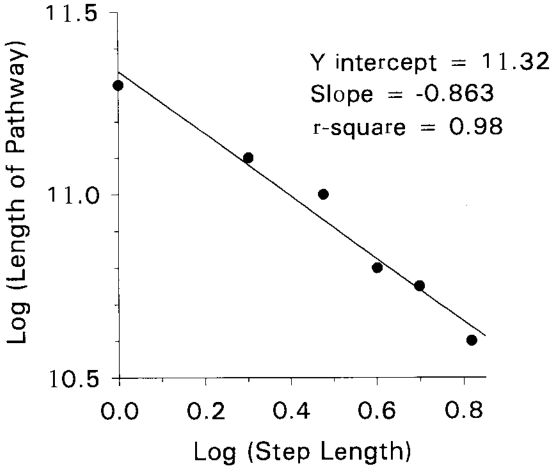

Fig. 3. Example of regression of log *L* (Step Length) against log δ (Total Length ofi Pathway) for a caribou movement pathway. The fractal dimension is calculated as, D = (1 - slope), and the standardized pathlength, *K*, as the y-intercept.

movements is the intercept of the log-log plot used to calculate fractal dimension (Milne, 1992). This measure, *K*, can be considered the standardized length of movement pathways (Wiens *et al.*, 1995). The fractal dimension, *D*, indexes the overall complexity of pathway configuration over a range of spatial scales, whereas, *K*, indexes a standardized measure of total pathway length.

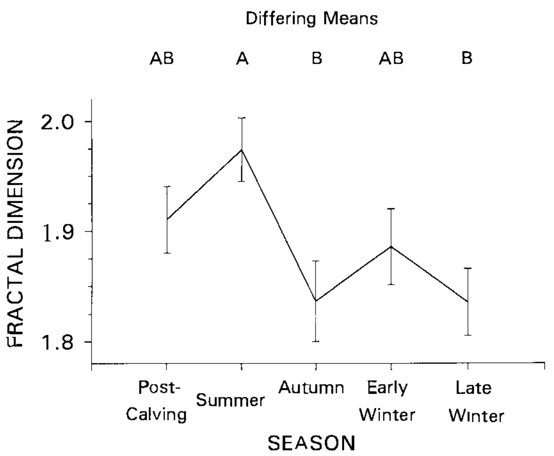

Fig. 4. Changes in fractal dimension of movement pathways over seasons for radio-collared female caribou, 1994-96. Data are presented as mean values ± S.E. and differing means are based on Tukey's multiple comparison test (α=0.05). Means with the same letter do not significantly differ. See methods for definition ofiseasons.

Statistical Analyses

Data were analyzed using SAS (SAS Institute Inc., Cary, NC) statistical software for microcomputers. We pooled data among years ($P > 0.15$) to assess the seasonal pattern. Standardized pathlength, *K*, was normally distributed (Shapiro-Wilk statistic; PROC UNIVARIATE in SAS: W = 0.98, $P = 0.10$) whereas fractal dimension, *D*, was not (W = 0.97, $P = 0.01$). Since neither log-transformation nor ranking improved normality for *D* ($P < 0.001$) we decided to use parametric statistics for both measures (see Stewart-Oaten 1995). We compared fractal

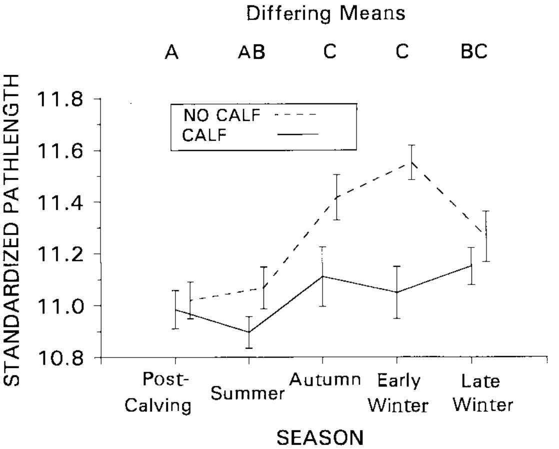

Fig. 5. Relationship between standardized pathlength of caribou movement pathways and season, and whether a female was wirh a calf or not, 1994-96. Data are presented as mean values ± S.E. and differing means are based on Tukey's multiple comparison test (α=0.05). Means with the same letter do not significantly differ. See methods for definirion of seasons.

dimension, *D*, and intercept, *K*, using analysis of variance (2-way ANOVA with season and reproductive class as effects). If differences were found within the ANOVA, then Tukey's multiple comparison tests were performed. For all tests, probabilities greater than 0.05 were considered not significant. Values are reported as mean ± SE.

Results

Fractal dimensions of female caribou movements varied with season ($F_{4,215} = 3.08$, $P < 0.02$) but not with whether or not a female had a calf ($F_{1,215} = 1.5$, $P = 0.37$), and no interaction was present ($F_{4,215}$ = 0.15, $P > 0.90$). During the summer season, cari-

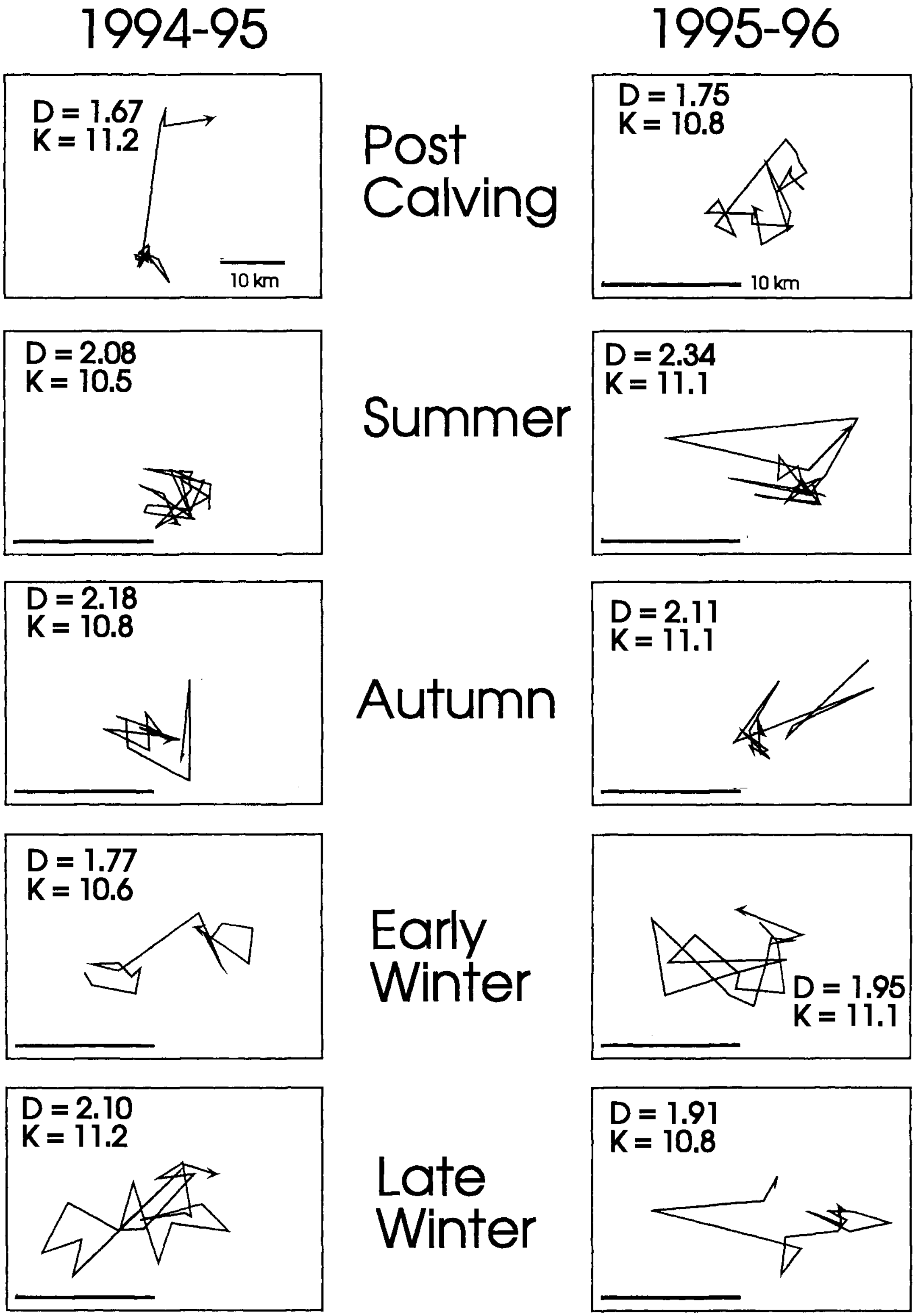

Fig. 6. Movement patterns for a female caribou with a calf in 1994-95 and without a calf in 1995-96, by season. Comparison of the fractal dimension of movement (*D*) and standardized pathlength (*K*).

bou movements had the highest fractal dimension indicating more random and irregular movements (Fig. 4). The lowest movement fractal dimensions were recorded during the late winter/spring and autumn periods suggesting that caribou movement was more directed and less irregular. These seasons coincided with the period when caribou moved from winter habitat to spring calving habitat and back again to winter habitat. During the post-calving and early winter periods, caribou movement was intermediate in terms of fractal dimension.

For the standardized measure of total pathway length, *K*, we found differences among seasons ($F_{4,217} = 6.39$, $P < 0.01$), and whether or not a female had a calf ($F_{1,217} = 19.4$, $P < 0.01$) with a possible interaction ($F_{4,217} = 2.31$, $P = 0.06$). Overall, the highest standardized length was for the early winter season while the lowest estimates came from the post-calving seasons (Fig. 5). Female caribou without a calf moved shorter distances (standardized measure, *K*) during the autumn and early winter periods (Fig. 5).

Fig. 6 depicts the movement pathway of a radio-collard female during 1993-94, when she successfully raised a calf, and in 1994-95 when she was observed without a calf. During the spring of 1994, when she had a calf, this female recorded her lowest fractal dimension of movement and highest standardized pathlength. Throughout the remainder of the year, the fractal dimension of movement was high (ca. 2.0) with the exception of autumn 1994. Generally, the fractal dimension of movement was higher for the female the following year when she was observed without a calf. Also, the standardized pathlength was higher for the female in 1995 when she was without a calf.

Discussion

Differences in the fractal dimension of pathways may reflect differences in the way caribou perceive environmental heterogeneity related to differences in resource availability and possibly predation risk. Therefore, the parameters, *D* and *K*, may indicate how an animal responds to, or perceives, environmental pattern within the range of spatial scales considered. For example, the movements of a female caribou with a calf are directed principally at keeping her calf safe from predators, whereas a female caribou without a calf directs her searching to maximize energy intake (Roby, 1978; Boertje, 1981; Bergerud *et al.*, 1984; Ferguson *et al.*, 1989). In the case of females with a calf, the need to provide protection from predators may reduce their movement rates (low *K*) and relatively rapid and direct movements between sheltering locations may reduce pathway complexity (low *D*) relative to females without a calf.

Animals will move in a more straight line through an area with an evenly distributed resource (i.e., small *D*; Wiens *et al.,* 1995). In contrast, animals searching for sparse but highly clumped resources will search in a subregion with greater relative resources resulting in a more convoluted search path (i.e., large *D*; Crist & MacMahon 1991). Following this argument, the greater linearity of female caribou pathways in early spring and autumn (lower values of *D*) may have the effect of increasing the likelihood of encounters among widely dispersed individuals. During winter, the greater fractal dimension indicates a more tortuous pathway and suggests that caribou may interact with environmental heterogeneity on a finer scale (smaller grain; *sensu* Wiens, 1990). The fractal structure of animal pathways shifts when fundamental behaviour changes in response to food density, social factors, predation, or physiological stress (Dicke & Burrough, 1988; Crist *et al.*, 1992).

Wiens *et al.* (1995) advised that researchers in animal behaviour complement the use of fractal dimension with other scale-dependent measures (see Li & Reynolds, 1995). Patterns of space use can be described by speed of movement. Mean daily distance travelled ranged from 3-26 km/day for two barren-ground caribou herds in Alaska-Yukon (Fancy & Whitten, 1991) and 2-3 km/day for 3 woodland caribou populations in Labrador (Harrington & Veitch, 1991). For both of these studies, daily distances of females were lowest during the calving period, highest during spring and autumn when moving between winter and summer range, and also increased after a female had lost her calf. Unpublished results support this same pattern, with distances moved by female caribou in central Saskatchewan being similar to other woodland caribou populations (data in prep.). Fractal dimension and standardized pathlength are scale-independent measures of movement behaviour whereas speed of movement varies with changes in scale. Also, the spatial pattern of movement behaviour is described by the fractal dimension.

We strongly urge researchers to consider spatial and temporal scale carefully when calculating fractal dimension from movement pathways. One operational problem of fractal dimension measurements relates to estimating the slope of the regression line from the log-log plot. The slope may change with step length (i.e. curved line). For example, our results for caribou and similar data for polar bears (*Ursus maritimus*; Ferguson *et al.*, in press), show that satellite telemetry data (temporal scale based on 4-6 day intervals) for large-bodied mammals estimates a fractal dimension of movement of $1.5 < D < 2$. In contrast, insect movement pathways measured on a temporal scale of minutes show fractal dimensions of $1 < D < 1.5$ (Wiens *et al.*, 1995). Turchin (1996) argued that these differences are scale-dependent and therefore fractal theory is not applicable to movement data (i.e., lack of self-similarity). Researchers can consider the following options: (1) test for self-similarity before using fractal methods (see Cox & Wang, 1993); (2) choose a particular straight section of the curve for the estimation of slope and assume that the straight segment is the range of scales over which fractal theory applies; and (3) use statistical methods (e.g., "broken stick"; Sibly *et al.*, 1990) to delineate the range of scales over which the log-log plot is linear.

The structural complexity of the environment influences the fractal dimension of movement processes (Burrough 1981; 1983; Palmer 1988). Remotely-sensed measurement of landscape patterns can be used to estimate fractal dimensions (Milne 1989; De Cola 1989) and such studies can focus on the consequences of heterogeneity for the movement of animals, resources, and energy. Consequences of heterogeneity probably result from similar processes for beetles as for ungulates although allometric considerations are necessary (Swihart *et al.*, 1988). Adding to the descriptive observations and experiments in movement pathways in relation to landscapes for a number of populations and species will help to understand basic ecological processes.

Are differences in movement patterns attributable to differences in predation, body mass, diet, life-history, physiology, vagility, or social organization? Can we relate the fractal geometry of animal movements to the fractal geometry of their landscapes? These are the important questions we need to address in the merging fields of behavioural ecology and landscape ecology (Lima & Zollner, 1996). We need to study animal space-use patterns in the context of scale; particularly animal-perceived scale or the animal's perceptual range and not the narrow range of human-perceived scale. This will help us to develop an understanding of the limits to extrapolation of the results of a study, regardless of the scale of which that study is conducted. Wiens & Milne (1989) proposed that we adopt a multi-scale conceptualization of landscapes by conducting studies over a range of scales, thereby defining the domains of scale that apply to particular patterns, processes, or phenomena. One method of determining the domains of scale relative to a particular process, is to analyze the fractal geometry of patterns over a range of scales and determine at which points the fractal dimension changes (e.g., Krummel *et al.*, 1987; Palmer, 1988; Horne & Schneider, 1995). A constant fractal dimension over a range of scales defines a domain within which the patterns, and perhaps the causative processes, are repetitive and predictable.

This approach can be applied to animal movement pathways. We would not expect animal trails ro be pure fractals since, in nature, hierarchical 'breaks' define the domains over which self-similarity occurs (Mandelbrot, 1990). For movement trails, natural hierarchical steps interrupt the pattern as a sequence in time and space (Dicke & Burrough, 1988; With & Crist, 1995). For example, we have estimated fractal dimension of caribou movement pathways using a spatial and seasonal scale. At a higher hierarchical level, home ranges, which are movement pathways over a larger area and a longer time, define another domain of fractals. Gautestad & Mysterud (1993) estimated the fractal dimension of the home range of domestic sheep (*Ovis aries*). They argued that fractal dimension of this annual temporal measure is approximately 1.5, like other physiological measures of time that are allometricaly related to body mass raised to the 1/4 power. At a lower hierarchical level, walking gaits, define another domain of fractal self-similarity (Hausdorff *et al.*, 1995). Therefore, spatial and temporal patterns, or trends in random directions, can be seen as a process of hierarchies: small-area, short-term trends may be imposed upon larger-area, longer-term trends, imposed on yet larger-area, even longer-term trends, and so on (Mandelbrot, 1983; Milne, 1992; Arino & Pimm, 1995).

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Trade-offs between wood supply and caribou habitat in northwestern Ontario

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Abstract: Woodland caribou habitat management in northwestern Ontario is a complex spatial problem. The Strategic Foresr Management Model (SFMM), a linear programming PC-based planning tool being developed in Ontario, was used to examine the impacts of alternative management strategies on caribou habitat. The management alternatives investigated included the cessation of timber management and maximising the present value of wood production without any explicit concern (in the model) for caribou. Three major findings are worth noting: 1) ttying to maintain prime caribou habitat within active Forest Management Units will come at a cost to wood supply but the cost will depend on the absolute amount of area affected and the spatial configuration of that land in relation to mills. The cost of maintaining catibou habitat in one management unit at a level about 25 000 hectares is roughly $324 000 per year (about 3 cents for each Ontatio resident). The imposition of an even-flow constraint on wood production is in fact potentially more costly; 2) Given the tegion is heavily dominated by sptuce aged 90 years and over, forest succession and fire disturbance will likely cause large declines in prime caribou habitat in the near to medium term (20 to 40 years) even if no timber harvesting occurs; 3) The complexities of the trade-offs in this resource management problem highlight the limitations of any single modelling tool to satisfactorily address all issues. Planners need to take advantage of a wide range of analyrical techniques to quantify the issues and formulate integrated policies.

Key words: caribou, habitat, wood supply, economic analysis, forest management.

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Introduction

Forest management planning problems tend to be large and complex. For example, wood growth and yield functions are required across many stands. Silvicultural costs and stumpage values may vary spatially and stand management options are usually numerous. When non-wood outputs (values) are considered the complexity increases. A common response to this problem in forest planning has been to use linear programming (LP) to explore the trade-offs implicit in forest planning (e.g. Davis, 1996; Buongiorno & Gilless, 1987; Johnson *et al.*, 1986; McKenney & Common, 1990). Linear programming is a tool which can efficiently search through the large number of possible management combinations and permutations that are typical in forestry to identify a particular scenario that maximises an objective subject to certain types of management constraints.

In this paper, we quantify some of the trade-offs between wood supply and caribou habitat across northwestern Ontario using a linear programming model. The overall area of interest includes 17 Forest Management Units, and over 7 000 000 hectares of land (Fig. 1). A large geographic perspective is required for this forest management problem because of the nomadic nature of woodland caribou and the relatively low densities of caribou remaining in the region (Cumming, 1992). The Ontario Ministry of Natural Resources (OMNR) is committed to maintaining species within their current ranges and have developed a set of proposed guidelines for Caribou management (Racey *et al.*, 1992). Caribou numbers have been declining for a number

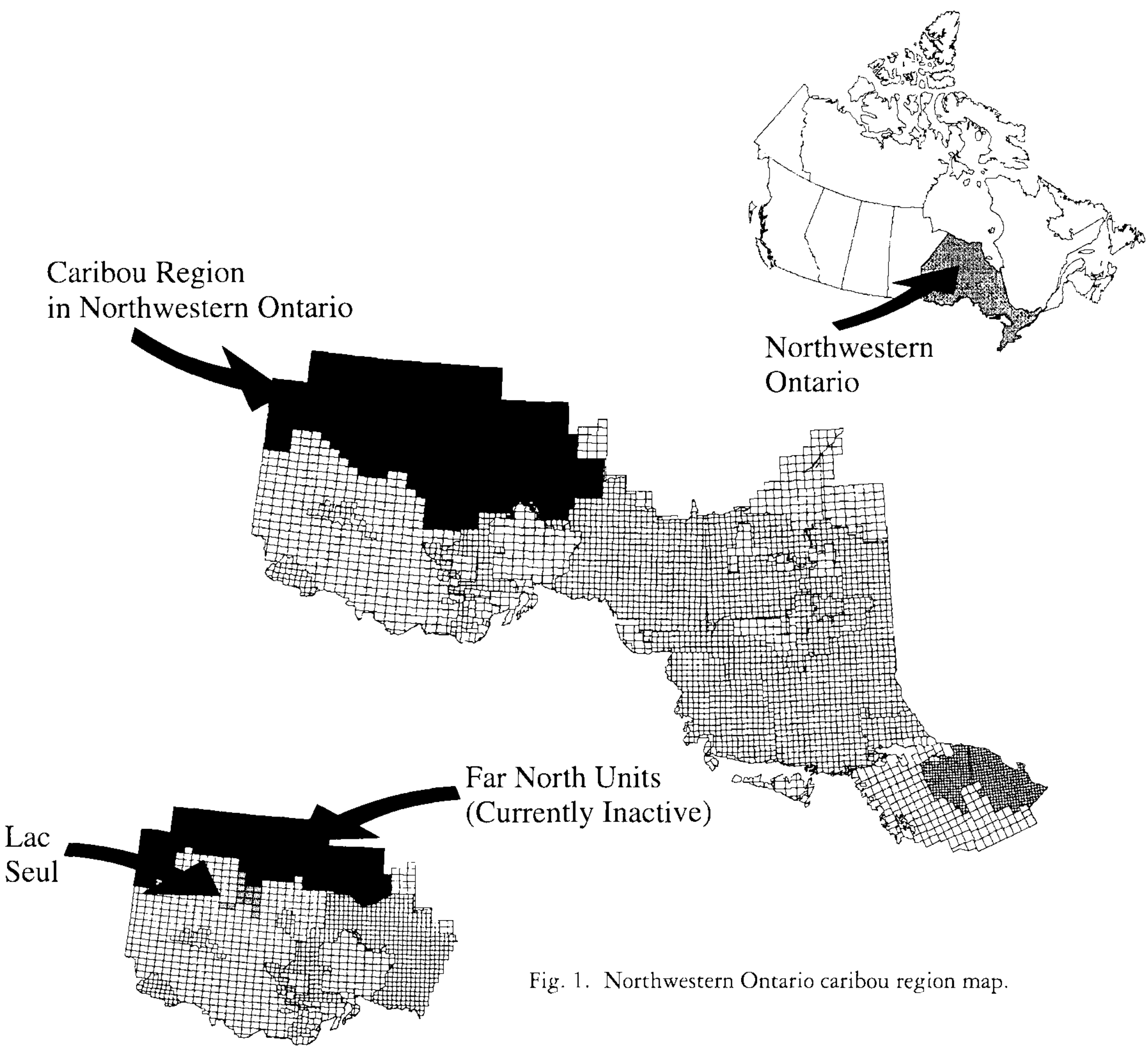


Fig. 1. Northwestern Ontario caribou region map.

of reasons but in a manner that roughly parallels the northern extent of timber harvesting operations. The caribou guidelines call for the maintenance of large tracts of older forest to provide for caribou habitat. These large tracts are identified in a mosaic which ensures special consideration of caribou winter habitat, areas used for calving and travel opportunities. This strategy suggests a set of spatial constraints to balance wood supply and habitat concerns that are somewhat different than most resource planning problems.

LP models allow the management problem to be set up in a number of ways although typically it involves maximising an objective such as the Net Present Value (NPV) of management activities through time. Effects of management on forest growth and yield are modelled for each land unit. The range of potential costs of management and benefits, usually a measure of stumpage value, associated with each land unit or activity are discounted by a rate of interest to derive a net value in today's dollars. In theory, the management strategy selected is the combination of activities through time that maximises the NPV. In practice, many scenarios and assumptions are examined to formulate actual management strategies.

Although it is possible to directly include nonwood values like wildlife habitat in objective functions of LP models, very few empirical studies actually do so. One reason is the difficulty in obtaining willingness-to-pay measures (i.e. prices) for nonmarket goods. Hence nonmarket values are usually identified as constraints on management in LP models. One example is maintaining a target total amount of area in particular age classes because some wildlife species associations prefer certain age classes. The cost of these constraints can be determined by running the model with and without the constraints. The difference in NPV represents the potential economic cost of that constraint. Decision makers can then use personal judgement and/or other information to assess whether the cost is worth while.

We examined changes in caribou habitat for one particular Management Unit in the region using three different objective functions, i.e. maximise net present value, maximise wood production, and maximise net present value subject to a constraint on changes in caribou habitat. A no timber management scenario is also presented. The second set of analyses simulates changes in caribou habitat on three far north management units in the region assuming no timber management. In this case the changes in caribou habitat arise as a result of fire regimes and natural forest succession. Data availability and the nature of LP make it difficult to explicitly examine some of the spatial aspects of this problem over the entire region.

Methods and data

The Strategic Forest Management Model (SFMM) is a PC based interactive forest modelling system that allows users to represent large forested areas at a strategic level (Davis, 1996). SFMM has been and continues to be developed by the Forest Resource Assessment Project of the OMNR. The modelling system is based on linear programming techniques, and is designed specifically for Ontario's forest conditions and strategic planning requirements. SFMM provides a flexible framework to represent a forest as it evolves through time, in response to natural dynamics and active intervention. Users can evaluate a variety of forest management objectives and targets, and explore long-term strategies and tradeoffs. Through a graphical interface, users can:

1. Define the current forest and non-forest land base;
2. Simulate the forest's natural development through time;
3. Describe their silvicultural options; and

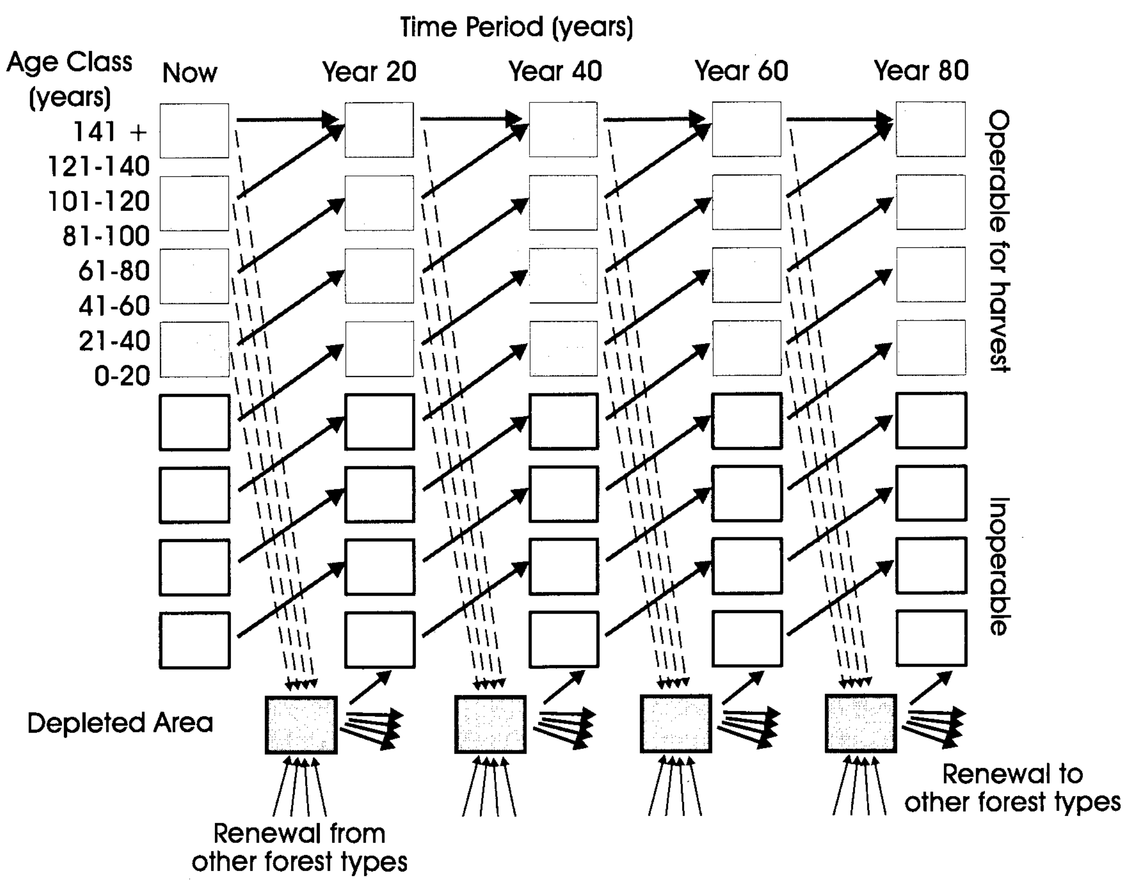


Fig. 2. A simplified view of SFMM's model III network srructure.

4. Explore management alternatives and scenarios to design a forest management strategy that provides an appropriate mix of benefits.

Results of a model run are provided through graphics and text in seven categories: forest condition, forest dynamics, areas treated, finances, volumes harvested, wildlife habitat and forest diversity.

The structure of SFMM is known as a "Model III" network (Fig. 2). The model is built upon a series of similar linked networks that together represent the various forest types within a large forest land base. The simplified network shown in Fig. 2 represents a single forest unit. Each box represents an age class within the forest unit. The arrows represent how area transfers between these age classes to represent growth, harvesting, and renewal through time. Linkages with other, similar networks (not shown) can also transfer to and from other forest types. Land might change in status from one forest type to another through natural succession, tending treatments, or harvesting and renewal treatments that do not return all the area harvested to the same forest unit.

Like most planning problems, four basic types of information were required for this study:

1. Forest Resource Inventory (FRI) data describing the forest stands within each township, base map or map unit in general in the region;
2. Projections of forest dynamics, i.e. growth and yield estimates, natural succession rules, and natural disturbance rates (probability estimates);
3. Information regarding eligibilities and costs of forest types for harvesting and renewal treatments; and
4. Standing timber values.

Forest Resource Inventory data

The FRI contains information on species composition, age, stocking and the area for each forest stand. These data for northwestern Ontario was obtained from the OMNR's Forest Resource Assessment Project. It was available in summary form by map sheet for the 17 active and currently inactive Management Units of interest for this analysis. Information on non-forested land types, and areas reserved from harvesting (e.g. protection forest) were also included as part of this analysis.

To simplify the model construction and interpretation, the FRI data was aggregated as: "White Birch" when it was 60% or more of the stand composition; "Jack Pine" when it was 60% or more; "Poplar" when 60% or more; "Spruce" when 60% or more black or white spruce and; "Mixed" for the remaining forest types which are primarily combinations of these species assemblages.

The region is heavily dominated by spruce age 90 years and older. However there is also a large amount of 50-90 year old jack pine and mixed forest.

Growth & yield estimates and forest dynamics

Growth and yield estimates describe the changes in timber volumes at different ages or through time for each of the different forest types. Very little is known about spatial variations in growth rates across northwestern Ontario, hence the same growth and yield estimates were used for each map unit. Average growth and yield estimates were developed for each of the forest types described above in consultation with OMNR Forest Resource Assessment Project. These values and assumptions regarding successional pathways, natural and fire disturbance rates were derived from previous work and historical data (see Arlidge, 1995). It is important to note that volumes decline over time as these forests become over-mature due to successional change.

Silvicultural options

Planning models developed previously by foresters in the region were used to derive the silvicultural options for this study. These included specific options and costs for forest harvesting and renewal treatments. Forest renewal options were $10 per hectare for basic; intermediate renewal at a cost of $300 per hectare, and intensive renewal at a cost of $1300 per hectare (Arlidge, 1995).

Standing timber values

In most planning models that involve an economic component a value of standing timber is required. The value of standing timber to society has long been a subject of debate. Forecasting the value through time further complicates the problem. The stumpage fees that are charged by the OMNR are administratively set, not through a competitive market process. The implication is that these fees would therefore not correspond to the true value of standing timber by standard economic criteria. Although the OMNR has recently changed its pricing policy to more closely correspond to current market conditions, determining the actual numerical value of standing timber to wood producers remains a contentious and difficult issue. A residual value approach is commonly used to determine standing timber values and has been applied in Ontario (Nautiyal *et al.*, 1994). This approach quantifies the difference between the final product value and the cost of producing the good. For example in the case of lumber, the standing timber value would be the market value of lumber less the cost of harvesting, transportation to the mill and an allowance for profit (Nautiyal *et al.*, 1994). This number represents the maximum amount the firm would be willing to pay for the right to harvest the standing timber.

A variant of this residual valuation approach was used to derive standing timber values for the study areas:

MWTP = (Starting MWTP - Hauling Cost)

where MWTP stands for "Mill Willingness to Pay" ($ per cubic metre), and "Starting MWTP" is intended to represent the maximum amount a mill would be willing to pay for standing timber if it was situated next to the mill. Given the difficulty in determining a single number this approach enables different views of long run standing timber values to be considered. Results presented here used a starting MWTP of $30 per cubic metre and existing mill locations (see McKenney & Nippers, 1996 for additional analyses). These MWTP values were adjusted by hauling costs for each map unit. The average of these values was then calculated to determine the average MWTP for the entire Management Unit. There is an inherent, though debatable, assumption, that harvest costs would not vary spatially.

Hauling costs are the $ costs/cubic metre of transporting wood from the harvest site to the mill. The further away wood is from a mill, the more it will cost to haul. Hauling costs were calculated as follows:

HAULING COST = (Distance to mill (km) * 0.0772(cents/cubic metre/km))

0.0772, the transportation cost factor used was based on Nautiyal *et al.* (1994) and OMNR, 1994). Distances were calculated using a Geographic Information System (GIS) algorithm and data on road locations and map units. The distance from each map unit centroid to the nearest major road was calculated for each map unit (e.g. township or Ontario Base Map). The GIS also calculated the distance to the mill that had primary rights to the standing timber for each Forest Management Unit. The distance to the mill used in the hauling cost calculations was the sum of these two values i.e. the "map centroid to nearest primary road distance" and the distance from there to the mill.

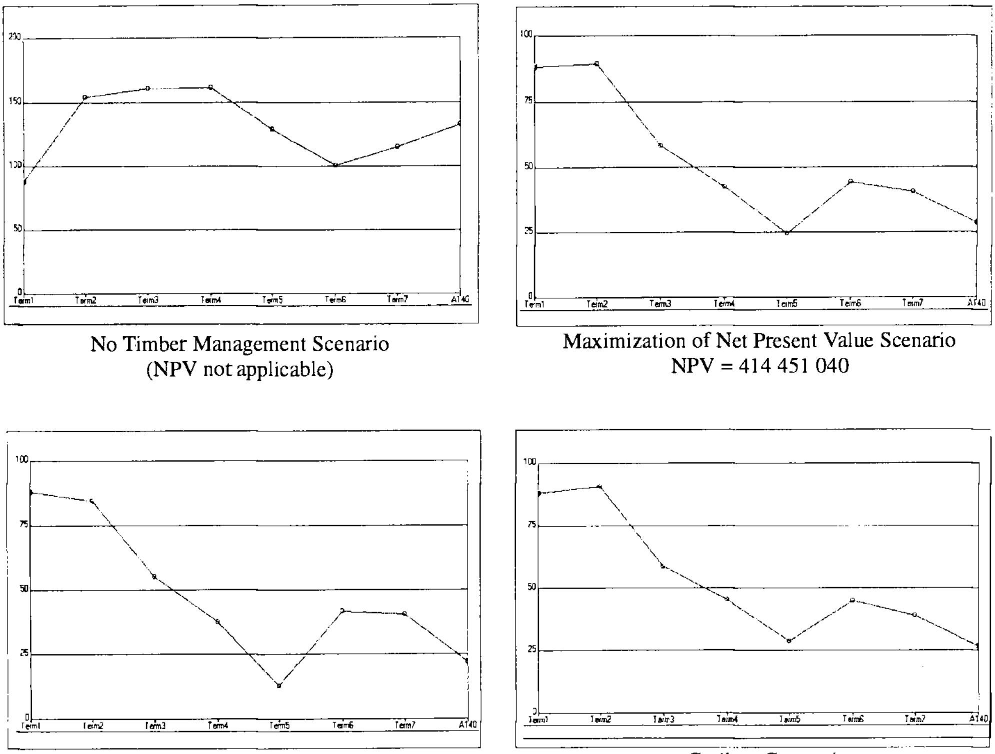
In summary, the general SFMM caribou model template tracked caribou habitat by using growth and yield projections based on other SFMM analyses in the region, inventory data summarised at the Map Unit level, standing timber values that were adjusted by hauling distance for each Map Unit and possible silviculture costs ranging from $10/ha-$1300/ha. Planning periods were 10 years and the planning horizon was 100 years. Prime caribou habitat was defined as hectares of spruce, jack pine and mixed forest aged 80 years and older.

Several SFMM analyses were performed on the Lac Seul Management Unit representing different objectives: no timber management (NTM), maximise NPV, maximise timber harvest volumes (MTH), and maximise NPV subject to maintaining a specified amount of caribou habitat in each planning period. This Unit was assumed to be representative of the active Management Units in the region. A major challenge in this type of analysis is sifting through the large volume of output to focus on the major issues. The results presented here are particularly salient. In addition some no timber management scenarios were run for 3 far north units which are not currently being harvested (see Fig. 1).

Results and discussion

Fig. 3 portrays the likely aggregate changes in caribou habitat over time for the different possible management strategies on the Lac Seul Unit. In the NTM scenario, caribou habitat fluctuated between 100 000 and 150 000 hectares. In the timber management strategies, caribou habitat dropped from near 100 000 ha currently to below 13 000 ha. After several trials, a set of constraints were developed that maintained total caribou habitat above 28 000 ha. No constraints could be found that would maintain a higher level of habitat.

The habitat results are driven by changes to the aggregate projected age class distributions. The NTM scenario skews the age classes to the older levels. Timber management scenarios result in very little of the older classes by the 5th decade. The magnitude of the drops could not have been easily



No Timber Management Scenario
(NPV not applicable)

Maximization of Net Present Value Scenario
NPV = 414 451 040

Maximization of Total Harvest Volumes Scenario
NPV = 292 120 347

Caribou Constraints
NPV = 406 373 488

* x axis = planning period; y axis = 000's of hectares of prime caribou habitat

Fig. 3. Lac Seul caribou habitat summaries.

ascertained without this type of modelling tool. SFMM makes such assessments straightforward.

The total NPV of various scenarios can be used to gauge the cost effectiveness of different management strategies. The cost in terms of NPV of the maximise timber harvest objective is approximately $122.3 million. This is the difference between maximise NPV scenario and the MTH run ($414.5 million versus $292.1 million). This amount should be weighed against the difference in the amount of caribou habitat between scenarios (which appears relatively insignificant - see Figure 3). In fact, prime caribou habitat reaches the lowest levels in the maximise timber scenario. The NPV of the habitat constraint scenario is $406.4 million. Thus, the cost of maintaining this level of habitat is $8.1 million over 100 years or roughly $324 000 per year (using a 4% discount rate). This translates into 0.07 percent of the NPV. This value represents what Ontario residents would have to be willing to pay to justify the constraint on economic efficiency grounds (about 3 cents per person in Ontario per year). Interestingly, additional analyses (not shown) which included even-flow, plus or minus 20%, timber constraints had much lower net present values $90 to $115 million depending on harvest constraint. Even flow constraints are often used in forest management to try to reduce volatility in harvest levels (Buongiorno & Gilless, 1987). In these runs caribou habitat reached low levels comparable to the MTH scenario.

Whether this 25 000 or 50 000 hectares of habitat in the Lac Seul Unit are sufficient to sustain the caribou population in the larger region is an important biological question but beyond the scope of this analysis. There may be alternative, more cost-effective means to maintain a population of caribou in the region at large. For example, timber harvesting could, in principle, be restricted in the far-north units. This fibre is potentially less valuable to industry because of the large hauling distances involved and may therefore involve less of a sacrifice if forgone. However, even if timber management was eliminated from these units, natural forest succession and fire patterns will affect habitat quality and quantity over time.

To investigate this issue, no timber management scenarios were developed for several far north management units (Ogoki, Lake St. Joseph and Berens River units - see Fig. 1). These scenarios examined potential changes in habitat given minimal fire suppression activities and natural succession. The fire probability disturbance rate was 0.015 as compared to 0.004 85 in Lac Seul where fire suppression activities are more common (Tithecott, pers. comm.).

Fig. 4 shows the implications of no timber management on 3 far north units on the expected aggregate amount of caribou habitat over time. Except for the Berens River Unit, caribou habitat substantially decreases over time relative to current levels. This is attributed to the existing old forest condition (age class structure) of these units. Note that the absolute amount of caribou habitat varies considerably across each of the units. More research is likely required to understand the actual spatial variation in habitat quality across these units. For example, would 50 000 hectares of "caribou habitat" in the Berens River Unit be better than 100 000 hectares in the Lake St. Joseph Unit because of the quality of overwintering areas?

Conclusions

This paper demonstrates how a generic linear programming based forest planning model can be used to investigate caribou, wood supply and forest economic issues. The implications of the proposed caribou guidelines are difficult to quantify in precise terms over such a large region. There is a complex array of trade-offs between wood supply and the value of standing timber and the spatial arrangement of caribou habitat. Models such as SFMM and other forest planning tools help planners and stakeholders to clearly identify and organise what is known and not known. This quantifies trade-offs more clearly. What makes the caribou management problem unique is the nomadic nature of the animal hence many Forest Management Units could be affected by policy directives. Wood supply issues may need to be co-ordinated over a much larger geographic area than is currently taking place.

The Lac Seul analyses presented here suggest that it will be difficult to maintain caribou habitat in a single management unit once timber harvesting occurs depending on the amount of habitat explicitly required. The results support the notion that coordination among management units may be necessary to maintain caribou range across the currently

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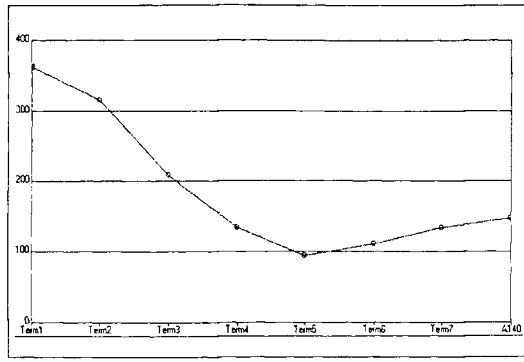
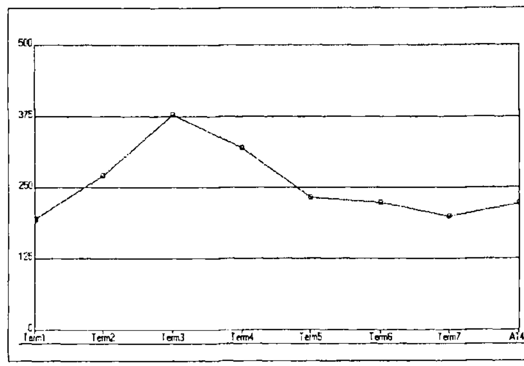


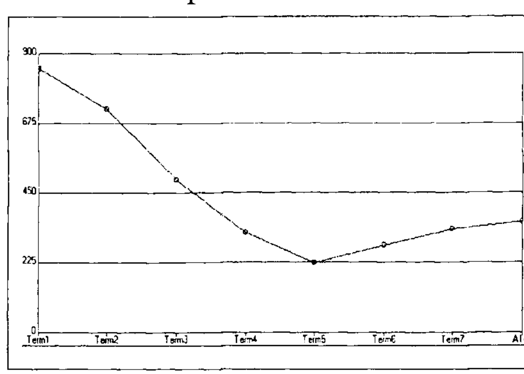
Potential Caribou Habitat over time

Berens River



Potential Caribou Habitat over time

Lake St. Joseph



Potential Caribou Habitat over time

* x axis = planning period;
y axis = 000's of hectares

Fig. 4. Caribou habitat in far north units with no timber managemenr.

occupied portion of northwestern Ontario. Extrapolating this result to other Forest Management Units in the region is nevertheless difficult. The composition (species) and structure (age classes) of each unit is different. Maintaining small patches of habitat within harvested areas across the entire region may in fact be a less cost effective approach to maintaining the species (see Hyde, 1989 for a similar recommendation in the context of a forest dwelling bird species). More analyses are required to investigate this assertion.

The no timber management scenarios on the far north units also suggest that prime caribou habitat is likely to fluctuate considerably over the next 100 years regardless of timber management activities. This is due to the preponderance of mature/over mature spruce forest in the region that is susceptible to fire. Woodland caribou may be more reliant on these areas than they have been in the past because of harvesting activities south of these units. Despite the likely declines in prime caribou habitat, timber harvesting may not be an economically viable proposition for these units. Restricting timber harvesting in these far north units may still be the most cost effective way of maintaining caribou in the region at large.

Clearly maintenance of caribou habitat in any given area that includes timber harvesting will require rigorous spatial analysis on the layout of harvest patches. Co-ordinated planning efforts with surrounding Management Units is necessary to minimise the impacts on both wood supply and habitat. Linear programming by itself will likely be of limited value in such broad scale planning. Forest planners will need to take advantage of a wider range of tools such as Geographic Information Systems, and other simulation and optimization tools to provide additional insights. (e.g. McKenney & Nippers, 1996).

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Analysis of forest stands used by wintering woodland caribou in Ontario

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Abstract: Two summers' field surveys at 9 locations in northwestern Ontario showed that woodland caribou (*Rangifer tarandus caribou*) wintering areas supporred jack pine and black spruce stands with low tree densities (mean 1552 trees/ha, 39% of a fully stocked stand), low basal areas (mean 14.14 m^2/ha), low volumes (mean 116 m^3/ha, 68% of Normal Yield Tables) and short heights (95% of stands 12 m or less). Ecologically, most sights were classed V30. Significantly more lichen (averaging 39% lichen ground cover) was found on plots used by caribou. Three measured areas showed few shrubs, possibly enhancing escape possibilities and reducing browse attractive to moose. An HIS model predicted known locations of caribou winter habitat from FRI data with 76% accuracy. Landsat imagery theme 3 (open conifer) produced 74% accuracy. Combining these methods permitted prediction of all 50 test sites. The low volumes of timber found in caribou wintering areas suggest that setting aside reserves for caribou winter habitat would not sacrifice as much wood product value as might at first appear.

Key words: *Rangifer tarandus caribou*, landsat, habitat, timber stands, HSI.

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Introduction

During the last 2 decades, forest managers have broadened the scope of their activities to include many uses previously ignored. Providing habitat for woodland caribou constitutes a recent challenge (Cumming, 1992). Unlike white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) which associate primarily with young stands and thus can thrive in a managed forest, caribou frequent even earlier ecological stages (moss, lichen) that paradoxically may not show up until forests are old and sometimes breaking up. Forest management for woodland caribou, therefore, involves some of the problems associated with managing old forests for other species (Cumming, 1994).

To meet these challenges, caribou biologists have often recommended that portions of the forest be reserved from cutting (Johnson *et al.*, 1977; Simpson *et al* , 1985; Ritcey, 1988; Servheen & Scott, 1988; Ministère du Forêts. Ministère du Loisir, de la Chasse et de la Pêche, 1991; Cumming & Beange, 1993; Cumming, 1994). In Ontario, some biologists (Racey *et al* , 1992) have proposed caribou habitat management by scheduled cutting in large blocks, rather than specific reserve systems, but this scheme also requires delaying wood harvesting of occupied winter habitat until alternate habitat becomes available. The situation is made more urgent by the finding that only about 1800 woodland caribou remain in the commercial forests of Ontario (Cumming, in press).

These considerations raise important questions for those who wish to manage forests to retain caribou winter habitat: what kinds of forest do woodland caribou inhabit in winter? What losses of wood products can be expected if cutting in caribou wintering areas is deferred? Can potential winter habitat be predicted? To answer these questions, we applied standard forest mensuration techniques, augmented by lichen and sighting surveys, to 9 caribou wintering areas known from previous aerial surveys to be frequented by caribou (Cumming & Beange, 1987). We then proposed a habitat suitability index (HSI) for predicting potential caribou habitat in forest planning.

Study areas

The Royal Commission on the Northern Environment (1980) describes the area around Lake

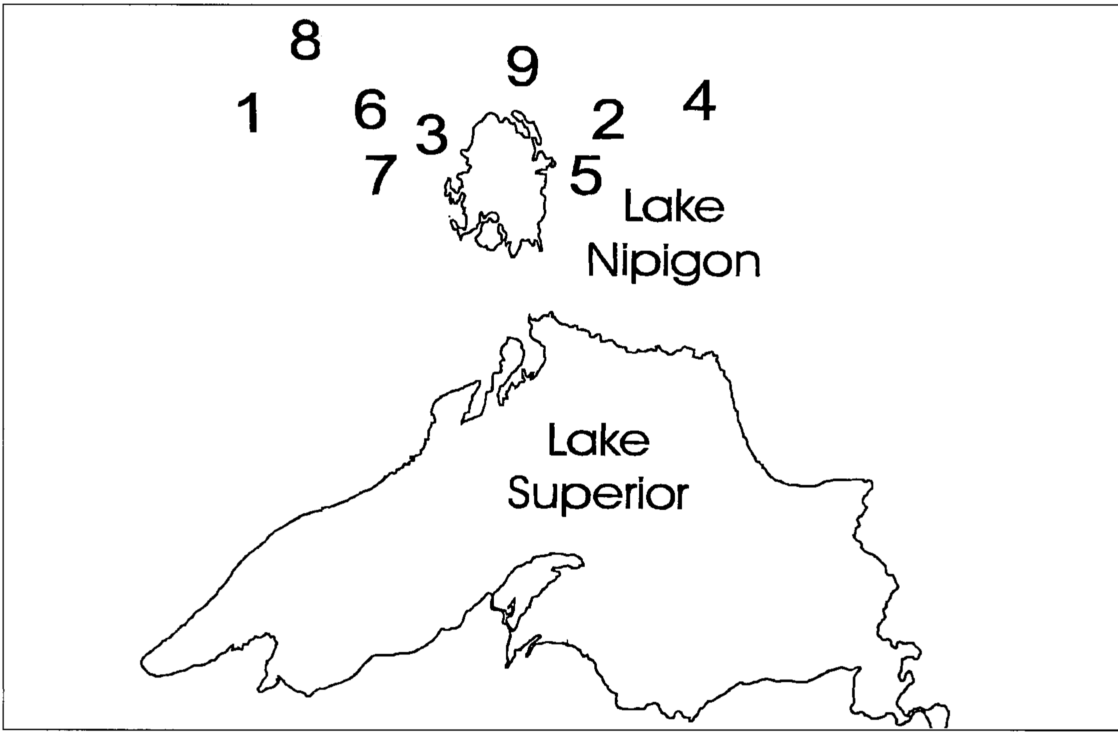

Fig. 1. Locations of study areas relative to Lake Nipigon, in the order they were examined. Location code: 1 Elf Lake, 2 O'Neil Lake, 3 Armsrrong Old, 4 Molison Lake, 5 Crocker Point, 6 Armstrong North, 7 Armstrong South, 8 Wabakimi Lake, 9 Lamaune Lake.

Nipigon (from Wabakimi Lake to Molison Lake, Fig. 1) as Canadian Shield made up of granitic rock partially covered by lacustrine sediments and the occasional ground moraine. The mean daily temperature for January is - 19.5 °C. Snow covers the ground for 160 to 200 days of the year. The area receives 160 to 280 cm of snow fall annually. During the years in which surveys determined locations of caribou for this study, maximum snow depths ranged from 35 to 65+ cm (Cumming & Beange, 1987).

Nine study areas were chosen from results of earlier research that documented locations of wintering areas over 4 winters by telemetry and aerial mapping of tracks (Cumming & Beange, 1987) . Four of the chosen areas had been used by caribou all 4 winters; 2, 3 winters; 1, 2 winters; and 2, 1 winter (Fig. 1). The Lamaune Lake study area was clear-cut in 1963, and another area at Springwater Creek that had been selectively logged in part during World War II and in part during 1980 was investigated for lichen regeneration only. All other locations supported virginal stands in the boreal forest zone (Hosie, 1973). The study areas represent the southern limits to the range of woodland caribou in the Lake Nipigon area (Cumming & Beange, 1987).

Methods

To learn what signs of caribou winter use looked like in summer, we marked, during February, 1980, winter feeding craters south of Armstrong and revisited them the following May. We then measured horizontal and vertical distribution of trees in the 9 locations during the summer of 1980. When a wintering area was chosen to be sampled, its boundaries were located on a map and on aerial photographs. The following sample design was used in all areas studied. Three transect lines (400 m long and 100 m apart) were laid out on the photos before the area field work commenced. The starting point was randomly located. Lines were established at right angles to the topography, both to provide for representative sampling and to minimize the need for slope corrections. Each line consisted of 14 sample plots, 10 m long and 20 m apart. This sampling intensity was chosen because it met the guidelines of the Ontario Ministry of Natural Resources

(OMNR) for sampling vertical transects (Ontario Min. Nat. Res., 1980), based on Bickerstaff (1961). Therefore, each study area contained 3 lines with 14 vertical sampling plots and 42 corresponding ground lichen and caribou usage plots. The only exception to this sampling design was at Lamaune Lake where access difficulties reduced sampling to 10 plots located 30 m apart on a single transect across the stand.

Up to 6 collection and analyses strategies were employed at each location. Ontario Forest Resources Inventory (FRI) data were collected (Ontario Min. Nat. Res., 1978) for a detailed description of caribou wintering areas. Vertical distributions of trees were measured using the vertical transect method described by Husch *et al.* (1982). Briefly, this method involves the tally by height class and species of all trees subtended by a vertical angle of 45 degrees. The sampling is carried out on a continuous strip with observations at right angles to the line of travel. Intensity of sampling varied with the size and heterogeneity of the stand. We sampled 100 m/ha, a rate that had been found suitable in the boreal forest (Day, pers. comm.), and agreed with suggestions by Husch *et al.* (1982).

Horizontal profiles of the forest stands were examined in conjunction with the vertical transect sampling, following Avery (1967) and Husch *et al.* (1982). We followed their recommendation in using a small BAF prism (2 m^2) to reduce possible bias. From the horizontal sampling results stand descriptions similar to those used by FRI were developed.

In 1992, we re-assessed these areas using the newly developed Northwestern Ontario Forest Ecology Classification (NWO FEC) for standardization of ecological site characteristics (Sims *et al.*, 1989). Ten plots were located in each of 8 measured locations. V-type plots (NWO FEC) were located at 30 m intervals along the sampling transects. The descriptions of the various vegetation types found in Stocks et al. (1990) were used to confirm the site assessments. Crown closure was estimated from the ground in accordance with the guidelines and charts provided by Sims et al. (1989).

In addition to the forest stand sampling, ground lichen and caribou usage were also measured as follows: (1) 10 - 1 m^2 plots were located along the line used for vertical stand sampling; (2) plots 1, 5, 10, were "framed" using 4 - 1 m sticks and then occularly assessed for the percentage of ground lichen; (3) evidence of woodland caribou winter use, including pellet groups, browsing, antlers, and bush thrashed trees, were recorded on each plot. Although arboreal lichens may be important to caribou in some places, summer efforts at evaluating use proved too inaccurate for further pursuit, and arboreal lichens were not included in this study.

Visual sighting measures, and lichen regeneration quadrat data were also collected in the summer of 1992. To help assess the impacts of these wintering conditions on the caribou themselves, and to obtain a rough measure of shrub availability, visual sighting measures were taken in conjunction with the NWO FEC plots at Crocker Point, O'Neil Lake, and Molison Lake. An 8 1/2" by 11" aluminum clipboard was held at breast height (1.3 m) at the plot centre. This height was chosen because it is the approximate height of a caribou's eye (Godwin, 1990). In each case, we recorded the distance along the transect line at which the clipboard could no longer be seen. If the distance was greater than 30 meters it was recorded as 30+ m. Comparative measures in fully stocked mature black spruce stands were taken near Shebandowan Lake, 100 km west of Thunder Bay, Ontario.

Due to wide interest in times required for lichen to grow again after trees are cut, the Lamaune Lake study area was examined for lichen regeneration 30 years after harvesting. In addition, the cut areas at Springwater Creek were examined on the ground in 1980 and 1992. During the second visit, we ran a transect line through each of the 2 cut-overs (12, 50 years old) at right angles to their common boundary. In each cut area, we established 10 sampling stations spaced 5 m apart, and at each station we measured 2 side by side plots, 1 m^2 in size.

We built our HSI model on FRI data because of their wide availability. Our model was derived from HSI models for moose in the Lake Superior Region (Allen *et al.*, 1987) and for woodland caribou year round habitat in Saskatchewan (Yurach *et al.*, 1991). To test the predictive ability of the FRI stand descriptions against known wintering areas, we obtained stand descriptions for "good habitat" values from the habitat suitability index model and then attempted to locate similar sites in the forest.

Another approach was made possible by Timmermann (pers. comm.) who provided Landsat imagery for Northwestern Ontario that had been developed, analyzed and summarized into 15 possible themes (for forest fuel analysis) for fire management. The Landsat MSS data with a 50 m resolution were corrected to UTM co-ordinates and a supervi-

Table 1. Forest Resources Inventory descriptions, Forest Ecosystem Classifications, and lichen ground cover percentages on 9 locations where caribou repeatedly concentrated during winter.

Survey location[a]	Plots showing use by caribou (%)	FRI Description: Working Group	Age (m)	Height closure	Crown Class	Lichen ground cover (%): Site by caribou	Plots used[b] by caribou	Plots not used
1	31	Pj	90	11	40	4	43.1[c]	13.7
2	33	Sb	60	6.5	50	3	27.3	0.6
3	21	Pj	70	18	60	2	50	22.7
4	36	Pj	98	15.1	40	3	30.9	1.9
5	26	Sb	90	12	40	2	24.5	1.9
6	40	Pj	65	13.2	80	3	41.6	31.5
7	40	Pj	65	13.2	80	3	63.1	8.9
8	26	Sb	87	11.4	50	3	24.8	2.1
9	60	Sb	25	4.2	40	3	45.6	29.1
Mean	35		72	11.6	53		38	12
S. D.	11		22	4.2	0.17		12	12

[a] Area code: 1 Elf Lake, 2 O'Neil Lake, 3 Armstrong Old, 4 Molison Lake, 5 Crocker Point, 6 Armstrong North, 7 Armstrong South, 8 Wabakimi Lake, 9 Lamaune Lake.

[b] Signs indicating caribou use of a plot included pellet groups, browsing, anrlers, and brush-thrashed trees.

[c] We used original data because square root, logarithmic and arcsin transformations did not substantially improve normality plots.

sed classification was performed to produce 15 forest fuel classes by the OMNR. The dates of the imagery ranged from 1976 to the mid- 1980's. The classified data (data which had already been analyzed into specific classes or themes) were downloaded onto a Sun workstation. The accuracy and reliability of forest fuel mapping by Landsat was checked by contacting the OMNR fire control centres in Thunder Bay and Sault Ste. Marie, Ontario. The only testing available was operational. The mapping system worked very well and met operational requirements (Mr. Turner & Mr. Checkley , OMNR fire control officers, pers. comm).

Test sites for these approaches were located in the vicinity of Wabakimi Lake, Ontario, where winter use by woodland caribou was well documented. Fifty locations where winter activity(feeding craters, telemetry locations, track aggregations, and visual sightings) had been observed were chosen from 8 winter surveys of caribou activity from 1978- 1984 and 1989-1991 (no surveys were conducted from 1985-1988, Gollat, pers. comm.) to compare with FRI data and Landsat theme areas.

Results

Three of the 9 surveyed wintering areas were situated on deep sand, the remainder on bedrock. Eight of the 9 were of fire origin. The NWO FEC class V 30 (Jack Pine-Black Spruce/Blueberry/Lichen) described a portion of every study area (half were entirely V30), totaling to 86% of the plots. Class V31 (Black Spruce-Jack Pine/Tall Shrub/ Feathermoss) occurred with V30 on 1 study area (6% of the plots), and V 32 (Jack Pine-Black Spruce/Ericaceous Shrub/Feathermoss) on another (5%). Class V 28 (Jack Pine/Low Shrub) shared an area with V30, V 32 (1%), and V 34 (Black Spruce/Labrador Tea/Feather moss) with V30, V 31 (1%). Non-V30 areas were usually located on water catchments between humps of exposed bedrock, where the slope difference was often sufficient to change the classification on the 10m x 10m sample plots. The mean estimated crown closure (from the ground looking up) was 25% (S.D.=10). Ground cover consisted of 33% (S.D.=18.08) feathermoss (*Pleurozium schreberi* and *Dicranum polysetum*) and 52% (S.D.=20.80) ground lichens (*Cladina* spp.). For further details see Antionak (1993).

Working groups (based on most common species) classed 5 study areas as jack pine, 4 as black spruce. Ground surveys using Ontario's FRI classes indicated that ages of fire-origin stands ranged from 60-98 years (Table 1); the sole harvest-origin stand at Lamaune Lake was 30 years old. Apart from Lamaune Lake (height 4.2 m) heights ranged from

Table 2. Vertical distribution (stems/ha) of all tree species by area and height class compared with Plonski's (1981) Normal Yield tables.

Area	3m	6m	9m	12m	15m	18m	Total	Normal Yield Table[a] Values (stems/ha)
1	619	329	442	127	90	16	1623	3584
2	1302	627	138	28			2095	5140
3	250	56	151	190	283		930	1611
4	1310	645	907	240	2		3106	3673
5	516	552	809	369	3		2249	3099
6	158	83	90	105	237	71	744	3490
7	143	48	190	335	128		844	1815
8	333	492	796	433	16		1981	4020
9	190	119	85				394	9495
MEAN	536	328	401	228	108	44	1552	3992
S.D.	439	241	325	132	106	28	834	2194

[a] Plonski (1981).

6.5-15.1 m. Forest site classes ranged from 2-4, crown closure from 40-80%. Within each study area, plots showing winter use by caribou comprised a mean of 35% (range 21 to 60) .

Vertical distribution of the forest

Descriptions of forests include vertical and horizontal measurements. Measures of vertical distributions showed that all trees were relatively short (Table 2), with no stands reaching the height-over-age ratios required to be included in site class 1 (Plonski, 1981). Overall, 99.9% of the trees were in the 15 m height class or less, and 95% in the 12 m height class or less. Vertical distribution surveys showed no significant difference between the used and unused plots (t=1.71, df=8, P>0.1). Therefore all plots within each study area were combined for an overall description of the area (Table 2). Species composition within each study area and between study areas showed no significant differences (t=0.32, df=16, P>0.5; t=.59, df=16, P>0.5). All stands were black spruce and jack pine mixed stands. Other species within the study areas included white birch, trembling aspen (*Populus tremuloides*), larch (*Larix laricina*) and balsam fir (*Abies balsamea*). None of these, nor any combination in total, constituted more than 5% of the stems in any of the study areas. When stems per ha by height class and study area were tested, the ANOVA showed no significant difference between study areas (f=1.411, df=8, 45, P=0.2181) but, as suspected, a highly significant difference among height classes within study areas (f=5.82, df=5.40, P=0.0004).

Vertical distribution of total stems per ha (Table 2) on the plots compared with values from Normal Yield Tables (Plonski, 1981) showed study areas always with fewer stems per ha (t=2.75, d.f. 8, P<0.05) averaging 38.8% of a fully stocked stand. Woodland caribou winter in a range of stem densities which are significantly fewer than fully stocked stands (Table 2).

Horizontal distribution

Differences in horizontal distribution between plots with signs of caribou and those with no evidence of use were not significant (t=1.32, df=8, P>0.2). Therefore the data from these categories were amalgamated (Table 3). Only 1.7% of the total volume was composed of species other than black spruce or

Table 3. Horizontal distribution: volume/ha by species.

Area	Black Spruce m^3/ha	Jack Pine m^3/ha	Others m^3/ha
1	71.06	21.18	3.31
2	51.59	4.31	
3	15.22	128.48	
4	169.03	5.79	
5	129.96		8.35
6	19.91	97.27	
7	16.28	92.53	
8	142.4	5.94	2.1
9	37.01	28.38	
Mean	72.5	47.99	4.59
S.D.	56.2	46.71	2.34

Table 4. Horizontal distribution (volume) and basal areas of plots used by caribou in winter compared with those not used and with normal tables by Plonski (1981).

Location	Volume (m^3/ha)			Percentage of normal volume (Plonski, 1981)
	Caribou sign		Total Volume	
	Present	Not present		
1	51	85	94	61
2	75	42	56	72
3	137	150	144	48
4	93	219	175	71
5	99	178	138	56
6	188	109	117	59
7	116	164	109	55
8	100	179	150	97
9	32	54	65	98
Mean	99	131	116	
S. D.	43	58	37	

Location	Basal area (m^2/ha)			Percentage of normal yield (Plonski, 1981)
	Caribou sign		Total Basal Area	
	Present	Not present		
1	11.3	11.7	12.2	51
2	9.7	10.9	10.7	54
3	16	16	9.6	37
4	9.3	26.3	20.7	87
5	12.7	21.7	17.2	50
6	22	12.6	17.6	78
7	13.5	19.2	13.3	59
8	12.7	14.7	18.7	64
9	5.3	21.7	7.2	51
Mean	12.5	17.2	14.1	
S. D.	4.4	5	4.4	

jack pine. An ANOVA showed no significant difference in volume between study areas (f=1.248, df=8, 117, P=0.2774) but a highly significant difference between diameter classes within study areas (f=7.528, df=13, 104, P=0.0001). This is to be expected with the larger volumes occurring in the upper diameter classes. Total volume per ha from all study areas, compared with volumes from Normal Yield Tables (Plonski, 1981), showed that the study areas would yield significantly lower volumes than expected (t=3.91, df=8, P<0.01). On average they supported 68% of the volume listed as Normal Yield Tables (of the same site class) and ranged from 48% to 98% of the table volumes (Table 4).

Basal areas did not differ significantly (t=1.68, df=8, P>0.05) between plots showing usage and those that did not (Table 4). The basal areas for study locations when were significantly lower (t=6.42, df=8, P<0.01) than those from the Normal Yield Tables (Plonski, 1981). The study areas had a mean basal area of 14.14 m2/ha which is less than the mean table value of 24.00 m2/ha. The differences ranged from 37% to 87% below the table values.

Caribou signs revealed a highly significant tendency to occupy plots with a greater coverage of lichen (t=6.54, df=8, P<0.001). The average percent of ground covered in lichen in plots that showed caribou usage was 39% (S.D.=12.4) compared with a covering of 12% (S.D.=11.7) in the unused plots.

Visual sighting measures

Standard forestry measurements do not indicate thickness of understory, therefore, at 3 study areas

Table 5. Lichen regeneration quadrats in 50+ year old and 12 year old cutover stands at Springwater Creek.

Plot no.	Percentage of plot covered with lichens			
	Old Cutover		Recent Cutover	
	Quadrat 1	Quadrat 2	Quadrat 1	Quadrat 2
1	80	70	60	30
2	60	80	0	0
3	10	0	0	0
4	10	40	0	0
5	5	15	0	0
6	40	10	0	0
7	0	0	0	0
8	80	50	0	0
9	30	60	0	0
10	0	0	0	0

special measurements were taken of sighting distances. Mean visual sightings from 10 measurements in each location were 22.4 m (S.D. 8.2), 24.3 m (S.D. 7.0), and 19.2 m (S.D. 5.4). Ten of the 30 determinations showed visibility beyond 30 m. Since no significant differences were found within locations (ANOVA F=1.226, df=2, 27, P=0.309), they were combined to calculate a mean visual distance of 22.0 m (S.D. 7.3), which proved to be significantly (t=4.76, df=38, P<0.001) longer than in the unused spruce forest, mean of 10.8 m (S.D. 1.9), with which it was compared

Regeneration of lichen

Caribou use had been recorded in parts of a stand along Springwater Creek in 1979 that was clear-cut in 1980. Subsequently, neither aerial surveys (Cumming & Beange, 1987) nor ground inspections showed further use by caribou. Our ground surveys in 1992 found that 12 years after the 1980 cutting, lichens grew in only 10% of the plots. In the 50 years following the 1940's selective logging, 80% of the 20 plots had established ground lichens (Table 5).

Assignment of HSI values

In forming an HSI equation we assumed that lichen is the key to winter stand usage (see discussion by Cumming, 1992). The HSI values, then, rate the ability of FRI descriptors to predict the likelihood of ground lichen. The overall HSI value for each stand is determined by multiplying all variable HSI values togethet, as follows:

HSI (overall) =
((species comp. HSI)(site class HSI)(age HSI)(crown closure HSI))$^{1/4}$

The variables were multiplied because any 1 variable has the potential to decrease the positive attributes of all other variables when indexing stands for potential wintering areas. The product was then taken to the quadratic root to eliminate the effect of 4 multiplicand decimal multiplication. As a result, HSI overall values fall between 0<>1.0. Potential woodland caribou habitat can then be rated on a scale: 0-0.33 poor; 0.34-.066 fair; and 0.67-1.0 good.

With the equation in place, results of the field research were used to assign values. Maximum HSI values for species age, crown closure, composition, and site class were based on the authors' data and the findings of Racey *et al.* (1992). Zero values were omitted because a single 0 would make the overall HSI value 0, and there is always a chance that a caribou can be anywhere. The major change points were derived from the results of this study and from other values in the literature. Survey results suggested that stand age values should be assigned as follows: from first establishment, when little or no lichen would be present, 0-20=0.01 (mid-range value, Fig. 2). When a stand is fitst being established there is little or no lichen and therefore a very low value is assigned 0-20=0.01(mid-range value), medium age 20-60=0.5 (mid-range value), mature forest, when lichen availability would be high 60-100=1.0, and older stands that would have a diminishing amount of lichen over time 100-150=(mid-range value) 0.75 (Fig. 2a).

Stands ranging from no crown closure to the development of a canopy would be very young and were rated as 0-10%=0.5 (mid-range value). Maximum lichen growth requires an open canopy, therefore 10%-70%=1.0. As the canopy closes the amount of lichen decreases with the corresponding values 70%-100% = (mid-range value) 0.45 (Fig. 2).

Species composition was expressed as total percentage of jack pine and black spruce in the stand. HSI considerations follow. Since no caribou winter activity was found in mixed stands, a low value was assigned to them 0 - 70% = (mid-range value) 0.025. The constraints of timber mapping often demand that small pockets of deciduous trees be included in what would otherwise be a pure conifer stand. As the conifer component (suggesting a dry

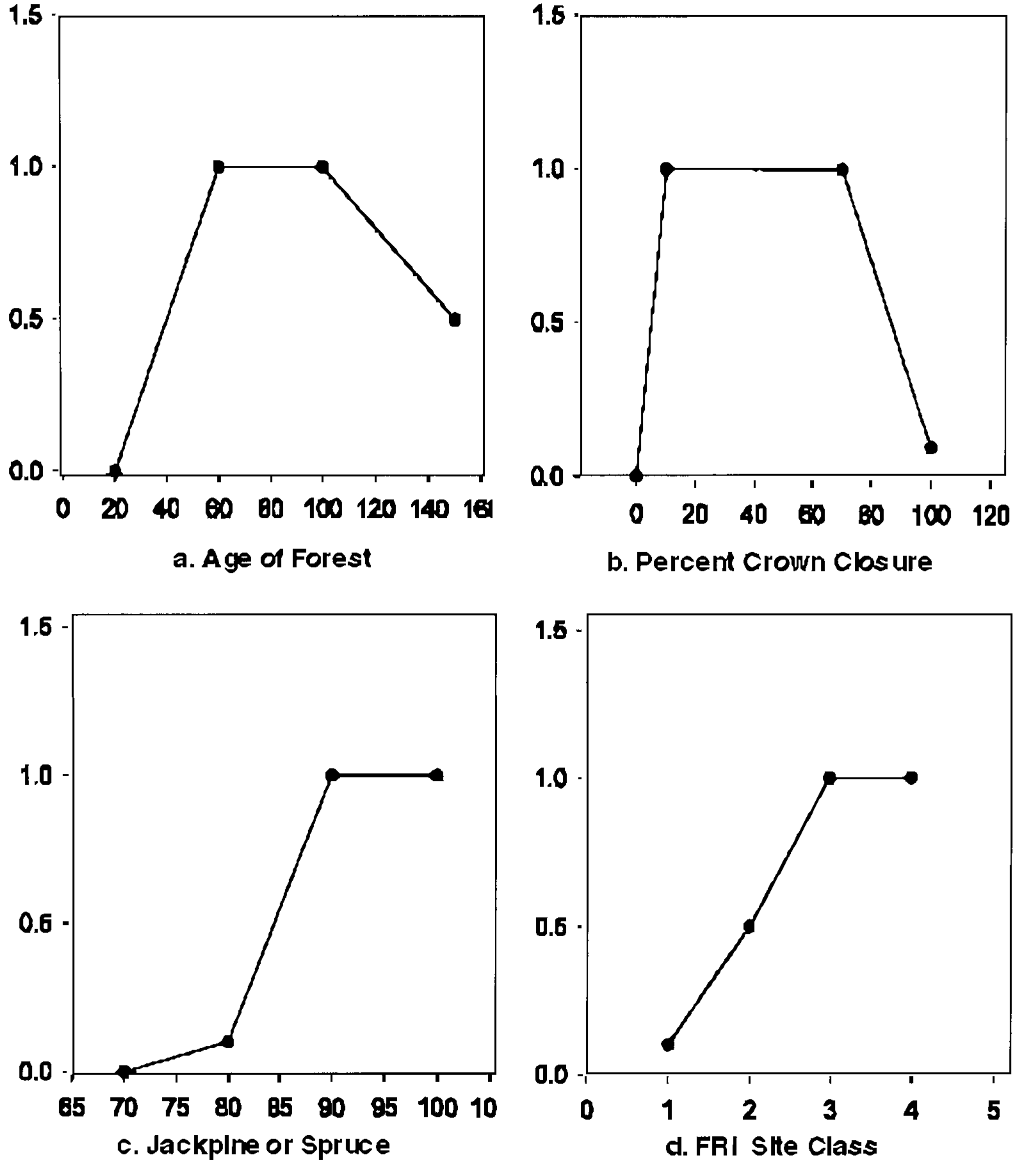

Fig. 2. HSI relationships for places where woodland caribou winter in Ontario. HIS scales are on the verricle axes.

site) increases there is an increase in the likelihood of lichen presence (Sims et al 1989) and the following values were assigned: 70%-80%=0.05 (mid-range value), and 80%-90%=0.45 (mid-range value). Pure conifer stands were currently being used, thus they were given the highest rating 90%-100%=1.0 (Fig. 2c)

Site classes based on the relationship of tree height over age (Plonski, 1981) are affected by the moisture and nutrients available on a site. The lower the site class the drier or poorer the site which makes it more suitable for lichen. Since no caribou were found in site class X or 1 they were assigned the lowest values: X and 1= 0.1. Since 2 of the 9 study areas were site class 2 they were assigned a medium value 2= 0.5. The remaining site classes, 3 and 4, made up 78% of the study areas and were given the highest values 3=14=1.0 (Fig. 2d)

Tests of FRI Data and Landsat Imagery

Use of the HSI model with FRI data predicted 38 of the 50 known caribou winter areas. In a total area of

516 000 ha for which Landsat imagery was available, 107 000 ha (21%) was water, 346 000 ha forested land. In the latter, 22% was classified as theme 3, which predicted 37 of the 50 locations correctly. However, these were not all the same locations as predicted with FRI. When both approaches were combined, the known caribou-use stands were predicted 50 times out of 50.

Discussion

Answers to our questions were obtained from our results. Caribou chose mainly V30 type forests for winter habitat (a finding that supports Morash & Racey, 1990), and our FRI data confirmed this conclusion. Horizontal distribution analysis showed low basal areas and volumes, modest densities, and relatively short heights (95% are 12 m or less), all characteristics that tend to make the stands of little interest economically. Maximum recovery of wood products would be no more than 2-3 m-sawlogs per tree from the tallest trees in the stands. Even so, the quality would be low. Poorly stocked stands produce trees that are heavily limbed with tapering trunks (Stoddard, 1978), factors that reduce their value as sawlogs. Near Armstrong, the forest might be economical to harvest because of existing road access and the flat sandy country which allows for low harvest costs. But even here low wood volumes might make individual stands unmerchantable.

The distribution of trees across a number of height classes suggested that these uneven aged stands (overstory of shade intolerant jack pine, understory of black spruce), once cut, might be difficult to replace. To insure the return of a similar forest, the slash would have to be spread across the site to distribute the serotinous and semi-serotinous cones so that heat near the ground would open them (Burns, 1983). This action would simulate regeneration after fire better than planting and would leave lichen on site. Sims *et al.* (1990) suggest a rotation age of 70 to 80 years on low growth jack pine and black spruce stands, but this would entail harvesting during the peak period of caribou benefits. For caribou, the rotation age should be extended to over 100 years.

The HSI model might have a number of uses. It could be combined with a GIS digitized FRI map to locate potential woodland caribou wintering areas and to predict how changes in forest stand composition would affect woodland caribou winter habitat. The latter might be expanded to model changing forest conditions on computer GIS programs as the forest is "grown" and "harvested", permitting managers to see compare present inventory with predicted consequences management action. Since high HSI value stands indicate correspondingly low economic worth, concentrations of high HSI stands might suggest a candidate places for non-timber management objectives, such as park land or wildlife areas. However, this was a first attempt at such a model and the HSI values assigned to the variables may require modification for different areas. Other variables such as predation and snowfall could be added to further define the winter habitat of woodland caribou.

The value of the described stands to the caribou remains speculative, but we suggest some possibilities. The finding of significantly more lichen on plots used by caribou supports the suggestion that lichen presence may represent a benefit. Lichen growth is limited by the amount of sunlight that reaches the ground. Hale (1961) estimated that lichens contain between 10% and 25% the chlorophyll of regular plants, and thus require large amounts of sunlight for growth. Apparently the amount of sunlight in the study area stands was sufficient for fruticose lichens. The mean density of 1552 trees per ha allowed a 39% lichen ground cover; the maximum value obtained of 3106 trees per ha still showed 31% lichen cover. Yet Moore and Vesrspoor (1973) found that tree densities between 3080 and 4840 per ha constituted a transition range between lichen and moss as ground cover, and suggested that a mid-point of 3960 per ha might be the limiting density for lichen growth. Furthermore, Rencz & Auclair (1978) in northern Quebec found that a mean black spruce density of 556 trees per ha resulted in a 97% ground cover of lichen. Thus, the densities of trees in our study areas may be near the maximum that lichen can tolerate.

Few lichens were recorded 12 years after logging but some lichen was present after 30 years and heavy lichen regeneration was present on sites selectively cut 50 years ago. Although the sample is small results agree with Carrol & Bliss (1982) in northern Saskatchewan who found successful lichen regeneration 45 years after fires. Rencz & Auclair (1978) in northern Quebec reported 47 years. In northwestern Ontario, Webb (pers. comm.) and Harris (1996) observed that lichen regeneration may be sooner after logging than by fire, because the lichen is already on the site and does not have to re-invade the site. Racey *et al.* (1996) found caribou using stands 40 years after logging, in the same area.

If these stands are near their maximum, why do caribou not move to more open areas? Perhaps there is a difference between lichens on the ground and lichens available to caribou. Conifer forest canopy reduces the hardness and thickness of snow cover (Schaefer & Pruit, 1991) when compared with open sites. Caribou move into these stands in the winter because of the more favourable snow conditions (Darby & Pruit, 1984). Therefore these low density conifer areas produce lichens which are easier to access for food in winter. The range of height distributions within our study locations may alter snow conditions during different times of winter and in different years, and such a range may provide optimal feeding throughout the winter and over a series of different winters. Choosing a specific canopy density may not provide the best winter habitat for all snow conditions. An overhead canopy which is open enough to allow lichen growth in the summer yet closed enough to reduce ground snow depths is may be the optimum.

Another possible benefit from these forest stands might relate to the observed lack of shrubs and good visibility. The 3 measured areas showed almost total lack of shrub understory to block ground vision, a condition that might have several benefits: the ground is not shaded allowing good lichen growth; caribou should be able to detect predators (wolves) more easily; and, caribou escape will not be hindered by understory. The lack of shrubs in these areas also suggested a reduction of amounts of browse available for moose. Allen *et al.* (1987), modeling moose habitat, calculated that a moose would require 3 kg of browse per day in concentrated patches to survive. Although browse volumes were not measured in this study, it seems doubtful that our study locations would grow such browse densities; these areas would probably not support many moose in the winter (Harry, 1957; Dodds, 1960; Telfer, 1974; Crete & Bedard, 1975; Miquelle & van Ballenberghe, 1989).

Implications for management

The low volumes of timber found in this study suggest that setting aside reserves for winter caribou habitat would not sacrifice as much wood product value as might at first appear. Cumming & Beange (1987) found that caribou wintering areas totaled 5-9% of whole forests. These stands on average supported only 68% of normal yield. Therefore, the loss in wood product value from reserving these stands might be in the neighbourhood of 3-6% of total volume. Loss of dollar values from these volumes should be further reduced since the timber values of stands being used as wintering areas by woodland caribou are not high. Seventy-eight percent of the stands studied were either site class 4 (protection forest, which is already set aside from harvesting) or site class 3 which is the most fragile and least productive of the merchantable stands. The stands are slow growing, low density, and on dry, fragile sites (sand and bedrock) that would be hard or impossible to regenerate to fully stocked stands. Considering the low product value, the cost of harvesting trees of low densities would make these stands economically marginal at best. Managing such stands for caribou management purposes might require that the areas being removed from production because optimizing regeneration and growth would not be in the best interests of caribou winter habitat production.

Managing forests for caribou may require optimizing lichen production while retaining a suitable canopy to reduce snow depths and hardness. At the same time, it appears that the stands should have an open canopy and understory to allow for predator detection and escape, and to reduce browse supplies that might attract alternate prey for wolves. Harvesting of natural stands should not occur during the peak lichen period between age 60 to 100 years. Yet later harvesting might be better than no harvesting. It may return the areas to winter habitat for caribou in a shorter time than natural fires, and may accelerate lichen regeneration, but further studies are needed to ascertain if adequate crown closure can be developed to coincide with peak lichen development. The wintering areas would require a range of canopies to provide adequate micro- winter habitat to allow for changing snow conditions.

Forest harvesting in known wintering areas should occur only in locations where caribou have alternate habitat away from the disturbance. Erikson (1975) recommends winter harvesting to reduce lichen disturbance and provide arboreal lichens for food, but these factors may be outweighed by the negative aspects of winter disturbance. In our view, harvesting should be carried out in late summer to reduce poaching and road kills, to eliminate plowed winter roads providing easy access for poachers and wolves, and to minimize impacts on other birds and mammals that might result from harvesting during the spring reproductive period (Telfer, pers. comm.).

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Progress towards the experimental reintroduction of woodland caribou to Minnesota and adjacent Ontario

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Abstract: Woodland caribou (*Rangifer tarandus caribou*) are native to Minnesota but started to decline in the mid 1800s and disappeared from the state by 1940. Their demise had been attributed to extensive timber harvest and ovethunting; but more recently mortality from the meningeal worm, *Parelaphostrongylus tenuis*, carried by white-tailed deer (*Odocoileus virginianus*), and increased predation by timber wolves (*Canis lupus*) and black bears (*Ursus americanus*) have been suggested as additional causes. We describe a current initiative to explore feasibility of restoring caribou to the boundary waters region of Minnesota and Ontario. Feasibility studies have been conducted under the guidance of the Notth Central Caribou Corporarion (NCCC), a non-governmental organization with representation from relevant state, federal, Native American, and Canadian agencies. Results indicate a) Within Minnesota the most suitable site for woodland caribou lies within the eastetn sector of the Boundaty Waters Canoe Area Wilderness (BWCAW), and this is contiguous with a similarly suirable sectot of Ontario's Quetico Provincial Park: Together these comprise the recommended 1300-km^2 Boundary Waters Caribou Region (BWCR); b) Vegetation in the BWCR has changed little since the 1920s when caribou were last present other than effects of fire suppression; c) Level of white-tailed deer, hence the meningeal worm, is so low in the BWCR that this factor is unlikely to impede survival of re-introduced caribou; d) While wolf numbers within the wider region are relatively high, their impacts may be minimized if caribou are released in small, widely scattered groups; in addition, an abundance of lakes with islands affords good summer-time predation security; e) Threat to calves from black bears, probably more numerous rhan in earlier times, appears lessened by the security of lakeshores and islands; and f) A simulation model, combining knowledge from elsewhere with the BWCR assessment, suggests that released animals have a 0.2 to 0.8 chance of increasing in numbers during the first 20 years post-release. Strategies for maximizing success are identified. NCCC has concluded that the only practical approach that temains for determining restoration feasibility is through experimental releases or caribou. While promise of eventual success appears only moderate, the NCCC feels that costs and uncertainties associated with the experiment are justified by the environmental benefits from a success. Even if the effort fails, valuable knowledge would acctue for conservation biologists in general. An action plan is outlined, and progress and problems in selling the caribou initiative are discussed.

Key words: woodland caribou, restoration, Minnesota, Quetico, survival assessment, agency support.

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Introduction:

Native woodland caribou of Minnesota began declining in the mid 19th Century and disappeared completely by the early 1940s (Fashingbauer, 1965). The species disappeared earlier from other regions of the northeastern states: northern New England, upper Michigan, Wisconsin, and Isle Royale, Michigan, in that sequence. In the west, a resident herd in the Selkirk Mountains of northeastern Washington and northern Idaho numbered >100 in the 1950s, but declined to about 25 by the 1980s, and these last animals were transient between the U.S. and British Columbia (U.S. Fish & Wildlife Service, 1994). Over the past 15 years, woodland caribou from British-Columbia have been released into both Idaho and Washington in a co-operative restoration effort among provincial, state, and federal agencies; but there has not been the anticipated increase in population size (U.S. Fish & Wildlife Service, 1996).

This report updates progress in a current effort to determine the feasibility of restoring woodland caribou to a small sector of northeastern Minnesota, and, by proximity, to a sector of adjacent Ontario. The driving justification is a commitment to restore biota that have been lost since European settlement.

Background

Disappearance of caribou from Minnesota

At the time of the first European exploration, woodland caribou were fairly common in northern Minnesota, being found as far south as Mille Lacs and Kanabek counties; however, by the late 1800s they had receded to a region near the Ontario border, from Lake Superior to Red Lake (Fashingbauer, 1965; Bergerud, 1978; 1988). Hunting of caribou was regulated by the state: with declining numbers in the 1880s, limits and seasons were sharply reduced, and by 1904 all hunting was prohibited. By the late 1920s no animals remained in northeastern Minnesota; and the last caribou, centered around Red Lake in the northwest, disappeared in the early 1940s (Fashingbauer, 1965). During the early 1980s, two caribou were seen for about a year around Hovland, Minnesota, some 50 km south of Ontario near Lake Superior (Fig. 1, inset) (Mech *et al*, 1982). At that time, the closest breeding population was 250-300 km north around Armstrong and Lake Nipigon, Ontario (Fig. 1, inset). The subsequent fate of the Hovland caribou is unknown.

Demise of Minnesota's caribou was at first attributed to overhunting (Trygg, 1966 *vide* Heinselman, 1996:164) and to habitat changes from logging, wildfires, and clearing for agriculture (Fashingbauer, 1965). More recently, strong evidence indicates that a parasite may have been a primary factor as well: the nematode, *Parelaphostrongylus tenuis* or the meningeal worm, is normal in white-tailed deer and transmitted through an intermediate gastropod, but is fatal to caribou (Anderson & Strelive, 1968). The decline of caribou coincided with a marked northward extension of whitetails during the past century (Bergerud, 1974). Also, the increase of deer in northern Minnesota apparently expanded the prey base for timber wolves, leading to a rise in their numbers. This in turn, according to Bergerud (1974), would have increased the threat to caribou, particularly to populations already stressed and declining. After 2 decades of legal protection, wolves are now relatively abundant in northern Minnesota, but it is doubtful they played a significant role in extirpation of caribou earlier in the century, because they were then bountied and subject to unregulated trapping and shooting. Another potential predator was the black bear, whose ability to impact caribou was not fully understood until somewhat recently (Ballard, 1993), as in Maine where, during the 1980s, animals released in a restoration project suffered significant losses from bears (McCollough & Connery, 1990). Whether bears contributed to the extirpation of caribou in Minnesota is unknown.

In summary, the loss of woodland caribou from Minnesota will never be explained with certainty. It is likely that human impacts upon populations and, in some regions, upon habitats was the key factor during the 19th Century, while the meningeal worm may well have been the leading cause behind continued loss and ultimate extirpation during the 20th Century.

Restoration assessment and the status of caribou elsewhere in the region

Currently several populations of woodland caribou exist within the Lake Superior region of Ontario: the Armstrong-Lake Nipigon herd, 225-250 km north of eastern Minnesota (Cumming & Beange, 1987), and several insular populations in Lake Superior, the closest to the BWCR being on the Slate Islands some 65 km north and 300 km east of Minnesota (Fig. 1, inset). Starting in 1982, Ontario undertook several releases on other islands in Lake Superior (Darby *et al.,* 1989; Gogan & Cochrane, 1994).

Feasibility of caribou restoration was assessed for two U.S. national parks in the region. For Isle Royale National Park in northwestern Lake Superior (Fig 1, inset), where caribou were last known in 1928, it was concluded in the early 1990s that, although white-tailed deer were absent, wolves were too numerous and security habitat inadequate for caribou to succeed there (Cochrane, 1996). For Voyageurs National Park near International Falls, Minnesota, some 90 km east of the BWCR, it was concluded that abundance of white-tailed deer, hence the threat of meningeal worms, was probably too great for caribou to survive (Gogan & Cochrane, 1994).

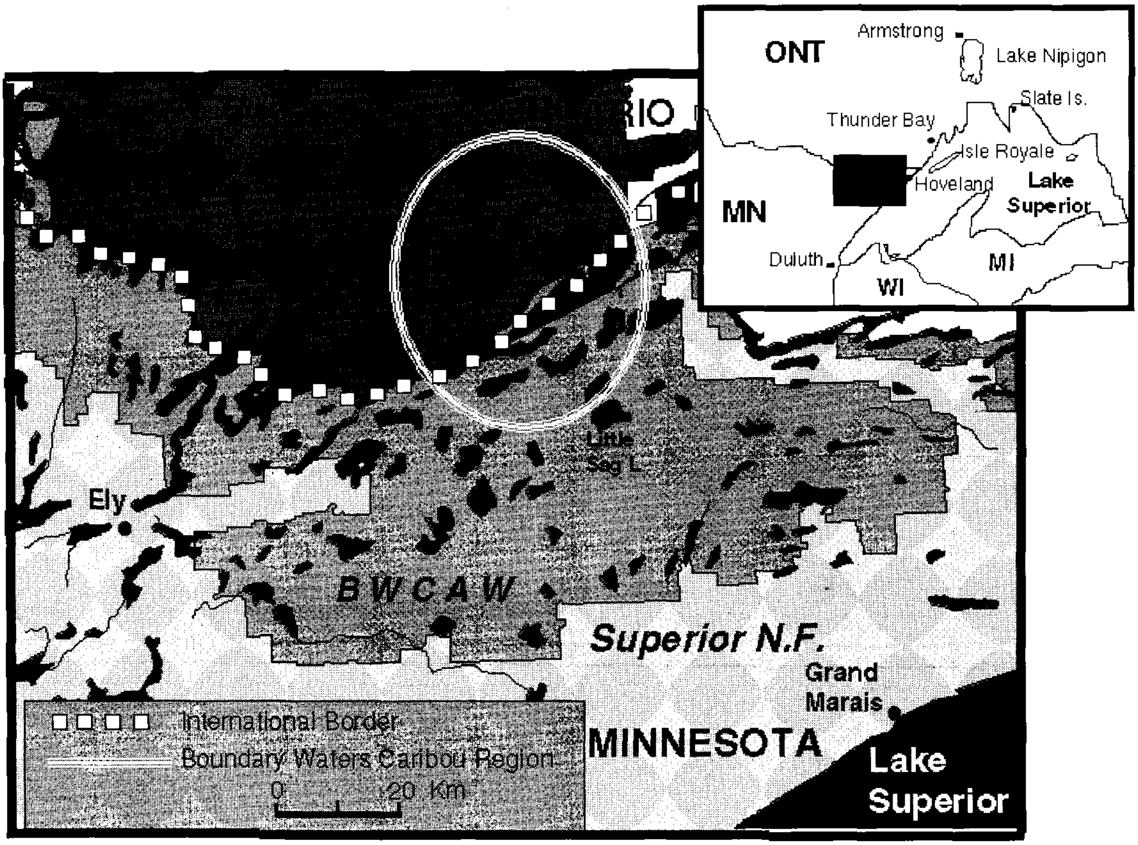

Fig. 1. The Boundary Waters Caribou Region (BWCR), lying across the Minnesota-Ontario border, rhe southern sector being wirhin the Boundary Waters Canoe Area Wilderness (BWCAW) of the Supetior National Forest and the northetn sector within Quetico Provincial Park. The 1300-km^2 BWCR represents the estimated contiguous zone of favorable habitat for caribou.

An earlier study for restoring Minnesota's caribou

During the 1970s, a comprehensive assessment of caribou-restoration feasibility was carried out by the Minnesota Department of Natural Resources (DNR) in consultation with several North American caribou experts (Karns, 1980; Karns & Lindquist, 1986; Gogan *et al.,* 1990). From a survey of four regions of northern Minnesota that apparently possessed suitable vegetation and topography, only one, located in the northeastern corner of the state, appeared to have all the required habitat components for caribou. The restoration initiative did not, however, progress further. At that time it was believed that if wild-caught animals were released, they would disperse far from the intended region; consequently it was assumed that animals for release must be captive-reared yearlings. Funding was not available for establishing a nursery herd, so the attempt was terminated. Subsequently, it has been shown elsewhere that released, wild-caught adults will remain localized, as in the Maine restoration attempt (McCollough & Connery, 1990).

Progress in the current caribou-restoration initiative

The North Central Caribou Corporation

In 1988, a group of Minnesota citizens formed the North Central Caribou Corporation for exploring a new effort to restore caribou to the state. The Corporation's board of directors included representation from relevant state, federal, Native-American, and Canadian agencies plus one citizens' organization. While the earlier caribou-restoration assessment (Karns & Lindquist, 1986) served as an important guide, the NCCC carried out its own feasibility analysis. The work was funded mainly by the Duluth Safari Club (independent of Safari

International), which had disbanded in order to form the Caribou Corporation. Research was done collaboratively among the U.S. Forest Service, the Natural Resources Research Institute, and the University of Minnesota. These analyses with resultant conclusions and recommendations were compiled as a report by the North Central Caribou Corporation (Raven, 1993) and are summarized below.

The Boundary Waters Caribou Region

The site recommended by the NCCC for caribou restoration (Raven, 1993) covers some 1300 km^2 (500 mi^2) and is referred to as the Boundary Waters Caribou Region or BWCR (Fig. 1). It extends across the international border, from within the Boundary Waters Canoe Area Wilderness (BWCAW) of the Superior National Forest in Cook and Lake counties, Minnesota, to the southeastern portion of Quetico Provincial Park in Ontario. The BWCR coincides with the area in Minnesota that was recommended for caribou restoration in the earlier assessment (Karns, 1980), but it defines more clearly the extent of suitable habitat within the Ontario portion.

Both the BWCAW (Heinselman, 1966; Lewis *et al.,* 1996) and Quetico Park (Anderson & Lime, 1984) are managed as wilderness, a status unlikely to change in the foreseeable future. Human presence within the BWCR is currently restricted to canoeists, skiers, and hikers (Anderson & Lime, 1984). Logging was never intensive within the BWCR, and has been completely banned for some decades.

The Caribou Region is vegetated primarily with upland and lowland boreal forest, but includes some mid-successional upland aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Forest structure, while not strongly affected by past logging, has been altered through prevention of natural fires on both sides of the border (Woods & Day, 1976, 1977; Day, 1990; Heinselman, 1996). Within the BWCAW, the Superior National Forest is now committed to restoring the natural pattern of fire (U.S. Forest Service, 1997), but that will probably be somewhat constrained due to concern for adjacent commercial timber.

Suitability of vegetation and landform

Landform and vegetation in Minnesota's northeastern border region were analyzed for presence and juxtaposition of factors critical to woodland caribou as defined by Bergerud (1978) and Bergerud & Mercer (1989). Broschart & Pastor (1992), working with satellite imagery, created a geographic information system (GIS) data base centered on the designated BWCR but including several thousand km^2 of adjacent area as well. They analyzed for spatial associations among mature conifers, lowland bogs, and lakes with islands. They concluded that the BWCR not only offered a favorable landscape for caribou, but that it met these criteria better than any other area of comparable size within the region. In particular, the widespread presence of lakes with small islands offered an abundance of potential summer-season protection from both wolves and bears. Bergerud *et al.* (1990) state that such habitat is critical for the security of young calves, as was found by Cumming & Beange (1987) around Lake Nipigon, Ontario. Also, the landscape-suitability analysis of Broschart and Pastor agrees with the conclusions of caribou biologists A.T. Bergerud and V.F.J. Crichton concerning the best region within the state for caribou (Karns & Lindquist, 1986).

Deer and the meningeal worm

To estimate the threat of the meningeal worm to caribou, Pitt & Jordan (1995) made wide-ranging, semi-systematic surveys for deer and meningeal-worm larvae within and adjacent to the BWCR. For deer presence, all current sign was recorded, but primary emphasis was on locating fresh fecal dropping (pellets), since they related to both deer densty and source of the parasite. During summers of 1989 and 1990, > 250 km^2 of the BWCR within Minnesota were covered, plus a sampling of adjacent regions. LandSteward and Timmermann (1991) made a shorter but similar survey within the Quetico portion of the BWCR in 1990. All evidence from both sectors suggests that summer deer-density within the BWCR was < 0.5/km^2. Frequency of encountering current-season pellets outside the BWCR where deer density was reportedly around 5/km^2 was about 1 group/hr, while in the BWCR it was roughly 0.1 group/hr. Furthermore, during the snow season, deer were apparently absent from the Minnesota portion of the BWCR according to Nelson & Mech (1992) who made repeated aerial surveys for wolves there. Their report to the NCCC was restricted to winters 1989-90 and 1990-91, but absence of deer in winter there is believed to hold over the longer term.

For estimating levels of meningeal-worm larvae, deer pellets and gastropods were collected throughout the Minnesota portion of the BWCR; from several sites in which at least some ofı the BWCR winter; and from scattered intermediate locales having higher summer deer densities than the BWCR (Pitt & Jordan, 1995). Larvae were found in 27% of 15 recent pellet-groups from the BWCR and in 57% of a larger sample of pellets from the wintering areas. In samples of terrestrial gastropods comprising several snail and slug species, none from the BWCR (n=56) showed of larvae, while 0,8 % of those from elsewhere within the region (n=744) did show larvae.

It was concluded that the low density of deer found within the BWCR, together with the negligible presence of meningeal-worm larvae, indicated that mortality from this parasite would not be great enough to prevent a caribou population from growing within the BWCR, but such would probably not be possible elsewhere in the region. Furthermore, there is an unknown but realistic possibility that habitats used by deer in summer differ sufficiently from those of caribou, so that caribou exposure to meningeal-worm larvae would be even lower than projected from the survey data, e.g., if caribou cows with calves are mainly on islands, while deer do not use these islands. Finally, all caribou being introduced, plus animals subsequently captured for marking or re-marking, could likely be protected temporarily from the meningeal worm with the anti-helminth drug, ivermectin, in a form designed for slow release (see "Capture and Release," below).

Wolf predation

As part of intensive, long-term studies of wolf dynamics in northeastern Minnesota (Mech, 1986; Mech & Goyal, 1995), Nelson and Mech (1992) reported that in the early 1990s wolf density within the Caribou Region was around 16-20/1000 km^2. While woodland caribou elsewhere have been judged unable to expand their numbers under this level of wolves (Bergerud,1980; Bergerud & Elliot, 1986), in those cases there was not an abundance of lakes with islands providing critical security from predation during summer. During winter, according to A.T. Bergerud (pers. comm.), as long as numbers of caribou in a given locale remain relatively low, e.g. in groups of < 10-20, then wolves are not likely to concentrate on this prey. It is also important that other prey are not locally abundant to attract wolves. In Pukaskwa National Park, Ontario, wolves in winter are apparently localized near moose that are wintering some distance inland from Lake Superior; while a small number of caribou reside along that lakeshore, relatively free of wolf predation (G. Eason, pers. comm.). Absence of deer in the BWCR, plus a relatively low density of moose, may well serve the same function, with wolves being focused mainly on the wintering grounds of deer that lie no closer than 20 km from the BWCR. However, as pointed out below, there remain no reliable means for determining the potential of wolves to severely reduce introduced caribou other than with experimental releases. Before European settlement, caribou had obviously co-existed with wolves, as well as with Native Americans hunters, throughout this region.

Bears and island security

Black bears are a potential threat to caribou, particularly where they have easy access to calves (Ballard, 1993). Security from bears would presumably be along lakeshores and on islands when calves are in their early months. However, in the BWCAW and Quetico the many campsites for canoeists are located on islands and lakeshores. Bears regularly visit these campsites, having presumably been conditioned to the availability of campers' food. While the effect of camp-food on bear populations in the BWCR region has not been studied, in nearby non-wilderness areas. Rogers (1987) showed that the bear sows feeding regularly at garbage dumps were significantly more productive than others. Otherwise, lake islands of the region should not have food sources that would particularly attract bears. Almost none have been recently burned or cut-over, hence would not likely have abundant berries, and none have oaks or other good sources of mast.

Pitt & Jordan (1996) documented frequency of black bears using islands and lakeshores, based on visits to stations baited with bacon. They found that bears commonly swim to islands, but only to those with permanent camp sites. Likewise the only stretches of shoreline regularly visited by bears were those with campsites. Regulations in both the BWCA and Quetico restrict canoeists to a limited number of designated camp sites, and bears seem habituated to these. Since the survey indicated that bears did not visit islands or segments of shore lacking campsites, such areas should be relatively safe for caribou calves in summer. And it is assumed that caribou would avoid the proximity of campers.

Furthermore, if and when a bear does encounter a cow and calf along a shoreline, the latter have quick access to the lake for refuge.

Future hunting

Since objectives of the NCCC's caribou restoration do not include harvest of caribou, this source of mortality was not considered in the feasibility analysis. That some caribou in the BWCR might be illegally killed is unlikely due to the area's relative inaccessibility. If some animals do disperse into adjacent, non-wilderness regions, they might be subject to poaching. However, such animals should be more vulnerable to the meningeal worm than to being shot because of the high deer levels outside the BWCR.

Simulations of post-release population dynamics

To estimate probabilities of survival and increase in caribou after release, a dynamic population model was generated based on mortality factors from our feasibility studies plus studies elsewhere. Precise predictions cannot be expected from such models, but they are valuable for identifying whatever mortality factor(s) may prove most critical. They also serve to identify priorities in ecological research critical to management planning (Starfield & Bleloch, 1991; North & Jeffers, 1991).

Our model was structured to estimate, under varying scenarios, the probability that within 20 years after release, caribou numbers will have increased (Raven 1993; 1994). Several scenarios were used for starting the simulations. Number of releases and numbers of animals per release plus age and sex ratios were set at different levels. Presence of wolves and of bears, plus availability of suitable islands, were also varied. Probabilities of population growth projected by the model indicate that with both bears and wolves present, population success was closely tied to how consistently calving cows moved to islands or suitable shorelines, and whether wolves would swim out to islands, a behavior not well understood. Multiple releases increased the estimated probability of achieving a self-sustaining population. Overall, the modeling suggests that caribou released into the BWCR have a 0.2 to 0.8 probability of surviving and increasing in numbers over ther first 20 years. As a postscript, the inputs here do not reflect information subsequently discovered concerning a caribou release in Grands Jardins, Quebec (formerly called Laurentides Park), where caribou restoration succeeded in the presence of both wolves and bears, but with deer being absent (Cantin, 1991).

The modeling for this analysis addressed the potential for population growth rather than a quantification of total numbers that might be supported within the BWCR. Estimating the total potential of the BWCR to support caribou would require knowledge of an average carrying capacity for the region, plus the total expanse of suitable landscape, i.e. just how accurate the estimate of 1300 km^2 actually is. Consequently, the model's estimates of an increase within the first 20 years were based simply on natality minus mortality, without regard to total habitat capacity. For example, if 75 animals were introduced, and the area's total capacity was only 75, the model's predictions on growth would not be applicable. However, the model's output can still be used as an indication of long-term viability within whatever expanse of habitat there may be.

Summary and conclusions from the feasibility studies

Despite serious uncertainties about success in restoring caribou to the Boundary Waters Caribou Region, the majority of NCCC Board of Directors agreed in 1996 that it was still fully reasonable and worthwhile to undertake experimental releases. Their conclusion reflected the following considerations: a) After the comprehensive feasibility studies, the only practical means left for better estimating whether this restoration will succeed is through experimental releases and follow-up monitoring; b) Considering the high environmental benefits from a successful restoration, the estimated level of risk is judged fully acceptable; and c) Regardless of outcome, such experimentation would provide important scientific information for restoration efforts in general; and, should released animals fail to sustain themselves, habitat deficiencies– apparently not present 70 years ago– could be identified.

Proposed experimental restoration

In 1996 the NCCC prepared a draft strategy for experimental release of caribou under a set of broad guidelines:

a) Stock for release should come from one or more free-living caribou population whose habitat is closely similar to the BWCR, and preferably that has been exposed to some predation;
b) Multiple releases should be made over 3 years, involving up to 20 mature cows and 5 mature bulls each year; and

c) Within and among years, releases should be spaced widely, with no more than 4-6 animals released at any one locale.

Source of animals for release

The most reasonable source of woodland caribou for a Minnesota release is from the Slate Islands, Ontario, an isolated archipelago in northern Lake Superior (Fig. 1, inset). Either the NCCC would formally request a donation of Slate-Islands caribou from the Ontario government, or, more likely, such a request would be made by an agency of the United States government. NCCC Board member, H.R. Timmermann (pers. comm., 1996), a former Ontario Natural Resources biologist, believes this would be acceptable because the Slate-Islands population has long been judged too numerous for its forage resources (Euler *et al.*, 1976).

In winter 1994-95, 2-3 wolves dispersed to the Slate Islands where wolves had not previously been known (Euler *et al.*, 1976). For 1 or 2 years these wolves reportedly preyed heavily on caribou, particularly calves. However, after winter 1995-96, none were seen there (Bill Dalton, pers comm.). Thus, being exposed to wolf predation should have improved the adaptability of Slate-Islands caribou for the BWCR environment, but then the subsequent disappearance of wolves should lead to the previous circumstance of over-abundance, hence the reasonableness of this herd being a source of stock.

Because caribou on the Slate Islands have most likely been genetically isolated, at least since 1907 (Euler *et al.*, 1976), the population may now be inbred. To insure satisfactory genetic diversity in the BWCR, caribou stock from elsewhere should be added. Possible mainland sources for this include the Lake Nipigon-Armstrong herd, Ontario, or, less likely, the Sasaginnigak Lake population in southeastern Manitoba, since that herd was recently given endangered status (V.F.J. Crichton, Manitoba Ministry of Natural Resources, pers. comm.).

In making the request to Ontario for a donation of animals, it would be argued that restoration of caribou immediately south of Quetico Provincial Park should serve to create a new population within Ontario as well, since some animals would undoubtedly disperse across the border. This is also in line with the current provincial commitment to protect caribou in northwestern Ontario (Racey & Armstrong, 1996), as reflected the policy statement: "..this can be achieved by supplementing small existing populations and establishing new ones in areas of former range, where they could be self-sustaining, through relocation of animals." (Darby *et al*, 1989).

Capture and release

Caribou could be captured on the Slate Islands in box traps or by netting of swimming animals from a boat (Timmermann, 1985). Captured animals would be tranquilized and, as soon as practical, transported by float plane directly to the release sites. For capture of adults on the mainland, procedures would be under advisement of Ontario or Manitoba biologists, who have recently had good success with helicopter-netguns (Carpenter & Innes, 1995).

For importing animals from Canada, a prolonged quarantine might be required by the U.S. Department of Agriculture. However, a waiver would be requested on the basis that caribou in northwestern Ontario or southeastern Manitoba were unquestionably contiguous with those present in Minnesota just 60 years ago, or those that apparently dispersed from Ontario into northeastern Minnesota just 20 years ago (Mech *et al.*, 1982). It is similar to the caribou-restoration project in Washington state where animals were imported from British Columbia without a quarantine-holding requirement (U.S. Fish & Wildlife Service, 1996). Apparently a similar agreement was reached by the U.S. Fish and Wildlife Service for the recent "hard release" of wolves from western Canada into Idaho. Furthermore, when moose from Ontario were used for restoration into Upper Michigan in 1985, each animal was treated with antibiotics against bacterial infection and ivermectin against nematodes and ticks (Schmitt & Aho, 1988). Blood was sampled to test for a wide variety pathogens considered threatening to livestock. Thus, after release, any animal found positive for a threatening pathogen could be relocated and destroyed, since all were radio-collared – as would be the case for all releases in this project.

Transporting of caribou to release sites within the roadless BWCAW would be practical only by float plane. Because landing planes is currently prohibited in the BWCAW, a waiver would be needed from the U.S. Forest Service. Should a waiver for float-plane landing (or quarantine-holding) be denied, then release just across the border in Canada would be considered. In an ecological sense, this would be little different from a release in Minnesota. However, were all releases made in Canada, the ability to attract needed public and financial support could be considerably reduced in Minnesota and elsewhere in the U.S.

To provide some relatively short-term protection from the meningeal worm, all animals released or recaptured would be treated with the anti-helminth drug, ivermectin, in the form of a slow-release implant that should be effective for over a year. While such technology had not been investigated at the time of this report, a consultant veterinarian (T. Kreeger, pers. comm.) indicated that it should be feasible.

Monitoring and research

For comprehensive monitoring, all experimentally released caribou would be equipped with highly dependable radio transmitters. These would be equipped with a mortality-mode function that permits rapid location of newly dead animals to determine cause of death. Such monitoring should continue at for least a decade after the last releases to document not only survival and mortality of released animals, but also their reproductive success andtheir seasonal use of the landscape.

Monitoring radio-marked large mammals in remote regions has in the past involved periodic relocation by searching for transmitter signals from a small aircraft, with maximum range of reception generally < 25 km. Disadvantages of this method include cost of frequent flights, interruptions by bad weather, and general inability to account for individuals that disperse far from the study region. Advantages are relatively lower cost of equipment, good precision in locations, and opportunities for direct observation. A newer system involves signals from transmitters being received by satellites and then forwarded as ground-location points to the investigator. Locational precision with this system is only within a few km, but it has the advantage of giving readings at a prescribed interval so, regardless of flying weather, mortality information is regularly available. Also, regardless of how far some animals may move, they can always be located. Although equipment and satellite charges make telemetry costs higher, this is partly offset by greatly reduced flying costs. A more recent and quite expensive system is based on Geographic Positioning System (GPS) technology: the animal's radio automatically accumulates information that is received from satellites and then is converted into precise location coordinates. The animal is periodically located by direct telemetry, usually from a small plane, and, upon radio-interrogation, the collar transmits the stored location data (Moen *et al.*, 1997). This system provides the most precise location data; however, of greater importance in a restoration experiment is having rapid access to mortality information and knowledge of animals moving far from the study region, as with the satellite system.

To monitor reproduction, each marked cow would be located for direct observation during late spring and again in late summer to determine birth and subsequent early survival of a calf. This would initially be from the air for a general locale, followed by radio-tracking on the ground or from canoes in the known vicinity of each radioed cow.

For evaluating the population over a sufficient time span, a sample of offspring should be radio-collared during the decade of continued monitoring. Under BWCAW and Quetico regulations, such capture would be most practical from canoes. From mid-spring into summer, locations of known radioed cows with calves would be identified; then such animals, presumably on islands or along lake shores, would be radio-located by a canoe party. If telemetry location from the water proved difficult, the search could be aided by communication with airborn telemetry operators. The animal pair would be pursued on foot into the water, where the calf would be hand-captured from a canoe, as done elsewhere from motor boats (Timmermann, 1985), and towed to shore for processing; immobilization should not be necessary.

Developing agency and public support for caribou restoration

Legal status of caribou

For Minnesota, the woodland caribou is surely a species in jeopardy, having completely disappeared some 55 years ago. However, since there were no animals extant in 1973 when the U.S. Endangered Species Act took effect, this species is not under mandate to be listed. In contrast, caribou in Washington and Idaho are "endangered," since a few animals were still present in the 1970s. In Minnesota, any animals released for restoration would be classified as "experimental" under provisions of the Endangered Species Act; this circumvents responding to federal regulations requiring special protection or habitat enhancement on public lands. For a restoration, the inconsistency of not listing locally extirpated species has mixed implications. Caribou have no federal status in Minnesota, so it would be less complicated for both state and federal agencies, since they would not be faced with constraints and expenditures associated with a listed species. On the other hand, there is no legal mandate for agencies to work towards restoration of a non-listed species.

Partnerships and support

Today the primary effort towards caribou restoration in the BWCR has moved from research on ecological feasibility to building of partnerships for governmental agreements and public support. First, among key agencies, the Minnesota DNR and the Superior National Forest must consent to restoring caribou to the BWCR. Then the Province of Ontario would hopefully agree to contribute the caribou stock. Concomitant permits from federal agencies are needed for importation of wild animals. In parallel, a major program will be undertaken to inform the public and to seek political and funding support from a diversity of sources. High among such groups are Native Americans of the region, who are considered partners in the caribou restoration, since this animal was an important component of their environment prior to European settlement.

Detailed planning for the restoration and monitoring would be directed by a full-time coordinator. State and federal funding would be sought, particularly since caribou restoration would conform with responsibilities under current policies for protection and restoration of natural biodiversity and endangered species on public lands. At the same time, due to uncertainty about state or federal funding, the NCCC will vigorously seek financial support and volunteer help from the private sector.

Issues of possible concern by government or private interests

While a formal announcement, along with detailed public information about the proposed restoration, has not been released by the NCCC, some reports have appeared in the media, and relevant agencies have been kept abreast through participation on the NCCC board. The points that follow are not in response to any formal statements from government or private sources, but they do address questions that have been informally raised or may be as planning proceeds:

a) Timber harvest: Unofficial comments from leaders within the Minnesota timber industry suggest there is fear that habitat protection for restored caribou may entail restrictions on timber harvest, particularly within the Superior National Fotest. Unlike potential conflict between the forest industry and caribou management in northwestern Ontario (Racey & Armstrong, 1996), this fear has no basis. Allthough release sites would be within the Superior National Forest, all these sites plus the region in which caribou could survive are managed entirely as wilderness – on both sides of the border: thus there could be no logging or opportunity for logging within the BWCR. Furthermore, the NCCC surveys clearly indicate that, were caribou to disperse from the BWCR into areas of managed forests in either Minnesota or Ontario, their survival would be in jeopardy from the meningeal worm (Pitt & Jordan, 1995) rather than from any possible timber practice. Consequently it is not possible to foresee any alteration of timber-harvest regulations regardless of where released caribou may wander.
b) Tourism Industry: Many resort owners and outfitters in northern Minnesota are aligned with groups opposed to almost any government regulations of natural resources or wildland uses. In the case of caribou within the BWCR, however, a successful restoration should have nothing but positive effects upon tourism. There would be no restrictions whatsoever upon tourism's current operations, while restoration of a native large mammal should markedly increase the attractiveness of these areas to canoeists. Hence, if anything, tourism-related businesses should be improved by successful establishment of caribou in the boundary waters country.
c) Sport Hunting: Concern that presence of caribou might restrict legal hunting within the BWCR is without basis. First, current hunting in that portion of the BWCAW is extremely low, since access requires at least 1 day of canoeing and portaging. Second, since the legal, large game, deer and moose, are relatively sparse, the area offers little attraction to most hunters, even those willing to deal with the wilderness challenge. And, third, those few hunters who do venture far into such wilderness tend to be environmentally knowledgeable, hence would be sensitive to possible disturbance of caribou, perhaps even more than many non-hunter canoeists in summer. Furthermore, any reduction of either deer or moose by hunting within the greater region would be in the best

interests of caribou, as it would reduce both the meningeal worm and the quantity of prey for wolves. Finally, there are good indications that Minnesota hunting groups will support the return of caribou, not as a future game animal, but simply to restore a native large mammal.

d) The Minnesota Department of Natural Resources: The DNR administers statewide programs for non-game, natural heritage, scientific and natural areas, and endangered species. Minnesota ranks high among U.S. states in the scope and effectiveness of conservation programs. At the same time, the DNR has indicated significant reservations about caribou restoration. This hesitancy may reflect one or more of the following:

i) Some DNR biologists feel that chances of restoration are poor, and a failed attempt, even if identified as a necessary experiment, would reflect badly upon that department despite the current initiative being of private origin. Citizens can and do mistakenly associate the caribou initiative as originating with the DNR rather than the NCCC.

ii) In 1979 a caribou restoration initiative by the DNR was based on the assumption that rearing a nursery herd was necessary (see "..recent restoration study.." above), and funding for this could not be raised. The DNR then removed caribou restoration from its agenda, perhaps reflecting frustration over having nothing to show for a considerable investment.

iii) A small herd of introduced elk or wapiti (*Cervus elaphus*), originating 100 years ago with a transplant from Yellowstone National Park into Itasca State Park in northwestern Minnesota, subsequently moved into farmland. These animals have caused minor but conspicuous damages that have led to annoying political problems for the DNR. Such experience leaves the DNR less than enthusiastic for experimenting with another ungulate restoration, even though caribou are never likely to disperse into farm areas.

iv) With funding problems typical of most state agencies, the DNR assumes that long-term management of a possible caribou population would become their responsibility, regardless of the future role of the NCCC. However, a restored caribou population should require minimal management expenditure. The species would not be listed as endangered (see "Developing agency and public.." above), hence no habitat attention would be required. In addition, even if desired, no habitat manipulations could be done because caribou would be within designated wilderness areas. Also, as discussed above, there would be no hunting to administer. Administrative costs should be confined to reporting whether the population is persisting or not. Data for this might well come from a systematic index generated voluntarily by a non-governmental organization that solicited and summarized canoeists' sightings of caribou.

On the other hand, the Minnesota DNR has contributed extensively to restoration of the peregrine falcon (*Falco peregrinus*) and the trumpeter swan (*Cygnus buccinator*); it has an active program of returning river otters (*Lutra canadensis*) to regions from which extirpated; and in 1993 the agency seriously considered releasing wolverines (*Gulo gulo*), another species long absent from the state. In a report of the Minnesota Endangered Species Technical Advisory Committee (Coffin & Pfannmuller, 1988), woodland caribou are listed as of "special concern," but it is stated that, "The difficulties inherent in maintaining a permanent population of caribou in Minnesota must be addressed before any serious consideration is given to reintroduction.." The NCCC believes it has now addressed these concerns.

e) The Superior National Forest: In general, U.S. Forest Service guidelines call for restoration of natural biodiversity and a natural-resource management approach based on ecosystem principles. In the most recent plan for the Superior National Forest (U.S. Forest Service, 1986), woodland caribou are listed as a species of "concern;" also in the plan is the statement, "Reintroduction of native species is desirable and acceptable."

However, administrators of this Forest have been relatively neutral towards bringing caribou back. They may be concerned that establishment of caribou in the BWCAW might lead to recommendations for reducing campgrounds or visitor numbers. Summer usage is already so great that reservations for entry are required. The plan prepared by NCCC does not recommend any change in visitor policy.

On the other hand, successful restoration of caribou within the Superior National Forest would attract national attention to that forest's environmental accomplishments. It would also add a new dimension to the experience of visitors in the BWCAW. In Idaho and Washington, close cooperation by the U.S. Forest Service in interagency programs for caribou restoration has contributed positively to the image of that agency.

d) Native Americans: Several bands of Native Americans reside in northeastern Minnesota. In recent years, native peoples have developed a renewed interest in the fauna present before Europeans so thoroughly altered their home region. While NCCC has a representative from one band on its board, detailed discussions with regional tribes need to be expanded. It is the intention of NCCC to actively involve Native Americans in the process of restoring an important animal that was once part their wildlife heritage.

Summary and conclusions

A thorough feasibility analysis for restoration of woodland caribou to the Boundary Waters Caribou Region of Minnesota and Ontario has been carried out. The North Central Caribou Corporation believes that an experimental release of woodland caribou in Minnesota is justified based on two general criteria: a) Its comprehensive assessment indicates a reasonable chance for successful restoration; and b) The valuable environmental benefits from successful restoration of caribou to the Boundary Waters region clearly outweigh the uncertainties surrounding this proposal.

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Using caribou knowledge in expanding the Wabakimi protected area

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Abstract: When Wabakimi Wilderness Park was created in 1983, conservation of woodland caribou (*Rangifer tarandus caribou*) was one of the primary considerations. Twelve years later, in April 1995, the Governmenr of Onrario announced that the Patk, measuring some 155 000 ha, was to be expanded into a ca. 890 000 ha prorected area. This was done following 2.5 yr of deliberations of the Wabakimi Park Boundary Committee. The Committee tried to reach consensus on an expanded protected area by examining a variety of options in terms of criteria related to a range of key values, one of which was woodland caribou. The analysis procedure involved dividing the 1.25-million-ha study area into more than sixty "assessment units". These were defined primarily on the basis of approximate sub-watershed boundaries. Each assessment unit was tanked on a five-level scale with respect to goodness for each value, including seasonal caribou habitat. High-value habitats fot wintering, calving, and migration dominated the assessment of habitat importance fot caribou.The initial assessment phase included six park expansion concepts ranging in size from just over 200 000 ha to about 1 million ha. One of the concepts (about 750 000 ha), was based specifically on the catibou value. In the second phase, four refined options wete examined, ranging from just under 600 000 to roughly a million ha. Two additional options were added to rhe four and submitted to the Ontario Ministry of Natural Resources for consideration. The Committee was, in the end, unable to reach full consensus on which of the final options to recommend. However, upon consideration of the Committee's final report and other input, the Ontario Government announced in April 1995 the more than five-fold expansion. The new prorecred area contains about 475 000 ha of high-value caribou habitat. Caribou were a key value in determining both the ultimate size and configuration of the expansion.

Key words: *Rangifer tarandus caribou*, parks, boreal forest, Canada, caribou habitat.

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Introduction

Natural resources decision-making works best when it is comprised of a productive blend of rational analysis and bounded politics (Lee, 1993). Analysis for decision-making normally consists of a protocol including: (a) identification of criteria and indicators by which potential solutions are to be judged; (b) creation of alternative potential solutions; (c) prediction of the state of each indicator under implementation of each alternative solution; and (d) evaluation of alternative solutions in terms of the predictions (Duinker & Baskerville, 1986). Selection and implementation of a preferred alternative solution then follow.

In 1992, the Ontario Ministry of Natural Resources (OMNR) established a public advisory committee - the Wabakimi Park Boundary Committee (WPBC) - to review the boundary of Wabakimi Provincial Park, located a few hundred kilometres north of Thunder Bay, and recommend improvements to that boundary. The Committee engaged in a 2.5-yr process that included both technical analysis and consensus building. In the technical analysis, eleven values (criteria) were chosen for evaluation of boundary-expansion alternatives. Among the eleven values was habitat for woodland caribou - *Rangifer tarandus caribou.* Early in the process, the WPBC members agreed that it was one of the highest priority values to consider, not only in its own right but also because it was felt to be closely linked with other biotic values.

This paper relates how caribou were treated by the WPBC in arriving at its conclusions about what expansions to recommend. After presenting back-

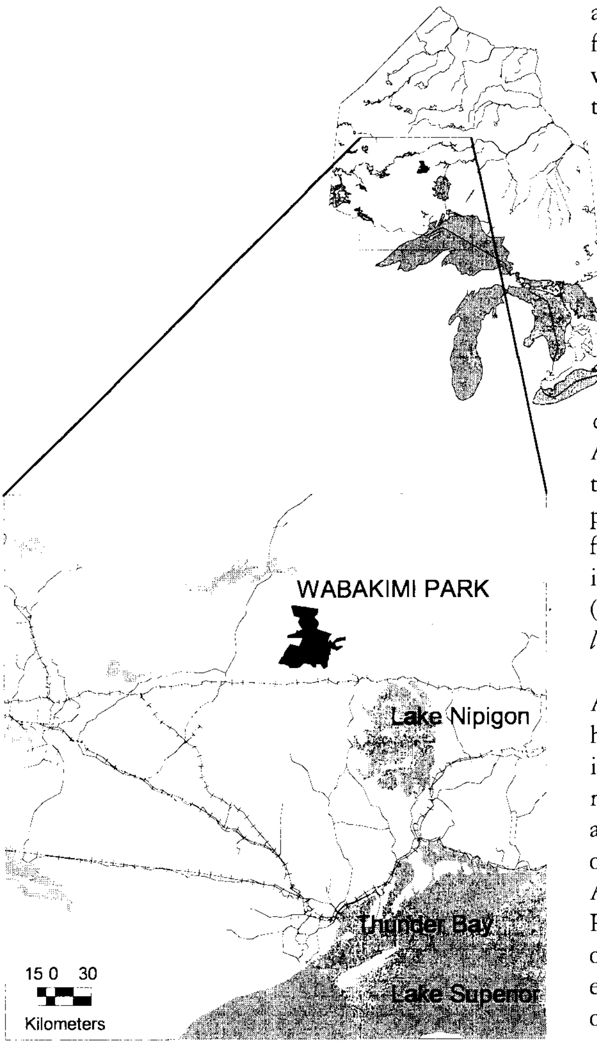

Fig. 1. Location of the original Wabakimi Park in Northwestern Ontario.

grounders on both the Park and the WPBC, we discuss current understanding of the status of caribou in the Wabakimi area. Then we describe the assessment protocol used for the caribou value, along with our view on how caribou influenced the various decisions of the WPBC. We conclude with recommendations for future exercises that might need to consider caribou in decisions for protected areas.

Background to the Wabakimi Wilderness Park

Overview of values in the area

The Wabakimi area (Fig. 1) contains a variety of unique and representative features - biotic, physical, and cultural - that have long been of great interest from park protection and representation perspectives (Lee Kam, 1993). Woodland caribou are found throughout most of the area, and were one of the primary considerations in the establishment of the original park (Cumming, 1987). Winter habitat, calving sites and summer habitat are distributed across the landscape (see below).

A variety of earth- and life-science features are found in the area. Especially significant in the context of the boundary review were the provincially significant moraines, spillways, and other glaciofluvial features associated with glacial Lake Agassiz (Teller & Thorleifson, 1983). Also found in the area are various kames, dune complexes, and peatlands. The area is representative of the boreal forest (Rowe, 1972), with the principal tree species including jack pine (*Pinus banksiana*), black spruce (*Picea mariana*) and trembling aspen (*Populus tremuloides*).

Much of the area has a history of traditional Aboriginal use, with one lake containing one of the highest known concentrations of native pictographs in Ontario (Dewdney & Kidd, 1967). Several communities surround and make use of the Wabakimi area, including four First Nations and the hamlets of Armstrong, Collins and Savant Lake. Armstrong, southeast of the current Wabakimi Park, is the largest community and is an area base of operations for many of the fly-in remote tourism establishments. Fishing and hunting are major uses of the landscape from both recreational and tourism perspectives. Many canoeists frequent the area because of the variety and quality of canoeing opportunities available. Although difficult to quantify, the area is considered to have high value for remoteness and for wilderness experiences.

Creation of the park

OMNR began working on the concept of a large wilderness park northwest of Armstrong in the mid-1970s, primarily to obtain protected-area representation of Site Region 3W (Hills, 1976). The Wabakimi Park concept evolved slowly, with a variety of names: Whitewater Lake Candidate Wilderness Area, Ogoki-Albany Wilderness, and, when Minister of Natural Resources of the day Allan Pope announced its creation in 1983, Wabakimi Provincial Park. Even with park establishment, there remained considerable public interest and controversy surrounding the park boundary. Many parks advocates felt that the park was much too small to be a self-regulating ecosystem, and that many significant earth and life science features remained outside its boundaries.

Background to the Wabakimi Park Boundary Committee

Rationale

During the past few decades, decision-making in natural resources in North America has been undergoing a shift from authoritarian and bureaucratic approaches to democratic and inclusive approaches (Johnson & Duinker, 1993). Such a shift has been welcomed and endorsed in forest decision-making in Ontario (e.g., Ontario Forest Policy Panel, 1993; Koven & Martel, 1994). Indeed, our experience is that the OMNR has been embracing such a shift in recent years, and the WPBC is a prime example.

Park advocates felt that the 1983 park boundaries were highly inadequate because they omitted critical caribou habitat, important recreational features, and other significant park values. Rather than conducting some classic public-consultation hearings and calling in written submissions, OMNR decided to put the issue in the hands of a group of local and regional people, carefully selected to represent a wide range of interests in the area. The WPBC was thus created in fall 1992.

Mandate and membership

The mandate of the WPBC was to review the existing boundary and develop a single, consensus-based boundary recommendation to OMNR's Regional Director for the Northwest Region. OMNR gave the WPBC a small secretariat and modest budget to support its activities, and did not constrain the WPBC as to any expected magnitude or orientation of a boundary adjustment. The WPBC comprised 16 local individuals representing the following interests and organizations:

- First Nations (3)
- OMNR district office (1)
- OMNR regional office (parks) (1)
- tourist outfitters (fly-in fishing and hunting, and canoeing and ecotourism (2)
- anglers and hunters (1)
- conservation and environmental groups (2)
- prospecting and mining interests (1)
- rural community interests (2)
- timber companies (2)
- outdoor education group (1)

Regional and provincial groups desiring participation in the park-expansion discussions were engaged through two workshops specially designed for their input. In addition, opportunities were extended to the general public for consultation and input.

Consensus-seeking deliberations

The WPBC used standard consensus-seeking techniques for its overall decision-making process. After six months of preliminary discussions, a facilitator was retained to move the process along more vigorously without losing sight of the consensus goal. Majority votes were avoided as much as possible, but were accepted as necessary when stalemate situations arose. Voting has the advantage of efficiency, at the expense of effectiveness in the sense of buy-in by the parties affected by decisions. On the other hand, consensus building is relatively inefficient but can be highly effective. The commitment of WPBC members (and the OMNR, to its credit) to consensus was so strong that the WPBC exceeded its original one-year deadline and took almost 2.5 years to reach its conclusion.

Landscape assessment units

Early on, the WPBC was considering an undefined study area of roughly a million hectares surrounding the current park of 155 000 ha. WPBC members were having difficulties dealing with the complexity of such a vast landscape. A common approach was needed for referring to discrete portions of the landscape, for defining boundary expansion alternatives, and for making detailed assessments of whether any particular location of the study area should be within or outside a park expansion. The group settled on the concept of landscape assessment units (AUs), defined as small (ca. 10-50 thousand ha) land/water areas that could be used for creating and assessing alternatives. For the most part, the group defined the AUs on the basis of subwatersheds, trying to maintain a reasonably consistent size. Thus, AU boundaries followed heights of land wherever possible and incorporated "complete" water systems. Some 65 AUs were delineated (Fig. 2), each named according to a dominant lake or river. The whole assemblage of AUs comprised an area of over 1.2 million ha (Fig. 2).

Option development

Option development began with consideration of alternative park sizes and configurations given cer-

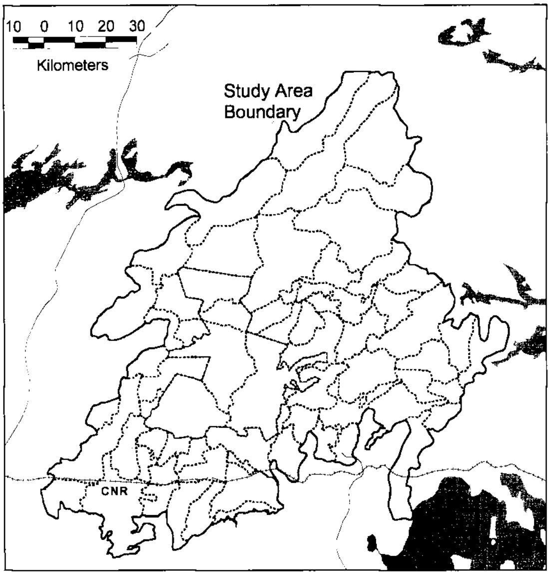

Fig. 2. Distribution of 65 assessmenr units within the study area of the Wabakimi Park Boundary Committee.

tain combinations of AUs. WPBC members quickly recognized the political ramifications of option development. Those who initially favoured a large park expansion were anxious to see some large alternatives developed and assessed, and were cool toward small options. Those who initially favoured a relatively small park expansion, or no expansion at all, were enthusiastic about creating such alternatives but were reluctant to accept more-generous expansion options.

With time, the group designed a set of six, first-round park-expansion options ranging in size from about 200 000 ha to about 1 million ha. These options were called "protected-area concepts", for two reasons: (a) "protected" areas rather than parks, because parks have narrow legal definitions and the WPBC was considering a wide range of options for protecting areas from roads, logging, mining, and hydro-electric development; and (b) the term "concepts" was considered more appropriate at this early stage of examining theoretical expansions, whereas "options" sounds more concrete and possible.

Once the six concepts were assessed by the WPBC, discussed in public forums, and reviewed by members of an invited scientific panel, the WPBC proceeded to develop four composite options for further assessment and discussion. The four options ranged from about 570 000 ha to 1 million ha. Essentially, two of the smaller expansion concepts were dropped, and the larger four were redesigned. One of the four options was based upon a combination of earth science features and woodland caribou habitat.

As the WPBC's work proceeded, full consensus on one new boundary appeared increasingly elusive. The WPBC was, however, able to agree on two options - one was based solely on conservation objectives (near 1 million hectares), and the other was a rather conservative option of almost 600 000 hectares. There was strong consensus that the latter option should be included entirely in any new protected area.

Values assessment

In its early work, the WPBC decided to group relevant area values into four classes: (a) ecological and watershed integrity; (b) landscape diversity and natural heritage; (c) recreation; and (d) sustainability of social and economic benefits. With time, the four classes gave way to the following eleven basic values which were used to assess both the first-round concepts and the second-round options:

– Aboriginal and traditional use
– canoeing
– woodland caribou habitat
– community development values
– Crown-land recreation
– earth-science values
– economic minerals
– life-science values

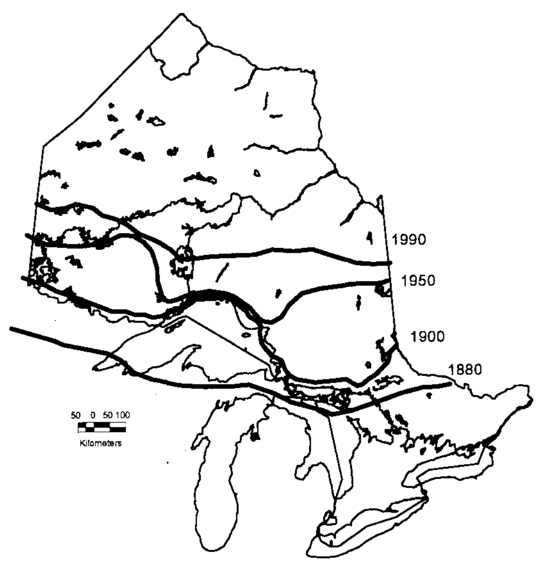

Fig. 3. Recession of the southern limit of continuous distribution of woodland caribou in Ontario since 1880 (source: Cumming & Beange, 1993).

- remote tourism
- remoteness
- timber capability

For each value, much time was spent gathering basic data and information on how the value was distributed across the study area and in each AU. In some instances, new data had to be collected. Then, members created schemes, in some cases quantitative, for rating the importance of each AU in terms of the value. For most values, a five-class system was used, so each AU could be rated low, low-medium, medium, medium-high, or high for a particular value. Maps showing the distribution of these classes became a vital source of information for WPBC members during assessment discussions. Besides the obvious utility of breaking down a complex task into more manageable bits, the AU approach facilitated greater objectivity in assessing and debating priorities for including AUs in an expanded protected area.

Caribou in the Wabakimi area

Most woodland caribou in Ontario live north of the northerly extent of roads and timber harvesting. The original Wabakimi Park (ca. 1983) lay near the southern edge of the line of continuous caribou distribution (Figs. 1, 3). Nonetheless, the original park contained a concentration of about 175 caribou (Bergerud, 1989). The size of the caribou population within the combined area of the proposed park expansion and adjacent caribou concentration areas such as Brightsand, Jojo Lake, and Lake Nipigon has been estimated at about 500 animals (R. Gollat, pers. comm., 1996). Frankel & Soulé (1981) have indicated that to avoid possible extirpation due to inbreeding in the short term, a minimum population of 50 breeding animals is required; to avoid long-term extirpations, a minimum of 500 breeding animals is thought to be required. Therefore, despite its large size and relatively high caribou concentrations, the largest possible Wabakimi Park could be at or below the lower limits of long-term caribou viability if the population were isolated. However, exchanges of genetic material may occur with caribou populations to the west, east and north.

There are generally agreed to be three critical habitats for woodland caribou: predator-free spring/summer calving areas, lichen-rich winter range, and corridors linking the two (Racey *et al.*, 1991; Cumming, 1992). The Wabakimi area is particularly well endowed with both winter and summer habitats. An arm of the ancestral Lake Agassiz extended into the area north of Armstrong, leaving a number of glaciofluvial features that constitute important caribou habitats, including peatland-dunefield complexes, outwash plains, glacial spillways, moraines, eskers, and extensive areas of wave-washed bedrock (Zoltai, 1965). Parks advocates have contended that many of the winter habitats are of high quality for caribou because of the shallow, dry and nutrient-poor soil conditions, resulting in low site index and low stocking, which in turn fosters prolific lichen growth (Morash & Racey, 1990). Antoniak (1993) found that many habitats could be well predicted using these parameters, and that virtually all actively used caribou habitats could be identified using a combination of standard forest resource inventory (FRI) data and remote sensing from Landsat.

Wabakimi's concentration of large lakes with convoluted shorelines and numerous islands offers many actual and potential calving sites and summer habitat (Timmermann, 1993a). The high density of lake chains and rivers constitute excellent travel corridors between winter and summer habitats.

Population studies on the Wabakimi-area caribou have only begun to become comprehensive for the entire area in recent years. Previously, several researchers documented the presence of some portions of the population. Following up reports by canoeists and oufitters, and with the added impetus of a 1978 proposal for a major logging road, Harold Cumming carried out the first scientific aerial surveys in the late 1970s and early 1980s, identifying some of the winter habitats north of the CNR line (Cumming & Beange, 1987). However, Cumming carried out few investigations to the west or south. These surveys had considerable influence upon the Ontario Parks Council and the Minister of Natural Resources in establishing the original 1983 park boundary. Likewise, surveys in 1989 (Bergerud, 1989) were limited to the extant park area, plus some area south of the park, but north of the CN rail line. Bergerud's (1989) population estimate (mean) was 171 animals in the extant park. Random aerial surveys from 1990 to 1993 (Hyer, 1997) showed that there were actively used winter habitats and corridors in the Wapikaimaski, Aldridge, and Loop Lake areas south of the CNR and north of the Kopka River. Also, a travel corridor from the Armstrong airport and Jojo Lake wintering range extending north via the Pikitigushi River to the Ogoki River was documented at this time (Hyer, 1997).

Additional studies on caribou populations and habitats in the Wabakimi area were conducted by OMNR, both during the years that OMNR was considering a boundary change and while the WPBC was deliberating. These surveys added many valuable data on winter habitat (much of which appeared to be unoccupied), and on caribou winter presence, including March migration routes (1992-94) and linkages between Wabakimi animals and those in the Brightsand, Kopka, and Savant Lake areas. Since the announcement of the park expansion in April 1995, additional work in the summers of 1995 and 1996 has identified yet more critical habitats outside the announced expansion areas to the west, south and east. Collared animals have confirmed that in 1995 and 1996 caribou wintering south of the tracks used Wabakimi habitats north of the CN line in all seasons (R. Gollat, pers. comm., 1996).

Incorporating the caribou habitat value in Wabakimi expansion deliberations

Assessment Protocol

The total area under consideration consisted originally of 65 AUs ranging in area from 1600 to over 50 000 hectares, and averaging ca. 17 500 hectares. This included five AUs representing the original park. The larger AUs were generally to the north (Fig. 2), where caribou habitat values were considered relatively low.

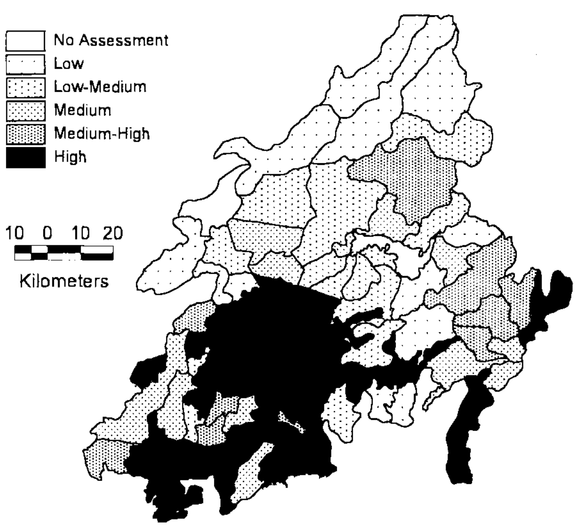

Fig. 4. Caribou habitat values ranked for each assessment unit within the study area of the Wabakimi Park Boundary Committee.

Information on caribou habitat values was compiled for the entire study area. This included information on winter habitat sightings, traditionally used wintering areas, summer sightings, calving sites, and documented and suspected travel corridors (between winter and summer range). The information came from a variety of sources using various techniques, e.g. winter caribou surveys, incidental caribou sightings during moose surveys, caribou research projects, calving site surveys on specific lakes, incidental reports of caribou sightings from forest users, Timber Management Plan values maps, and published and unpublished reports (e.g., Cumming 1987; Bergerud, 1989). Data coverage was not uniform, making quantitative comparisons difficult - the study area spanned four administrative districts and five Wildlife Management Units as defined by OMNR. Much of the information was recent, due to an increasing interest in caribou inventory and management in recent years. Little information was available for winter habitat utilization for large portions of the study area, particularly to the north and the east; specific winter caribou surveys were conducted in these areas to collect data using general transect survey methods (Timmermann, 1993b).

The overall value of each AU as currently utilized caribou habitat was evaluated - habitat potential, current or future, was not ranked. In some cases, the habitat was provided in only a portion of the AU, but the entire AU received the same ranking. An effort was made to provide consistent judgements across all AUs. AUs were ranked according to the following qualitative scale:

High:
- repeated winter use, or
- essential calving lake, or
- winter use and heavily used/linear travel corridor, or
- favoured habitat type and demonstrated use;

Med.-High:
- a value judged to be mid-way between high and medium;

Medium:
- significant winter use, or
- winter use and light/diffuse travel corridor, or

Table 1. Relative ability of four park concepts (G to J) and the proposed expansion to incorporate assessment units containing critical woodland caribou habitats. All figures include the area of the original park.

Park Concept *	Total Area (ha)	Area of AUs with High caribou habitat values (ha)	Area of AUs with M-H caribou habitat values (ha)	Area of AUs with Medium caribou habitat values (ha)	Proportion of critical caribou area within habitat is study the concept (%)
Original Park	155 700	123 250	0	32 420	23
Concept G	571 200	218 800	57 700	60 700	50
Concept H	763 600	284 400	80 400	134 700	74
Concept I	846 200	321 800	109 500	146 800	86
Concept J	1 038 600	312 500	153 300	149 000	91
Study Area	1 204 000	359 500	158 000	158 100	100
Expansion	891 500	243 500	114 500	118 700	71

* Original Park = Wabakimi Provincial Park as originally established in 1983.
Concept G = concept based on maintaining some high quality timber and mineral opportunities.
Concept H = concept based on tourism and recreation.
Concept I = concept based on landscape and biological diversity (including woodland catibou).
Concept J = concept based on maintaining ecological integrity.
Study area = total area considered by the Wabakimi Park Boundary Committee.
Expansion = territory included in the protected-area expansion announced by the Govetnment of Ontario in April 1995.

– habitat type with occasional use;

Med.-Low: – a value judged to be mid-way between medium and low;

Low:
- occasional or no winter use, and
- no known calving sites or travel corridors, and
- unfavourable habitat type.

Assessment outcomes

The ranking of caribou habitat values for all the AUs resulted in a ranking classification as follows: high - 18 AUs; medium-high - 8 AUs; medium - 10 AUs; medium-low - 14 AUs; and low - 15 AUs (Fig. 4). Three AUs were split and each section was ranked separately, because of the clumped spatial distribution of caribou habitat features.

Caribou habitat values for each of the four refined concepts (concepts G, H, I, J - Fig. 5) were compared to determine how well each concept incorporated caribou habitat values. Critical caribou habitat was considered to include the medium, medium-high and high rankings. The four park concepts incorporated from 50 to 91% of the critical caribou habitat considered to be within the approximately 1.2 million hectare study area (Table 1). Some qualitative assessments of the various concepts were also undertaken, to determine how well they incorporated specific habitat needs such as travel corridors to adjacent habitats, and linkages with Lake Nipigon (a major calving/summering lake). Concept I was judged to meet these qualitative needs best, an expectable result since development of this option most closely considered all seasonal caribou habitat values.

As part of the selective scientific review, responses were received from ten of 24 invited scientists. Five reviewers commented specifically on caribou habitat considerations relative to park expansion, and most were supportive (see summary in Table 2). Reviewers generally did not comment specifically on the relative merits of the various park concepts, but rather provided comments on caribou habitat protection and biodiversity conservation.

Subsequent to the development of the four concepts, the WPBC created two additional concepts (K and L) for OMNR to consider. These two concepts were further assessed by OMNR to determine their ability both to protect park-related values and provide resource-development opportunities. Caribou habitat concerns were again considered in this assessment, with regard to how they supplemented the caribou habitat incorporated within the

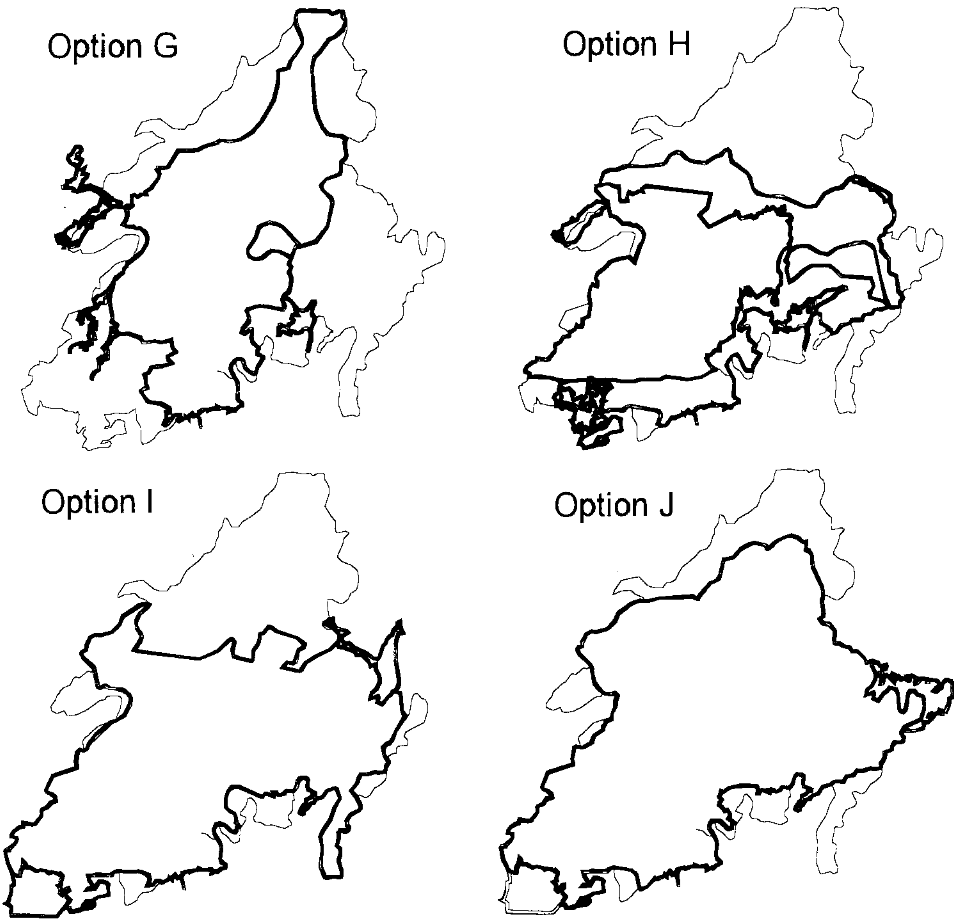

Fig. 5. Phase-2 options for protected-area expansion as derermined by the Wabakimi Park Boundary Committee.

existing park. The 577 100 ha Concept K added about 150 000 ha of critical (i.e., seasonal high-value) habitat to the existing park, and with the current park represented about 45% of such habitat within the study area. Concept L, which was over a million hectares, added almost half a million hectares of critical habitat to the existing park, and along with the current park represented almost 95% of the critical habitat within the study area.

In April 1995, Minister of Natural Resources Howard Hampton announced that Wabakimi Park was being expanded to an area of approximately 891 500 ha (Fig. 6). This included 475 000 ha of critical woodland caribou habitat, or 71% of the critical habitat identified within the study area.

Influence in boundary redefinition

In the process of developing and assessing park expansion options, the WPBC moved through three distinct phases. In the first phase, six options were used to stimulate response, but without conclusion. In second phase, four refined options emerged, and these moved the process ahead encouragingly. The final phase found general consensus on a minimum core expansion, but consensus could not be reached on a single new boundary. Caribou values remained key in all three phases.

Indeed, caribou were always central to all the WPBC deliberations, for two reasons. First, the evidence is clear that whatever factors may be implicated in the continuing northward regression of caribou range, the northern boundary of continuous caribou habitat coincides with the northern timber cut line. Consequently, the provincial policy that no species of flora or fauna be allowed to decline permanently in total numbers across the province as a result of forest management dictated that Wabakimi be considered an important caribou refu-

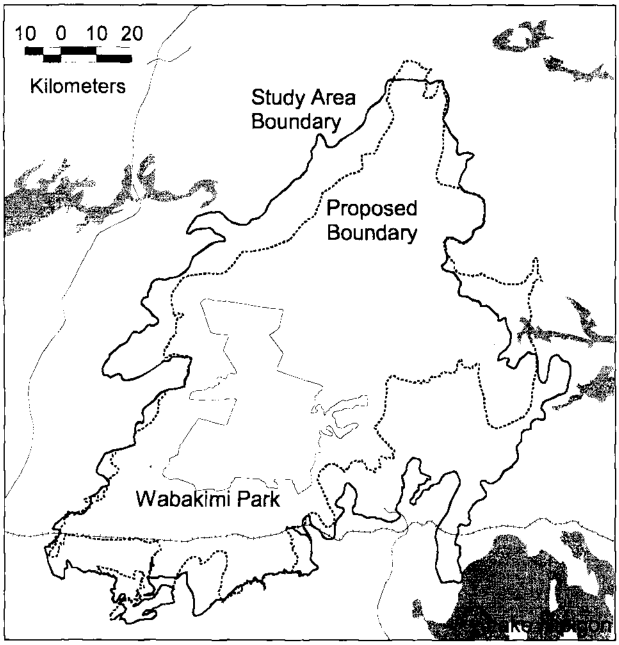

Fig. 6. Proposed boundary of a protected-area expansion at Wabakimi as announced by the Government of Ontario in April 1995.

gium. Protected areas are important in maintaining woodland caribou within Ontario's forests, as approximately one third of the documented caribou within the boreal forest are found within parks (Cumming & Beange, 1993). Second, park expansion advocates understood well the importance of public opinion associated with such a policy where an animal as appealing as the caribou is concerned.

Space is believed by many biologists to be the most important overall caribou habitat requirement (Bergerud, 1992). Within that space must be certain forested sites in a sequence of age classes renewed over time by disturbance (traditionally wildfire). As Table 1 shows, the larger the expansion option, the greater the inclusion of high-quality space for caribou. Option J, in addition, was aimed at providing sufficient area such that natural fire-disturbance regimes could operate and thus create a regional fire-renewing ecosystem. Preserving a remnant of the boreal forest as a benchmark area was also a key priority in Wabakimi expansion, but it may be only within such a large area that woodland caribou can survive over time.

We believe that the prospect of wide provincial, national and international interest in the caribou issue had a profound effect upon the final expansion decision. Thankfully, promises of mitigation of area and wood supply losses brought the forest-products industry onside, as it is doubtful the companies would have moved based upon caribou and other park values alone. Most participants and observers would agree with the statement made by Paul Gagné, Avenor's CEO, at the April 1995 announcement of the proposed expansion of the Wabakimi protected area: "The expansion of Wabakimi will create a world-class park and ensure the continued protection of unique land forms and wildlife habitats indigenous to the region." We are happy to report that the expanded park was officially regulated in July 1997.

Conclusions

Caribou habitat was one of eleven key values that commanded much attention during the deliberations of the WPBC. It was fortuitous from a park-expansion point of view that several park values (as opposed to resource-use values such as timber harvest and mining) overlapped spatially in roughly the same areas surrounding the former, 155 000-ha Wabakimi Provincial Park. Moreover, areas with favourable seasonal caribou habitat were also generally important in terms of earth-science, canoeing and remote-tourism values.

WPBC members were firm in their conviction that a reasonable outcome could be achieved through a combination of principled consensus-building and rational analysis of alternative park sizes and boundary configurations. Analytical progress was strong once the WPBC worked out the assessment-unit approach and methods to assess the values objectively, either quantitatively or qualitatively. The caribou perspective was incorporated into the technical analysis along with all the other key values, and played a vital role in shaping the new Wabakimi protected area.

We offer the following advice for participants in future exercises where caribou (or any other featured species, for that matter) may be a vital value in creating protected areas:

1. Information will always be inadequate, and decisions will always have to be made despite inadequate information. As early as possible, assemble extant information, analyze it, identify

Table 2. Summary of key points raised by five scientific reviewers regarding woodland caribou habitat values.

Park expansion
Park expansion to the south required to include additional winter and summer habitat.
Boundary must include important habitat and linkages for seasonal migration.
Caribou should be given top priority in re-defining the park boundary - require a network of viable caribou areas across northern Ontario.
To ensure long-term viability of the caribou population, must protect an area of sufficient size to maintain natural fire patterns.
To ensure the long-term survival of the herd, it is important to incorporate landforms that will provide future habitat.
Adjacent land use
Ecologically sustainable land use should be implemented on the landbase outside the expanded park to maintain landscape linkages.
Human disturbance
Human use of islands not considered a problem.
Winter snowmobile access should be restricted in some critical areas to avoid disturbance of caribou.
Park management
May wish to consider less restrictive park management policies that allow for vegetation management to maintain caribou habitat (eg. Lightly stocked stands, prescribed burns).
May wish to consider option of directly managing other wildlife populations to aid in caribou survival, e.g. wolf control, moose hunting.

critical information needs, get the new required information, and use the assembled information base fully.

2. Simple analytical approaches are efficient, and likely sufficient for strategic decisionmaking. Detailed and site-specific information should be compressed into more-usable forms at a regional scale.
3. Hasty analytical work in support of important decisions should be avoided. Useful analysis, supported by careful information gathering and incisive discussion, takes time, not to mention the negotiations in which analytical results are used. The WPBC overran four process deadlines, requiring substantial amounts of time to reach its conclusions. The biophysically sensible and politically feasible outcome that was reached would have been elusive, if possible at all, in a more rushed exercise.

Acknowledgements

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Preliminary analysis of habitat utilization by woodland caribou in northwestern Ontario using satellite telemetry

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Abstract: Locational data collected over a one year period from 10 female woodland caribou, *Rangifer tarandus caribou,* collared with Argos satellite collars in northwestern Ontario, Canada were superimposed on supervised Landsat images using Geographical Information System (GIS) technology. Landscape parameters, land cover classifications, and drainage were utilized to create the basemap. Using ARCVIEW software, all digital fixes from collared caribou with information of date, time, and activity status were overlain on the basemap to facilitate a preliminary analysis of habitat use in this species. Results supported the conclusions (1) that woodland caribou in northwestern Ontario select habitats containing high to moderate conifer cover and avoided disturbed areas and shrub-rich habitats, (2) that seasonal changes in habitat utilization occurs in females of this species, and (3) that satellite telemetry technology can be employed in the boreal forest ecosystem to assess habitat utilization by large ungulate species.

Key words: seasonal activity, habitat use, Landsat imagery

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Introduction

Recent cooperative initiatives between the forestry industry and provinical government to improve the image and efficiency of forest resource management has lead to the development of an integrated forest management policy, which considers the impact of forest harvesting practices on sustaining wildlife populations, and enhancing forest regeneration and harvest rotation time. In this regard, experimentation with new cutting practices has been initiated and research on regeneration and wildlife populations has been ongoing for the past few years. In northeastern Ontario, comparison of the impact of different cutting methods in the black spruce-lichen/moss forest community has indicated that small mammal species diversity and biomass can be maintained, if intermediate impact cutting practices (light residual and heavy residual) were employed (Courtin & Beckerton, 1994). In addition, earlier forest regeneration and shorter rotation periods between harvesting have been associated with these techniques.

However, the impact of various cutting practices on the activity and sustainability of larger boreal mammals is presently unclear. Research has shown that woodland caribou, *Rangifer tarandus caribou,* are the least tolerant of current logging practices and have been extirpated over much of their former range (Stardom, 1977; Chubbs *et al.*, 1993). An overview of habitat utilization by this species in northwestern Ontario would provide government and the forest industry with information required to manage and sustain this species. In addition, an understanding of the interactions associated with current forest harvesting practices, ungulate populations, and their primary predators would also aid in the development of sustainable forest management policy and expand our knowledge of the population dynamics and behaviour of these important species (Edmonds, 1988; Seip, 1992).

Recent advances in remote sensing technologies have presented new opportunities and challenges for researchers working on ungulate species inhabiting large diverse ranges in regions with limited accessibility. To date, few studies have examined the advantages and limitations of satellite telemetry in assessing habitat utilization and movement patterns in ungulates in the boreal forest ecosystem (Thompson *et al.*, 1980; Ferguson, 1991; Pearce, 1992) and only one study has been conducted on woodland caribou (Ellis & White, 1992). The application of GIS technology to research on woodland caribou has been conducted in Alberta (Bergerud, 1989; Chichowski & Banner, 1992) and has begun to be applied in northwestern Ontario (Antoniak, 1993; Cumming *et al.*, 1996).

The objectives of this study were: (1) to obtain preliminary estimates of annual and seasonal habitat utilization by female woodland caribou in northwestern Ontario, (2) to assess variation in seasonal activity patterns in females of this species, and (3) to assess whether satellite telemetry technology was able to identify habitat utilization by ungulates in the boreal forest ecosystem.

Methods

Three classified Landsat thematic map images with 25 x 25 m pixels were supplied by the Ontario Remote Sensing Office, Toronto, Ontario. Landsat image areas chosen represented locations where caribou fitted with Telonics Argos satellite collars occurred. Nineteen land cover classes were present on each image. Images were projected in pseudocolour and colour-themed using Image Legend Editor, ARCVIEW 2.1 (Stafford, 1994).

Data were collected weekly from 10 female caribou minimizing autocorrelation problems (Nau *et al.,* 1974). Caribou telemetry data were separated into four seasons: (1) Spring: March 1 - May 31, (2) Summer: June 1 - August 31, (3) Fall: September 1 - November 31, and (4) Winter: December 1 - December 31. The n values were as follows; Spring, n = 7; Summer, n = 11; Fall, n = 11; Winter, n = 10. Telemetry locations classified by Service Argos as LQ (Location Quality Index) 1 (+/- 1000 m), LQ 2 (+/- 350 m), and LQ 3 (+/- 150 m) were used. It was assumed that this approach provided a more accurate representation of caribou behaviour as sample size was increased and levels of error would overlap and cancel each other (F. Messier, pers. comm.). Location points were used to create the boundary of each polygon. Habitat use inside each polygon was established by associating the location point of each animal with the corresponding 25 x 25 m Landsat classification pixel (Litvaitis *et al.,* 1994). All latitudes and longitudes were transformed from decimal degrees to Universal Transverse Mercantor (UTM) units to correspond to basemap point locations. The number of satellite collared caribou locations in each habitat were transformed into percentages to estimate trends in seasonal habitat use. The Landsat land cover classifications were: Water/Ice, Shoreline, Wetlands, Open Fen, Shrub-Rich Fen, Treed Bog, Dense Deciduous Forest/Shrub, Dense Conifer Pine, Dense Conifer Spruce, Mixed Forest Deciduous, Mixed Forest Conifer, Sparse Conifer, Sparse Deciduous Cover, Recent Clearcuts, Recent Burns, Old Burns/Cutovers, Bedrock/Sand, Mine Tailings, and Urban/Roads.

Seasonal changes in activity patterns were determined from the telemetry information provided by Argos Service and animals were classified as resting (0 - 5), feeding (6 - 30), walking (31 - 36), and running (> 37).

Results

Spring

During the spring (March 1 - May 31), caribou were found predominately in 5 habitat types: Treed Bogs (22%), Old Burns (17.1%), Sparse Conifer areas (15.3%), Mixed Forest Deciduous areas (11.2%), and Dense Spruce areas (10.2%). These classifications represented 75.8% of the habitat used by caribou during this period.

In contrast, the 5 most under utilized habitats consisted of: Urban/Roads (0%), Mine Tailings (0%), Bedrock/Sand (0%), Dense Deciduous Forest/Shrub areas (0%), Shrub-Rich Fens (0%), and Wetlands (0%). These classifications were not used by caribou in the spring and represent habitats created by disturbance or containing a heavy deciduous shrub component (Fig. 1).

Other habitat types used by caribou ranged between 7.7% and 1% and included: Shoreline (7.7%), Dense Coniferous Pine areas (5.5%), Sparse Deciduous Covered areas (3.4%), Recent Clearcuts (2.6%), Open Fens (2%), Water/Ice (1.4%), Mixed Forest Conifer areas (1.2%), and Recent Burns (0.4%).

Summer

During the summer (June 1 - August 31), the 5 most common land classifications utilized by caribou were: Treed Bogs (18.7%), Mixed Forest Deciduous areas (16%), Dense Conifer Spruce areas (14.8%), Shoreline (13.3%), and Dense Conifer

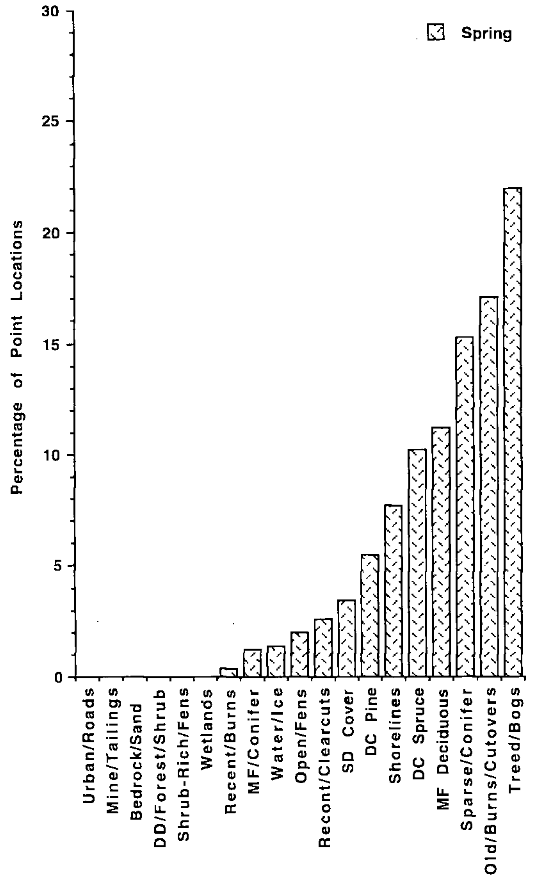

Fig. 1. Percentage of point locations in different Landsat land cover classes for woodland caribou during the spring of 1995 (March 1 - May 31) in northwestern Ontario (DD = dense deciduous; MF = mixed forest; SD = sparse deciduous; and DC = dense conifer).

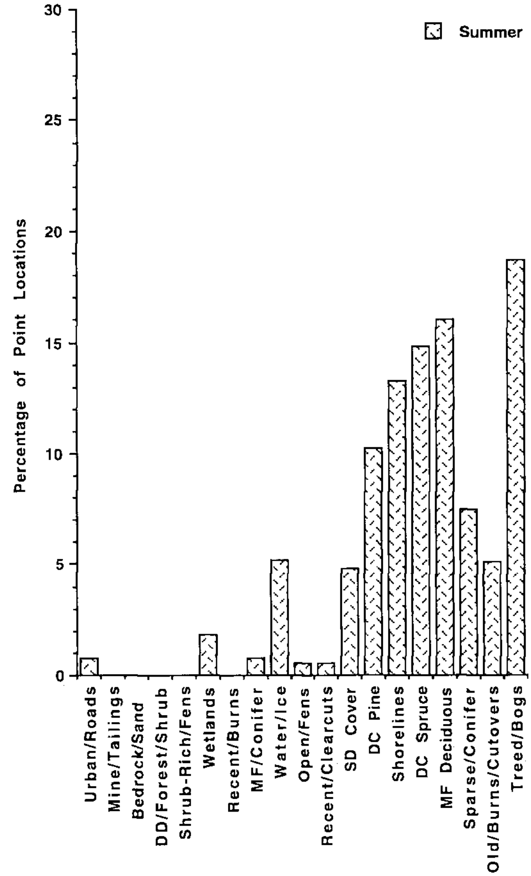

Fig. 2. Percentage of point locations in different Landsat land cover classes for woodland caribou during the summer of 1995 (June 1 - August 31) in northwestern Ontario (DD = dense deciduous; MF = mixed forest; SD = sparse deciduous; and DC = dense conifer).

Pine areas (10.2%). These classifications represented 73% of the habitats utilized by caribou during the summer (Fig. 2) and indicated caribou used both dense canopy cover and open sites during this period.

In contrast, the 5 least important land classifications used were: Mine Tailings (0%), Bedrock/Sand areas (0%), Recent Burns (0%), Dense Deciduous Forest/Shrub areas (0%), and Shrub-Rich Fens (0%). These habitat types were not used by caribou during the summer and represent habitats created by disturbance or containing a heavy deciduous shrub component (Fig. 2).

Other habitat types utilized by caribou in summer ranged between 7.5% and 0.3% and included; Sparse Conifer areas (7.5%), Old Burns/Cutovers (5.1%), Water/Ice (5.2%), Wetlands (1.8%), Urban/Roads (0.8%), Mixed Forest Conifer areas (0.8%), Open Fens (0.5%), and Recent Clearcuts (0.5%).

Fall

In the fall (September 1 - November 31), caribou were found in Dense Conifer Pine areas (29%), Dense Conifer Spruce areas (9.9%), Recent Clearcuts (9.9%), Treed Bogs (8.4%), and Shorelines (7%). These classifications represented 64.2% of the habitats used by caribou in the fall (Fig. 3).

In contrast habitats where caribou were found least included: Mine Tailings (0%), Urban/Roads (0%), Recent Burns (0%), Shrub-Rich Fens (0%),

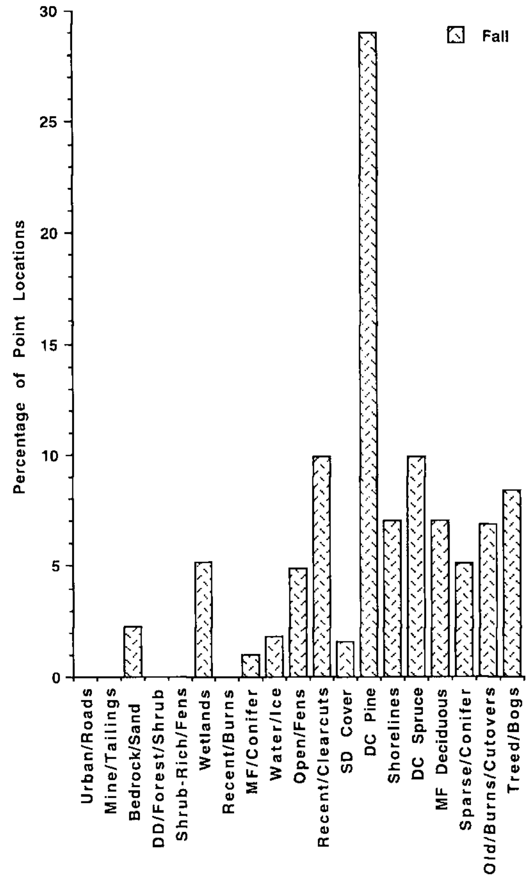

Fig. 3. Percentage of point locations in different Landsat land cover classes for woodland caribou during the fall of 1995 (September 1 - November 31) in northwestern Ontario (DD = dense deciduous; MF = mixed forest; SD = sparse deciduous; and DC = dense conifer).

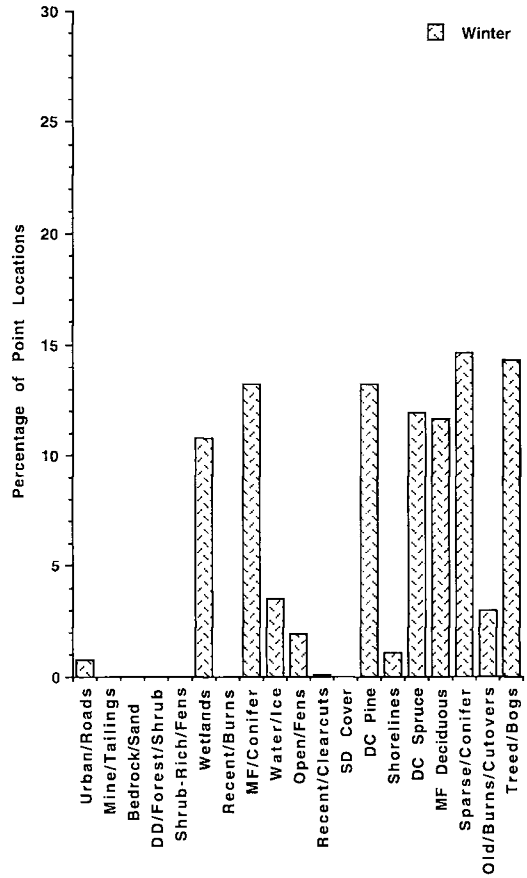

Fig. 4. Percenrage of point locations in different Landsat land cover classes for woodland caribou during the winter of 1995 (Decembet 1 - December 31) in northwestern Ontario (DD = dense deciduous; MF = mixed forest; SD = sparse deciduous; and DC = dense conifer).

and Dense Deciduous Forest/Shrub areas (0%). These habitats were areas of disturbance and areas of dense deciduous shrubs (Fig. 3).

Other habitats used by caribou during the fall ranged between 7% and 0.1% and included: Mixed Forest Deciduous areas (7%), Old Burns/Cutovers (6.9%), Wetlands (5.2%), Sparse Conifer (5.1%), Open Fens (4.9%), Bedrock/Sand (2.3%), Water/Ice (1.8%), Sparse Deciduous Cover areas (1.6%), and Mixed Forest Conifer areas (1%).

Winter

During winter (December 1 - 31), the 5 Landsat classifications most utilized by caribou were: Sparse Conifer areas (14.6%), Treed Bogs (14.3%), Dense Conifer Pine areas (13.2%), Mixed Forest Conifer areas (13.2%), and Dense Conifer Spruce areas (11.9%). These classifications represent 67.2% of the habitat utilized by caribou during winter (Fig. 4).

In contrast, classifications not used by caribou during winter were Shrub-Rich Fens (0%), Mine Tailings (0%), Bedrock/Sand areas (0%), Recent Burns (0%), Sparse Deciduous areas (0%), and Dense Deciduous Forest/Shrub areas (0%). These classifications represented areas of disturbance or contained heavy deciduous shrub components (Fig. 4).

Other land classifications utilized ranged between 11.6% and 0.25% and included: Mixed Forest Deciduous areas (11.6%), Wetlands (10.8%), Water/Ice (3.5%), Old Burns/Cutovers (3%), Open

Fens (1.9%), Shorelines (1.1%), Urban/Roads (0.8%), and Recent Clearcuts (0.1%).

Activity

Annual activity patterns of 10 females are represented in Figure 5. Mean annual percentages for the four behaviours were: resting (25.4%), feeding (37.6%), walking (11.5%), and running (25.5%). Resting activity ranged from 17% to 39%, reaching a peak during the summer months (June, 39% and July, 33%) and again in winter (December, 33%). Feeding represented the highest recorded activity ranging from 26% to 45% and was greatest in March (45%) and May (45%) and lowest in June (26%). Walking was less frequent and ranged between 6 - 22%. Running was most common during the fall (August - October) and ranged from 16% to 35% of the total activity.

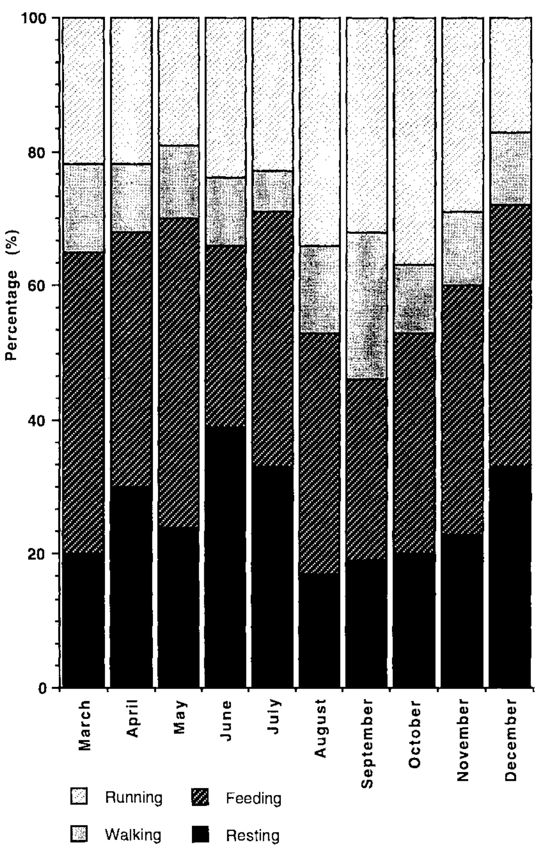

Fig. 5. Annual activity patterns of woodland caribou during 1995. Mean annual percentages for the four behaviours assessed were: resting - 25.3%, feeding - 37.6%, walking - 11.5%, and running - 25.4%.

Discussion

Although only preliminary data were available, woodland caribou in northwestern Ontario during 1995 appeared to utilize specific Landsat land cover classifications more, while others were avoided. The four Landsat land cover classes most used throughout the year in order of importance were; Treed Bogs (15.9%), Dense Conifer Pine (14.5%), Dense Conifer Spruce (11.7%), and Mixed Forest Deciduous areas (11.5%). These habitats were utilized during all seasons of the year and received 53.6% of all point locations. Similar findings have been reported by Bergerud & Butler (1975) and Cummings & Beange (1987) for woodland caribou herds associated with the Lake Nipigon region. In this area, winter concentration areas were found to occur on sandy flats containing 90% jack pine and 10% white birch, with a lichen understory. Further analysis by Darby *et al.* (1989) and Hyers (1997) indicated that the entire winter range of approximately 180 km2 was estimated to be composed of 61% conifer, 17% mixed forest, 11% deciduous forest, 7% muskeg and open habitat, and 4% water. Stardom (1997) working in Manitoba concluded that woodland caribou preferred open larch or black spruce bogs and intermediate to mature jack pine stands on rocky ridges or sand plains.

In contrast, the three Landsat land cover classes never or minimally utilized were; Mine Tailings (0%), Shrub-Rich Fens (0%), Dense Deciduous Forest/Shrub areas (0%), and Recent Burns (0.1%). These habitats were avoided during all seasons of the year and only received 0.1% of the point locations. Although data on habitat availability were not analyzed, the results support the conclusion that woodland caribou in this region select habitats containing high to moderate conifer cover and avoided disturbed areas (Mine Tailings) and shrub-rich habitats, such as Shrub-Rich Fens, Dense Deciduous Forest/Shrub areas, and Recent Burns. Recent Clearcuts which are known to support heavy shrub layers also appeared to be avoided and received only 3.3% of the point locations. In contrast, Old Burns/Clearcuts received 8% of all point locations. Hyers (1997) studying a caribou herd in northwestern Ontario impacted by winter log hauling and roads concluded that caribou temporarily avoid disturbance and human development, but return once development is completed. Similar results were found by Hill (1985) studying caribou in Newfoundland associated with the construction of a hydroelectric development. In this study, natural and man-made shrub-rich habitats with high levels of broad-leaf browse have been shown to be avoided by caribou, which is supported by the literature (Darby & Duquette, 1986; Godwin, 1990). These habitats favour moose and consequently increased wolf and black bear numbers, which may make caribou more vulnerable to predation. Bergerud (1983a, 1983b) and Seip (1992) have both presented data supporting this hypothesis.

Although seasons were only defined broadly within this study, trends in Landsat land cover class utilization were observed (Figs. 1 - 4). During the spring period, Treed Bogs, Old Burns/Cutovers, and Sparse Conifer habitats were most commonly used. These habitats have been found to be associated with calving females by other researchers and are thought to allow caribou to separate themselves from moose and associated predators (Shoesmith & Story, 1977, Fuller & Keith, 1981, Brown *et al.,* 1986, Parker, 1997).

During the summer post-calving period, Treed Bogs remained important, while Old Burns/Cutovers and Sparse Conifer habitats declined in importance and were replaced by Mixed Forest Deciduous areas, Dense Conifer Spruce and Pine areas, and Shorelines. In is interesting that the use of Shorelines was maximal during this period, when biting insects reach their greatest numbers. During the fall period, Dense Conifer Pine and Spruce areas were much more utilized than any other habitat type; however, Treed Bogs and Recent Clearcuts were a poor second. This combination of dense cover and open habitat may be associated with the rut, which occurs during this period. Winter habitats selected appeared to be more variable than fall land classifications and included; Sparse Conifer areas, Treed Bogs, Dense Conifer Pine and Spruce areas, and Mixed Forest Conifer areas. Wetlands also became important during this period when the substrate was frozen. As similar annual and seasonal habitat use have been reported by other researchers (Bergerud & Butler, 1975; Shoesmith & Story, 1977; Fuller & Keith, 1981; Edmonds & Bloomfield, 1984; Brown *et al.*, 1986; Cummings & Beange, 1987; Bergerud, 1989; Rominger & Oldemeyer, 1989; Hyers, 1997; Parker, 1997), it was concluded that satellite telemetry technology can be employed to assess habitat utilization by large ungulates in the boreal forest ecosystem.

Mean annual percentages for the four behaviours were: resting (25.4%), feeding (37.6%), walking (11.5%), and running (25.5%). Although these activity data were not calibrated, some trends were apparent. Resting reached a peak during mid-summer (June, 39% and July, 33%), when lactational requirements would be greatest and again in winter (December, 33%), when low quality forage and severe weather conditions would require the conservation of energy. Studies indicate that when forage intake declines, reindeer respond by reducing metabolic rate and energy expenditure (Fancy et al., 1989). In contrast, feeding remained relatively constant and the most frequent activity throughout the year (Collins & Smith, 1989). Walking and running were more frequent during the fall (August - October), when bulls spend most of their energy chasing and herding females (W.J. Dalton, pers. comm.).

In summary, the results support the conclusions (1) that woodland caribou in northwestern Ontario select habitats containing high to moderate conifer cover and avoided disturbed areas and shrub-rich habitats, (2) that seasonal changes in habitat utilization occurs in females of this species, and (3) that satellite telemetry technology can be employed in the boreal forest ecosystem to assess habitat utilization by large ungulate species.

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Ecosystem management and the conservation of caribou habitat in British Columbia

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Abstract: Woodland caribou (*Rangifer tarandus caribou*) in British Columbia inhabit a wide variety of forest ecosystems. Numerous research projects have provided information that has been used to develop caribou habitat management recommendations for different areas. Recenrly, the province has implemented guidelines to protect biodiversity rhat are based on an ecosystem management strategy of mimicking natural forest conditions. There is a great deal of similarity between caribou management recommendarions and biodiversity recommendations within different forest types. In mountain caribou habitat, both approaches recommend maintaining a landscape dominated by old and mature forests, uneven-aged management, small cutblocks, and maintaining mature forest connectivity. In northern caribou habitat, both approaches recommend maintaining some older stands on the landscape (but less than for mounrain caribou), even-aged management, and a mosaic of large harvest units and leave areas. The ecosystem management recommendations provide a useful foundation for caribou habitat conservation. More detailed information on caribou and orher management objectives can then be used to fine-tune those recommendations.

Key words: *Rangifer tarandus caribou*, habitat management, forestry, biodiversity.

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) conservation has been a high profile resource management issue in British Columbia (B.C.) for many years, primarily because of the conflict between forest harvesting and conservation of caribou habitat. That concern resulted in a large number of studies designed to provide information on how to integrate caribou habitat protection and forest harvesting. Those research results led to the development of numerous sets of guidelines and recommendations that have been implemented to various degrees throughout the province (e.g. Cichowski & Banner, 1993; Stevenson *et al.*, 1994). Forestry/wildlife guidelines have also been developed for various other high priority species in B.C. such as mule deer (*Odocoileus hemionus hemionus*) (Armleder *et al.*, 1986), and coastal black-tailed deer (*O. h. columbianus*) and Roosevelt elk (*Cervus elaphus roosevelti*) (Nyberg & Janz, 1990).

More recently there has been increased public concern about the impacts of forest management practices on the full range of natural biodiversity. Forest managers must now attempt to manage forests in a way that will maintain all native species, including vertebrates, invertebrates, vascular and non-vascular plants, and micro-organisms. Given this complex task, relying on single species guidelines is no longer a feasible approach. The habitat requirements of many native species are unknown, and even if they were, it would be impossible to integrate the individual requirements of thousands of different species, many of which have habitat requirements that are incompatible with the requirements of others. Consequently, an ecosystem management approach has been adopted as a more appropriate strategy to conserve natural biodiversity within managed forests in B.C. Ecosystem management provides the framework for the British Columbia Forest Practices Code Biodiversity Guidebook (British Columbia Ministry of Forests, 1995).

The British Columbia forest practices code biodiversity guidebook

The basic assumption of the Biodiversity Guidebook is that the more closely managed forests resemble natural forests, the greater the probablilty that all native species and ecological processes will be maintained. As natural ecosystems become increasingly modified by human activities, natural patterns of biodiversity become increasingly altered, and the risk of losing native species (including caribou) increases. Forest biodiversity is related to the age class distribution, patch size distribution (i.e. the size of contiguous, similar-aged areas of forest), and stand structure of the forest (Hunter, 1990). In natural forests, those factors were determined primarily by the frequency, scale and characteristics of natural disturbances such as fires, insects and disease. Thus, the Biodiversity Guidebook uses natural disturbance regimes as a model for forest management practices.

The degree to which natural biodiversity can be maintained within managed forests depends on how closely managed forests resemble natural forest conditions. As the forest age class distribution, patch size distribution, and stand structure become more like natural forests, the pattern of biodiversity will also approach more natural levels. However, moving along that continuum towards natural forest conditions usually has timber supply and economic consequences. Where we choose to be on that continuum becomes a social value judgement that considers the trade-off between biodiversity conservation and economic values. The Biodiversity Guidebook outlines three different options along that continuum, depending on whether biodiversity conservation has a high, intermediate, or low priority in a given area. The primary difference between those three options is the amount of old and mature forest retention. The High option maintains 75%, the Intermediate option maintains 50%, and the Low option maintains 25% of natural levels of old and mature forest in an area.

The Biodiversity Guidebook recommendations are intended to be applied at a landscape planning level. Forest Districts are subdivided into landscape units that are generally from 50 000 - 100 000 hectares in size. Landscape units must be quite large to represent the scale at which natural age classes and patch sizes were spatially distributed. The Biodiversity Guidebook provides recommended age class, patch size, and stand structure objectives for each landscape unit. Those recommendations vary depending on the natural forest characteristics (i.e. biogeoclimatic subzones; Meidinger & Pojar, 1991) and the biodiversity emphasis option for each landscape unit. The biodiversity emphasis option for each landscape unit is determined using a combination of ecological criteria, government policy on allowable timber supply impacts, and public input from strategic land use planning processes.

Ecosystem management and caribou habitat

Woodland caribou in B.C. live in a wide variety of ecosystems, but they can be broadly divided into a "mountain ecotype" and a "northern ecotype" (Fig. 1); (Stevenson & Hatler, 1985). Habitat management recommendations for the different caribou ecotypes have been developed based on specific information about caribou ecology in different areas. However, as will be discussed below, very similar recommendations would result from simply applying an ecosystem management strategy of trying to mimic the natural forest conditions in the areas where they live. The purpose of this paper is to discuss the value of an ecosystem management strategy for protecting caribou habitat.

Mountain caribou

Mountain caribou live in the southeastern part of the province (Fig. 1). The habitat use of mountain caribou has been the subject of numerous studies including Simpson *et al.* (1987), Servheen & Lyon (1989), Seip (1990; 1992a), Terry (1994), and Apps & Kinley (this volume). Mountain caribou spend most of the year at high elevations (generally above 1500 m) in alpine areas and subalpine forests of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). During the winter, snow depths are too great to allow cratering and the caribou feed almost exclusively on arboreal lichens. In some areas, caribou use lower elevation forests of western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) during early winter (November-December), but move to higher elevations as winter progesses.

These wet, mountainous landscapes had a very low frequency of stand destroying wildfires, and when fires did occur, most were relatively small in size. Thus, the landscape was naturally dominated by contiguous old forests, with early seral habitats relatively uncommon and small in size. Within

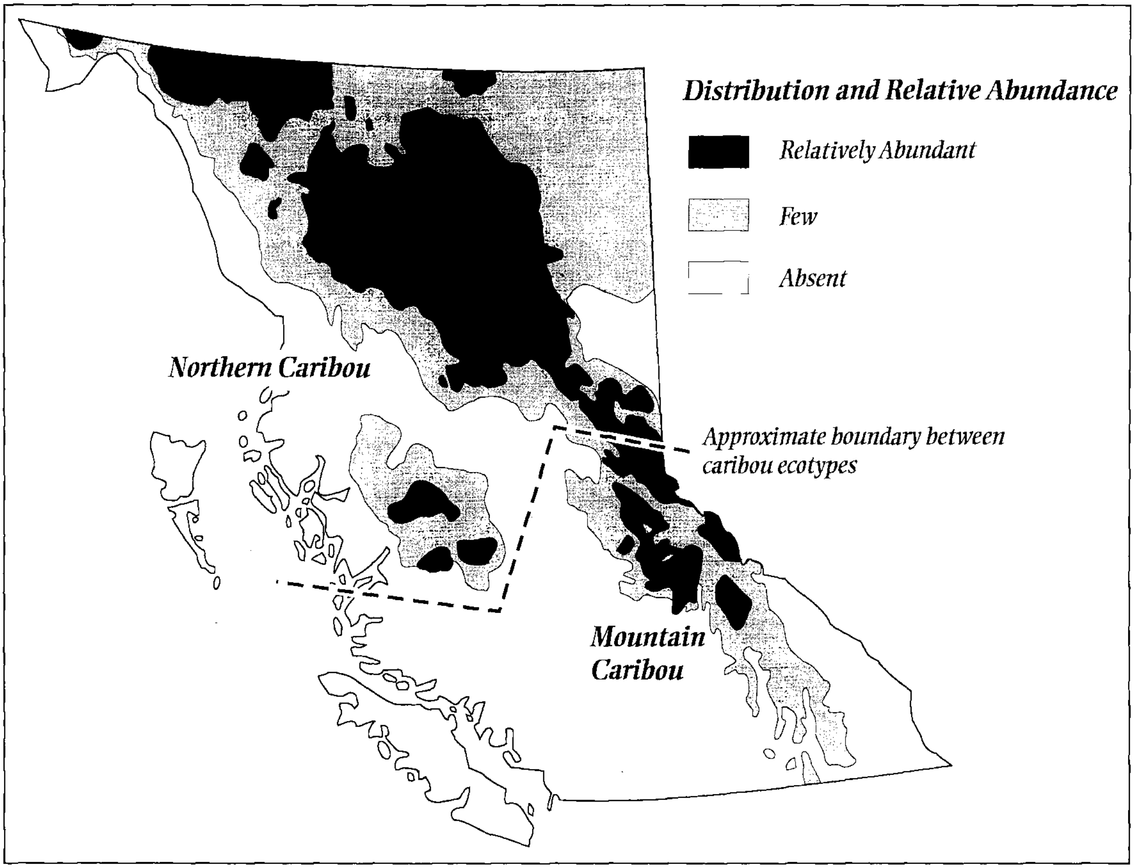

Fig. 1. The distribution and relative abundance of the mountain catibou ecotype, and the northern caribou ecotype, of woodland caribou in British Columbia (British Columbia Ministry of Environment, 1979; Stevenson & Hatler, 1985).

older stands, the death of individual trees or small groups of trees from small scale natural disturbances, such as insects or disease, created gaps in the forest canopy. Those gaps allowed trees to regenerate and grow in the understory resulting in the development of uneven-aged stands.

Arboreal lichens are most abundant in old forests (Antifeau, 1987) and are eliminated when those forests are clearcut or burned. Thus, maintaining old forests that provide arboreal lichen is an essential component of caribou habitat protection in these areas. Wolf (*Canis lupus*) predation is a major limiting factor of some mountain caribou populations, and caribou appear to be more vulnerable to predation when they live in close proximity to moose (*Alces alces*) because moose provide an alternative prey that sustains increased wolf numbers (Seip, 1992b). A similar situation probably occurs in the southern Selkirks and Monashee mountains where cougar (*Felis concolor*) predation is a major mortality factor for woodland caribou, and cougar abundance is associated with deer numbers (Compton *et al.*, 1990; Simpson *et al.*, 1994).

Moose, deer and elk numbers usually increase in response to the creation of early serai habitats by clearcutting and fires. Increased ungulate numbers may sustain increased populations of predators. There is concern that fragmenting caribou habitat into a patchwork of mature and early seral forests will bring caribou and early seral ungulate species into close proximity, sustain increased predator populations in the area, and thereby lead to an increase in predation on the caribou (Seip, 1991; Stevenson *et al.*, 1994). Consequently, maintaining large, contiguous tracts of old forest is generally seen as preferable to maintaining fragmented patches of mature forest interspersed with clearcuts.

A variety of strategies have been implemented to maintain large contiguous areas of old forest for mountain caribou in southeastern B.C. Many existing parks, especially Wells Gray Provincial Park, provide habitat for a substantial number of mountain caribou. British Columbia is in the process of increasing the amount of parkland to 12% of the provincial area (Anonymous, 1993). Many of the new parks which are proposed for southeastern B.C. will provide additional protection of caribou habitat so that in the future, a substantial proportion of the total mountain caribou habitat will be protected by parks.

Caribou habitat is also being protected in areas outside of parks. In some forest districts, the highest quality caribou habitat has been identified and is unavailable for harvest. The areas have been removed from the timber harvesting landbase and the allowable annual cut has been reduced accordingly (e.g. Prince George Timber Supply Area, Robson Valley Timber Supply Area). Most of the highest quality caribou habitat is high elevation subalpine forest that has relatively low timber productivity so these areas can often be protected with relatively modest impacts on timber supply. In some other areas, forest age class constraints are applied to caribou habitat to ensure that a substantial proportion of the habitat is old enough to provide arboreal lichens. For example, within medium quality caribou habitat in the Robson Valley Timber Supply Area, no more than 1/3 of the commercial timber volume can be harvested every 80 years. If clearcutting is being used, the constraint will ensure that at least 1/3 of the forest is greater than 160 years of age. Alternatively, partial cutting systems could be used to remove 1/3 of the volume from the entire habitat area every 80 years so long as the silvicultural prescription maintains caribou habitat attributes. In some areas, if clearcutting is to be used in areas of caribou habitat, small cutblocks less than 15 hectares in size are recommended (Simpson *et al.*, 1994). Some Forest Districts also require that mature forest corridors be maintained across valleys to provide connectivity between upper elevation areas of caribou habitat.

Those caribou habitat management recommendations are very similar to the Biodiversity Guidebook recommendations for those forest types. If a landscape unit is to be managed with a "*high emphasis*" on conserving biological diversity, the Biodiversity Guidebook recommendations for these forests include:

I) At least 54% of the upper elevation forest should be >120 years of age (i.e. at least 75% of natural levels). Lower elevation forest types that had a greater frequency of natural wildfires have a lower target for old and mature forest retention, but the target still represents 75% of natural levels.

II) No more than 17% of the upper elevation forest should be <40 years of age (i.e. no more than 1.5 times the natural level). More early serai habitat is allowed in lower elevation forests, but the target is still <1.5 times natural levels.

III) Partial cutting and uneven-aged silvicultural systems are preferred in the upper elevation forests to mimic the natural pattern of small disturbances within stands.

IV) If clearcutting is used, a range of cutblock sizes, up to 250 hectares in size, is recommended to mimic the size distribution of natural stand-destroying disturbances in these forests.

V) About 10% of the total area within each cutblock must be retained as mature forest remnants to mimic the structural features left behind by natural disturbances. Those remnants will provide habitat attributes, such as large diameter snags and arboreal lichens, within the regenerating stand.

VI) Mature forest corridors must be maintained to keep stands of mature and old forest connected into a contiguous "Forest Ecosystem Network".

These biodiversity recommendations are intended to maintain a relatively natural age class and patch size distribution wirhin the landscape unit. The stand management recommendations are designed to maintain natural stand structure and habitat attributes such as snags and lichens. The "Forest Ecosystem Network" is intended to partially maintain the contiguous distribution of old and mature forests on the landscape.

By maintaining many of the characteristics of natural forests, it is assumed that relatively natural levels of biodiversity, and relatively natural population levels of all native species will be maintained. In relation to mountain caribou, implementation of these biodiversity recommendations would maintain a landscape dominated by contiguous old and mature forest that would provide arboreal lichens for winter food, and allow caribou to maintain spatial separation from early seral habitats and thereby reduce the risk of predation. Thus, the ecosystem management recommendations provide a useful approach to conserving caribou habitat.

If a landscape unit is managed with an intermediate or low emphasis on biodiversity conservation, the mature and old forest requirement would be reduced (ie. 50% or 25% of natural levels respectively). Moving from high, to intermediate, to low emphasis biodiversity recommendations would increase the timber availablility, but would result in a greater impact on natural biodiversity, and increase the threat to various native species such as caribou.

Northern caribou

Northern caribou inhabit the northern and west-central areas of B.C. (Fig. 1). Historically the distribution was contiguous, but it became fractured during the past century due to the disappearance of caribou from portions of their range (Bergerud, 1978). Habitat studies of northern caribou are presented in Hatler (1986), Cichowski (1993), and Wood (1996). These caribou usually live in alpine habitats during the summer months but use lower elevation lodgepole pine (*Pinus contorta*) forests for at least part of the winter. During winter the caribou feed primarily by cratering for terrestrial lichens. The primary conflict with forest harvesting occurs on the low elevation winter ranges.

The low elevation forest types that provide caribou winter range experienced natural wildfires on average every 100-150 years. Those fires were often thousands of hectares in size. However, wildlfires did not burn 100% of the area, but rather, left small, unburned remnants of mature forest that constituted 5-15% of the total burn area (Eberhart & Woodard, 1987; Delong & Tanner, 1996). Consequently, the natural landscape was a mosaic of large, even-aged stands of pine that regenerated following wildfires. Within those stands there were remnants of older forest that had survived the fires.

Terrestrial lichens were usually destroyed by fires, but recolonized disturbed sites and became abundant in mid-aged to mature stands (Brulisauer *et al.*, 1996; D. Coxson, pers. comm.). Xeric growing sites support abundant terrestrial lichens for hundreds of years (Brulisauer *et al.*, 1996). However, on more productive sites, terrestrial lichens may be abundant in mid-aged stands but are replaced by mosses in older stands and thus require periodic disturbance to be perpetuated (D. Coxson, pers. comm.). Very productive sites are usually dominated by vascular plants and never produce substantial amounts of terrestrial lichens.

Habitat management strategies for these caribou must ensure that sufficient amounts of older forest are maintained to provide terrestrial lichens. However, on sites that naturally undergo a succession to moss cover, periodic disturbances of old stands are required to reestablish lichens. In addition, suitable foraging habitat should be maintained in large, unfragmented patches to keep the caribou spatially separated from early seral habitat where they would encounter increased exposure to moose and wolves.

Forest harvesting within the winter ranges of northern caribou in B.C. has been quite limited until now, but increased activity in those areas is anticipated. In response, a number of strategies have been implemented to protect winter habitat. Habitat for many northern caribou herds is contained within existing and proposed parks. There is an appreciation among Ministry of Parks biologists that maintenance of that habitat may require fire management plans that perpetuate natural wildfire regimes (D. Cichowski, pers. comm.). In areas outside of parks, forest age class constraints have been implemented in some Forest Districts to maintain old and mature forests that provide terrestrial lichens. For example, within caribou winter habitat in the Mackenzie Forest District, 25% of the forest must be older than 150 years. Similarly, in Ft. St. John Forest District 40% of the forest that provides low elevation caribou winter habitat must be older than 100 years. Those areas are available for harvesting, but on a rotation period that is long enough to provide terrestrial lichens for caribou. When harvesting is conducted, large harvest blocks of hundreds or thousands of hectares, offset with similar sized leave areas, are recommended to reduce habitat fragmentation (Cichowski & Banner, 1993).

Again, these caribou habitat recommendations are almost identical to the Biodiversity Guidebook recommendations which are based on mimicking the natural disturbance regime. Within landscape units that are managed with a *"high emphasis"* on conserving biodiversity, the Biodiversity Guidebook recommendations for the forest types that provide low elevation winter habitat for northern caribou vary (depending on the biogeoclimatic subzone and natural fire return interval) as follows:

I) At least 28-39% should be greater than 100 years of age (i.e. 75% of natural levels).

II) No more than 35-50% should be harvested within a 40 year period (i.e. 1.5 times the natural level).

III) Clearcutting with reserves is generally the preferred silvicultural system to mimic the stand stucture produced by stand destroying wildfires that contained unburned mature forest remnants. Generally, about 10% of the total area within each cutblock should be retained as mature forest remnants, similar to the pattern of wildfires.

IV) A range of cutblock sizes is recommended, but the majority should be relatively large (i.e 250-1000 hectares). This size distribution under-represents the frequency of much larger natural wildfires in these forest types, but the objective of mimicking natural patterns was balanced with public concern about large clearcuts.

By providing a relatively natural forest age class distribution, patch size distribution and stand structure, it is assumed that relatively natural levels of biodiversity will be maintained. For northern caribou, implementation of these guidelines would provide a perpetual supply of relatively large patches of mature forest that would provide terrestrial lichens for food, and some spatial separation from early seral habitats where predation risk is probably greater. If a landscape unit is managed with an intermediate or low emphasis on biodiversity conservation, the mature and old forest requirement would be reduced, and the risk to caribou and other native species associated with old forest would be greater.

Roads and disturbance

In addition to the forest management issues discussed above, there are concerns regarding impacts of roads, linear corridors, and disturbance on caribou. Roads and linear corridors clearly provide improved access to caribou for hunters and poachers, but may also increase access for predators. Disturbances such as snowmobiles can displace caribou and force them into more rugged habitats where they probably face increased energy expenditures and mortality risk from avalanches (Simpson, 1987; own obs.). However, these impacts can be quite subtle and almost impossible to demonstrate conclusively with research and monitoring. Although the cumulative effects of small increases in poaching, energy expenditures, vehicle collisions, avalanche deaths, and predation associated with increased disturbance may have a major impact on a caribou population over the years, it may be impossible to definitively show a direct cause and effect relationship. An ecosystem management strategy would assume that because roads, snowmobiles etc. are not part of the natural ecosystem, the more prevalent they become, the greatet the probablility that natural levels of biodiversity will be disrupted. Thus it would be prudent to minimize or prohibit roads and other disturbances in areas where maintaining natural levels of biodiversity, including caribou populations, is a priority, even if there is no conclusive research information that demonstrates a deleterious effect.

Predator control

Predation is often a major limiting factor of caribou populations and predator control can significantly increase caribou survival (Bergerud & Elliot, 1986; Farnell & McDonald, 1988; Seip, 1992b). However, use of predator control to increase caribou or other ungulates to unnaturally high levels is a disruption of natural biodiversity. It may be appropriate to manage predators in areas where society has decided to enhance natural ungulate populations at the expense of natural biodiversity. Also, it may be desirable to manage predators in areas where past human practices have reduced caribou populations, and predator control is to be used to restore natural caribou numbers. However, predator control to increase caribou herds to unnaturally high levels is inappropriate in areas where there is a priority to maintain naturally functioning ecosytems and biodiversity.

A general ecosystem management strategy

The following points outline the basic steps that are required to implement an ecosystem management strategy to conserve biodiversity in managed forests:

I) Delineate planning units that are large enough to allow landscape level planning objectives for age class and patch size to be applied. If the full range of forest age classes and patch sizes are to be maintained within a landscape planning unit it will have to be tens of thousands of hectares in size (B.C. Biodiversity Guidebook recommends 50 000 - 100 000 hectares).

II) Determine the management objectives for each landscape unit. If maintaining a high level of natural biodiversity, including caribou, is the priority, this will usually have a greater impact on timber production. Alternatively, an objective of maximizing timber production will have major impacts on natural biodiversity and caribou. An objective of enhancing early seral ungulates such as moose and elk may have negative consequences for some other components of natural biodiversity, including caribou.

III) Set forest age class and patch size objectives for each landscape unit. If there is a desire to maintain relatively natural levels of biodiversity within a landscape unit, the age class and patch size objectives should be as close to natural values as possible. Meeting other competing resource management priorities such as timber production or moose enhancement may require a significant departure from natural forest characteristics. That departure from natural forest conditions will result in significant changes in natural biodiversity, and an increased risk to caribou.

IV) Use silvicultural systems that mimic the dominant natural disturbances in the area, and retain stand attributes left by natural disturbances. For example, clearcuts with reserves can be used to mimic stand destroying wildfires that contained unburned mature forest remnants.

V) Minimize other habitat alterations which were not part of the natural landscape such as roads, other linear developments, and disturbance.

Fine-tuning ecosystem management guidelines for caribou

Although a coarse-filter ecosystem management strategy should provide suitable habitat conditions to maintain most native species, some species may require additional, more specific management practices to ensure their survival. Similarly, it may be desirable to provide more detailed management practices for species such as caribou that are a high management priority. In either case, however, there is no need to develop a completely new set of management guidelines. Rather, the coarse-filter ecosystem management guidelines simply need to be "fine-tuned" to better meet the needs of those species of special concern.

In areas of caribou habitat, landscape unit age class objectives could be modified to provide more mature forest than is recommended for more general biodiversity conservation (e.g. maintain 100% of natural levels of mature forest rather than 25-75%). Also, the location of mature forest retention within a landscape unit may be targeted towards sites that have the greatest potential to provide caribou habitat. A somewhat larger patch size objective may also be required. As mentioned above, the B.C. Biodiversity Guidebook recommends patch sizes up to 1000 hectares in size within northern caribou habitat. That size may be adequate for most species that require larger patches of forest, but for caribou habitat, a 10 000 hectare patch size mosaic as proposed for northern Ontario (Racey & Armstrong, 1996) may be more appropriate. Similarly in mountain caribou habitat, in areas where partial cutting is not feasible, cutblocks at the upper end of the recommended size range (up to 250 hectares) may be preferred to reduce fragementation effects and access concerns.

Earlier guidelines for northern caribou often recommended small clearcuts, which was inconsistent with the size of natural disturbances in those forests. Further research and understanding has supported a move to more natural sized disturbances to reduce predation risk. This is an example of why one should be cautious if habitat recommendations for a species are very different from the natural habitat pattern.

At the stand level, specialized site preparation guidelines may be appropriate in areas of caribou habitat. Natural wildfires often destroyed most of the terrestrial lichen groundcover whereas careful harvesting and site preparation methods have the potential to maintain much of the terrestrial lichen cover (Harris, 1996). Although an ecosystem management strategy would suggest that site preparation methods should mimic the natural pattern (i.e. broadcast burning), caribou management considerations may favour practices that retain the terrestrial lichen groundcover. Caution is required, however, because on sites where terrestrial lichens are replaced by mosses over time, periodic disturbances may be required to maintain lichens. On those sites, more aggessive site preparation techniques that reduce organic matter accumulations may be required to prevent succession by mosses from replacing lichens in the stand over time. Destroying lichens in the short-term may be necessary to maintain them in the long-term (Schaefer & Pruitt, 1991). This situation is another example of why habitat management recommendations that greatly diffet from natural patterns should be viewed cautiously. Diverging from natural patterns may have unanticipated, negative consequences that only become apparent after further study.

Naturally regenerating pine stands often had dense stocking which probably shaded out much of the lichen cover. It may be desirable to diverge from that natural pattern and use spacing to enhance lichen growth in regenerating stands.

Summary of ecosystem management and caribou habitat

I) Ecosystem management recommendations to conserve biodiversity are based on the assumption that the more closely managed forests resemble natural forest conditions (ie. age class distribution, patch size distribution, stand structure), the greater the probablility that relatively natural populations of all native species will be maintained.

II) Ecosystem management guidelines that have been designed to maintain the full range of native species in B.C. also provide many of the habitat requirements for caribou, and a strong foundation for the development of mote detailed caribou habitat management guidelines.

III) When the impact of a certain habitat alteration is unknown (e.g. linear corridors), and difficult to resolve by research, the most prudent approach would be to assume that maintaining the habitat in a more natural condition is the best strategy to maintain all species.

IV) If habitat management recommendations for a species are very different from natural habitat characteristics, one should be cautious. Diverging from natural patterns may appear beneficial on the surface, but have unanticipated, negative consequences that only become apparent after we have a better understanding of habitat relationships (eg. patch size and predation risk).

V) Detailed understanding of the habitat requirements of individual species, such as caribou, need not be used to develop an entirely new set of "single species" habitat management recommendations, but rather can be used to "fine-tune" ecosystem management recommendations that have been developed to maintain the full range of natural biodiversity.

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Integrating woodland caribou needs and forestry: perspectives of Alberta's forest industry

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Abstract: Much of Alberta's woodland caribou (*Rangifer tarandus caribou*) range outside protected areas is subject to commercial forest management. In this papet, I discuss some perspectives of the forest industry regarding caribou-relared issues. Six foresr companies holding Forest Management Agreements (FMAs) in Alberta wete polled. Fotest managers were most concerned about 2 aspects of caribou management: reductions of annual allowable cut (AAC) that may be necessary to provide for caribou habitat needs; and management of public access. Perceived information gaps fell into 3 categories: caribou demographics (population size, trends and densities); primary limiting factors of caribou populations (including the influence of human activity); and caribou habitat tequirements (including the effects of timber harvesr on caribou habitat). Increased costs associated with consideration of caribou have been incurred at the planning and operational levels. Howevet, those costs have been low, primarily because much proposed harvesr in caribou ranges has been deferred. Costs are expected to increase substantially in the future as timber from caribou ranges is required to meet harvest objectives. Other issues identified included: the desire for an adaptive management approach to caribou-forestry interactions; the need to incorporate natural-disturbance-regime models into forest planning; consideration of the cumulative effecrs on caribou of all industrial and recreational activities; and unmanaged harvest by Firsr Nations people. A list of caribou-related projecrs conducred or supported by forest companies in Alberta during the past 5 years is provided.

Key words: woodland caribou, *Rangifer tarandus,* forestry, forest management.

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Introduction

The woodland caribou (*Rangifer tarandus caribou*) was designated as an endangered species in Alberta in 1985. Since then, extensive natural resource development (forestry, oil and gas, mining, recreation, peat harvesting) has caused managers to become increasingly concerned about caribou populations throughout the province.

Much of Alberta's woodland caribou range outside protected areas is subject to commercial forest management (Fig. 1). Forestry has the potential to alter large areas of caribou habitat through timber harvest and the creation of access routes. To limit potential impacts, the provincial government has required forest companies to implement measures designed to reduce potential impacts to caribou and caribou range. Companies also have recognized the importance of maintaining caribou as a component of the province's ecosystem, and have started programs to learn more about caribou and their habitat.

The forest industry is an important sector that will help to determine the direction of woodland caribou research and management in Alberta. In this paper, I discuss the perspective of forest companies holding Forest Management Agreements (FMAs) regarding caribou-related issues, including perceived knowledge gaps, studies done to fill those gaps, the operational and financial costs of integrating caribou needs into forest practices, and other management-related concerns.

An FMA allows a company to harvest timber on a sustainable basis on a designated portion of public forest land (Alberta Environmental Protection, 1996). As part of the agreement, the company must consider the impact of logging on other forest

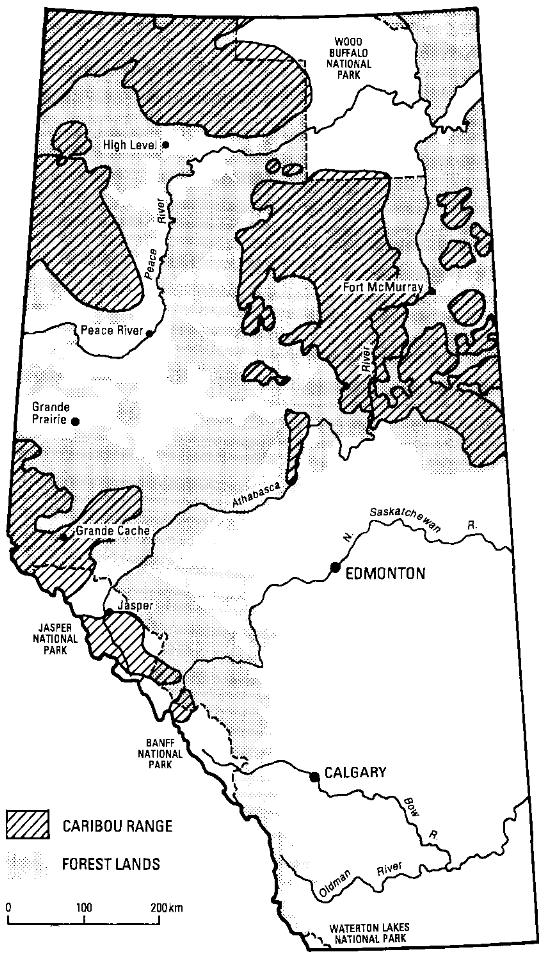

Fig. 1. Caribou distribution and forest lands in Alberta.

values such as fisheries, wildlife, and environmental quality. Maintaining adequate quality and quantity of caribou habitat is one component of that responsibility.

Methods

I sent a questionnaire to individuals responsible for caribou management for 6 forest companies holding FMAs in Alberta. The questionnaire was intended to provide information on the perceptions of forest managers about caribou management and its effects on forest planning and operations. Results were not analysed statistically. All information provided is included. Some answers were edited for brevity or combined with others that were similar, while attempting to retain the substance of the response. Responses under each heading are not necessarily ranked by importance, although those given more than once are listed initially in each category. In some cases, I have added annotation to summarize remarks and to contribute an additional perspective.

Results

Replies to the questionnaire were received from all 6 companies (Appendix 1). Responses are presented below by individual question.

1. Approximately what proportion of your FMA is considered caribou range?

There was a wide range among FMAs in the proportion considered as caribou range:

- 5-10% (*n* = 2 FMAs);
- 30% (*n* = 3 FMAs); and
- 75% (*n* = 1 FMAs).

The proportion of the annual allowable cut (AAC) contained within caribou range may be greater than the proportion of the FMA considered as caribou range because of the reliance of caribou on older-aged stands which have greater timber volumes per area of land than younger-aged srands. Companies with 30% or more of their FMA within caribou range have committed more resources to studies of caribou, but all acknowledge the importance of caribou issues and related investigations.

2. What are the 3 most important issues regarding caribou and forestry in your FMA?

Of the issues identified, the 3 most commonly cited were:

- Potential reductions of AAC (*n* = 3 responses);
- Finding ways to maintain long-term habitat supply (*n* = 4 responses);
- Access management (*n* = 4 responses).

Timber harvest has been deferred in known caribou range by most companies in an attempt to limit potential impacts. Deferrals reduce the effective land base for harvest and may require reductions in the AAC in both the short (annual) and long (rotational) terms. As an alternative strategy, harvest has been reduced in some parts of caribou range to limit habitat change. The reliance of caribou on older-aged stands has the potential to intensify the effects of deferrals or reduced harvest. Reductions in AAC represent additional planning costs, a loss of logs to the mill, and reduced capacity.

Finding ways to maintain long-term habitat supply for caribou included developing a better understanding of: caribou habitat needs; caribou use of merchantable timber stands; and the effects of timber harvest on habitat. Related operational questions included "what harvest patterns are most appropriate?" and "when is it appropriate to apply summer vs. winter logging?"

Roads and associated access generally are recognized as an important impact of natural resource development. For caribou, the intrusion of roads can mean increased hunting, both legal (by First Nations people) and illegal, and habitat fragmentation. There also is concern that compacted snow on trails or plowed roads can make caribou wintering areas more accessible to wolves. How roads are used once they are developed is crucial in determining their impact. Managing access is difficult and can be expensive.

Other important issues included the following points:

- The effects of forestry on large-mammal predator-prey relationships (in Alberta these systems may be complicated, involving up to 7 ungulate species and 6 potential predators);
- The effects on caribou of disturbance associated with development, including logging, oil and gas, mining, and recreational use; and
- Public perception regarding stewardship of caribou and caribou habitat.

In general, there is a concern by forest managers about the level of scientific knowledge available regarding caribou/forestry relationships. Important information gaps are considered below under question 3. Studies are underway to answer some questions (see question 4); however, results and conclusions are slow to be realized.

3. What are the 3 most important information gaps regarding caribou in your FMA?

The answers to this question fell into only 3 categories, including:

- Caribou population size, trends and densities (n = 6 responses);
- Primary limiting factors and how those interact to influence caribou populations (n = 4 responses);
- Caribou habitat requirements (n = 6 responses), including the effects of timber harvest on caribou habitat (n = 2 responses).

There was a consensus that a better understanding of caribou population sizes and trends is crucial. This requirement creates an important dilemma. The success of management efforts ultimately will be judged by the presence or absence of viable caribou populations. However, biologists have been attempting for years, with limited success, to devise adequate techniques for surveying caribou populations under dense forest cover. Population numbers or trends are difficult or impossible to discern (Thomas, 1998). Even the natural variability in caribou population sizes is difficult to determine in many instances. The management goal of maintaining viable populations will be difficult to realize if we cannot understand how management measures affect population change.

In a related aspect, forest companies wish to know what factors are acting to limit caribou populations. Forest managers would prefer to manage those elements over which they have direct control, such as habitat change, disturbance, and access. They have no mandate to deal with factors such as predation and no ability to deal with factors such as climate. However, because most limiting factors (predation, food, climate, insects and parasites, hunting, and human development; Klein, 1991) relate to habitat in some way, it is important that forest managers understand how those factors operate and how they are interrelated. For example, at least one company has changed their cut block design to reduce enhancement of moose habitat, thereby reducing the potential of altering predator-prey relationships.

Every respondent included habitat requirements of caribou as an important knowledge gap. This information is fundamental to understanding the impacts of forestry on caribou. The habitat relationships of woodland caribou have been the subject of systematic study for less than 20 years. In Alberta, the first detailed examination of ranges on provincial lands began in 1979. Other studies have been started since (see question 4, below), but progress has been slow due to the complex nature of caribou habitat selection, the inherent low densities of the animals, and environmental variability. Studies (e.g., Brown *et al.*, 1994; Edmonds, 1988; Stuart-Smith *et al.*, 1997) have shown that due to the wide range of movement and habitat-use patterns exhibited by caribou across the province, basic habitat relationships for each herd should be determined before the results obtained in other areas are applied.

4. What caribou-related projects have you undertaken or funded during the past 5 years to fill those, or any other, gaps?

- Much of the recent research conducted in the province has been related to caribou habitat selection, primarily in response to the information gaps discussed in question 3.

A list of projects supported by forestry companies during the past 5 years is provided in Appendix 2. Several studies based on radio-telemetry and back-tracking have been initiated recently to determine basic aspects of caribou habitat use. Many fundamental questions remain regarding caribou habitat needs at the landscape and stand levels, caribou food habits, influences of environmental variables on caribou habitat selection, and the short- and long-term effects of timber harvest on caribou habitat use.

The advent of regional standing committees has been important to caribou research programs in the province, and all of the FMA holders questioned have been supporters and active participants. The first multi-sector committee was organized in west-central Alberta in 1989 to increase knowledge and communication among industries, government managers, public interest groups and researchers, and to provide a framework for research and information gathering. Formalized standing committees then were formed across the province in the early 1990s, primarily in response to provincial government policy for oil and gas development on caribou range (Alberta Forestry, Lands and Wildlife, 1991).

The standing committees have come to coordinate much of the caribou-related research in the province. Three committees currently are active in separate regions. Recently, the research subcommittees in the northeast and northwest have cooperated to coordinate research efforts.

Participants in the standing committees include representatives of government agencies (wildlife management, forestry and mineral resources), and resource industries (forestry, oil and gas, and pipelines). Other representatives on some committees include other industries (peat extraction, mining), public interest groups, trapper and outfitter organizations, and researchers. Dissatisfaction regarding the committee process was expressed by one respondent. However, the development of a forum that involves most sectors with an interest in the land has been important in obtaining funding, sharing information, reducing unnecessarily repetitive research, and reaching agreements about caribou management measures.

Although much importance was placed on gaining more information about population numbers, population trends, and limiting factors (see question 3), forest companies have undertaken only a few studies to address those issues (e.g., Stuart-Smith *et al.,* 1997). This is largely because the responsibility for population management rests with the provincial government, and forest companies have considered those investigations beyond their mandate. By participating in the standing committees, forest companies will begin to contribute to population studies.

5. How has planning been affected by trying to incorporate caribou needs?

Measures have included:

- Deferral of harvest on caribou range;
- Changes in cutblock sequencing;
- Changes in the timing of harvest to avoid winter ranges or condensing the harvest period to ensure logging is completed before late-winter;
- Increasing cutblock sizes to reduce their attractiveness to moose;
- Development of access management plans; and
- In one case, the development of a specific "caribou protection plan."

To date, these measures have been considered easy to incorporate into planning. Changes in cutblock locations suggested by management agencies late in the review process have caused some complications for at least one company. Harder decisions related to deferrals and reductions in AAC may be yet to come as more is learned about the woodland caribou's need for habitat and space.

One company has started a relatively new approach to timber management on caribou ranges. For the purposes of planning, individual winter ranges will be treated as separate, sustained-yield units (i.e., each range will have its own AAC), with cutting sequences developed to ensure that intact "chunks" of habitat adequate in size and composition for caribou needs are maintained. The approach is in the early stages of development, and other factors such as relative geographic location, vegetation composition, and stand structure, have not yet been integrated. Until the critical characteristics of winter ranges can be defined, planners are designing harvest programs to more-closely resemble the natural landscape patterns of forest stand size, shape, and age.

6. What have the real effects been on operations, and how difficult have those changes been to implement?

All but one company has, at some time, delayed harvest in caribou range on their FMA. On at least one caribou winter range, the second harvest pass has been conducted earlier than originally planned. That strategy was taken to avoid entry into the remainder of the range, and to create a large block of approximately even-aged stands that will be available to caribou as the forest matures. The modification of logging techniques by implementing measures such as selective logging is being considered, depending on the effects of those measures on lichen regeneration trials (see Appendix 2). Implementation of these measures has been considered straightforward.

7. Please describe where additional costs have been incurred as a result of changes to planning and operations due to caribou-related concerns.

There are direct costs associated with measures to integrate caribou needs and forestry. Some areas in which additional costs have been incurred include:

- Active harvest by 2 companies has been stopped by government order;
- Increased annual and long-term planning costs and additional time have been required to accommodate deferrals, to make changes in road and cutblock design, and to identify effective harvest alternatives;
- Movements of additional logging equipment and loaders into the caribou zone has been necessary to ensure harvest is completed during the available operating window;
- Seasonal restrictions have been placed on timber supply due to winter-only harvest;
- Caribou-related research has required direct funding;
- Access management measures have been implemented;
- Additional road access has been built into areas outside of caribou range to replace deferrals;
- Silvicultural costs have increased due to restricted access following the reclamation of roads for access-management purposes; and
- Signs have been developed and installed to inform the public about caribou and the need for road closures.

8. Are there any other issues that you would like to have addressed or resolved with respect to caribou and timber harvest in your FMA?

Other issues that respondents wished to raise included the following points:

- An adaptive-management approach (Walters, 1986) to caribou was considered necessary. There exist no definitive answers about the long-term impacts of timber harvesting on caribou. Therefore, impacts must be monitored and approaches modified when necessary. An important issue arising from the adoption of an adaptive approach is the question of responsibility for the required monitoring. The forest company representative who raised this issue believes that the responsibility is jointly government's and industry's.
- The use of models for forest planning based on natural-disturbance regimes (i.e., attempting to more-closely emulate the natural range of variability of the ages, shapes and sizes, composition, structure, and distribution of forest stands) is being investigated. This approach would allow positive management action before a complete understanding of caribou habitat requirements is developed, and would address forest-management issues such as the conservation of biodiversity.
- Several respondents stressed that the cumulative effects to caribou of all industrial and recreational activities should be considered when developing management plans. They considered that to focus on forestry issues in a vacuum ultimately will be detrimental to the caribou populations.
- One respondent indicated a need for more information on sensory disturbance of caribou and the ability of caribou to habituate to predictable industrial activity.
- One respondent considered access management to be a "Band-Aid" solution, and that education to ensure that the public recognizes the need and role of access management may be a better investment.
- Although recreational hunting of caribou has been prohibited since 1981, caribou still may be harvested, without limit or timing restrictions, by First Nations people. Forest companies recognize that hunting by First Nations could negate other management initiatives.
- One respondent suggested that consideration be given to allowing no further coniferous tim-

ber allocation until issues such as caribou habitat supply are resolved.

Clearly, some of these issues are controversial, but the responses reflect the wide diversity of opinion among forest managers.

Conclusions

The forest industry and provincial agencies alike are concerned about maintaining woodland caribou in Alberta. Forest companies are attempting to find means of incorporating caribou habitat needs into forestry practices without experiencing serious reductions in AAC. Planning and operational costs have been increased by implementing measures to reduce the impacts of timber harvest on caribou and by conducting biological research. Those costs are expected to increase substantially as more is learned about the population biology and habitat relationships of caribou.

Specific concerns of forest companies relate to potential loss of AAC through deferrals or changes to harvest practices within caribou range, such as the alteration of seasonal timing, cut patterns, and rotation length. Access management within operating areas is of particular concern. Applied research projects that are underway relate primarily to caribou habitat requirements. However, forest managers also have a need for information on caribou population status, dynamics and primary limiting factors, all of which are difficult and expensive to study. Limited availability of funds makes research into those aspects more difficult. The formation of regional committees that include a wide range of land users has been important in dealing with that issue by obtaining funding from a range of sources, sharing information, reducing unnecessarily repetitive research, and reaching agreements about caribou management measures.

Woodland caribou occupy a wide range of habitats across the province, leading to a diverse pattern of habitat use and movement patterns. Respondents agreed that the transfer of information directly from herd to herd should not be done uncritically. Although there may be many similarities between populations, variations in habitat types and availability, distribution of other ungulates and predators, and environmental variables such as snowfall can have substantial effects on caribou behaviour.

Forest companies accept that adaptive-management models may be useful in dealing with caribou because many important questions remain unanswered regarding caribou-forestry relationships. If adaptive management is to be applied toward caribou in commercial forests, managers must ensure that proper experimental design and adequate monitoring are included in programs. The relative responsibility between the government and private sectors for that monitoring must be resolved. Some companies also are considering the use of natural disturbance models and cumulative effects analyses as management tools.

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Appendix 1. Questionnaire respondents.

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Daniel Gilmore, Canadian Forest Products Ltd., PO Bag 100, Grande Prairie, AB, T8V 3A3.
Randy Poole, Weyerhaeuser Canada Ltd., PO Bag 1020, Grande Prairie, AB, T8V 3A9.
Gordon Stenhouse, Weldwood of Canada Ltd., 760 Switzer Drive, Hinton, AB, T7V 1V7.
Shawn Wasel, Alberta Pacific Forest Industries Inc., PO Box 8000, Boyle, AB, T0A 0M0.
Bob Wynes, Daishowa-Marubeni International Ltd., PO Bag 2200, Peace River, AB, T8S 1Y4.

Appendix 2. Caribou-forestry projects undertaken by forest companies during the past 5 years in Alberta.

Alberta Newsprint Company

- Habitat suitability index (HSI) model designed to predict the occurrence of lichen on the basis of forest cover and soils.
- Support for the West-central Alberta Caribou Standing Committee to encourage information exchange and to fund research.

Alberta Pacific Forest Industries, Inc.

- Distribution and seasonal movements, including habitat preference and use of recently disturbed sites based on an intensive radio-telemetry program.
- Caribou population dynamics.
- Response of caribou to industrial disturbance.
- Access management and caribou distribution relative to linear corridors.
- Support for the North-east Region Standing Committee on Caribou to encourage information exchange and to fund research.

Canadian Forest Products Ltd.

- Support for the West-central Alberta Caribou Standing Committee to encourage information exchange and to fund research.

Daishowa-Marubeni International Ltd.

- Radio-telemetry studies of caribou to determine caribou distribution and movements.
- Back-tracking and fecal pellet analyses on caribou winter range to assess habitat use patterns.
- Caribou habitat analysis using GIS.
- Peatland classification for caribou habitat analyses.
- Support for the Northwest Region Standing Committee for Caribou to encourage information exchange and to fund research.

Weldwood of Canada Ltd.

- Effects of forest harvesting on lichen growth to assess lichen response after various harvesting strategies.
- Review of caribou habitat supply for west-central Alberta.
- Caribou habitat selection and the effects of logging on caribou distribution as a component of the Foothills Model Forest.
- Support for the West-central Alberta Caribou Standing Committee to encourage information exchange and to fund research.

Weyerhaeuser Canada Ltd.

- Detailed habitat assessments of 3 caribou winter ranges.
- Caribou distribution surveys on 2 winter ranges.
- Caribou habitat selection and the effects of logging on caribou distribution as a component of the Foothills Model Forest.
- Support for the West-central Alberta Caribou Standing Committee to encourage information exchange and to fund research.

The Seventh North American Caribou Conference,
Thunder Bay, Ontario, Canada,
19–21 August, 1996.

Integration of woodland caribou habitat management and forest management in northern Ontario - current status and issues

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Abstract: Woodland caribou (*Rangifer tarandus caribou*) range across northern Onrario, occurring in both the Hudson Bay Lowlands and the Boreal Forest. Woodland caribou extend south well into the merchantable fotest, occurring in licensed and/or actively managed Forest Management Units (FMU's) across the province. Caribou range has gradually bur continuously receded northward over the past centuty. Since the early 1990's, the Ontario Ministry of Natural Resources (OMNR) has been developing and implemenring a woodland caribou habitat management straregy in northwestern Ontario. The purpose of the caribou habitat strategy is to maintain woodland caribou occupancy of currently occupied range in northwestern Ontario. Long-term caribou habitat needs and predator-prey dynamics form rhe basis of this strategy, which requires the development of a landscape-level caribou habitat mosaic across the region within caribou range. This represents a significant change from traditional forest management approaches, which were based partially upon moose (*Alces alces*) habitat management principles. A number of issues and concerns regarding implications of caribou management to the forest industry are being addressed, including short-tetm and long-term reductions in wood supply and wood quality, and increased access costs. Other related concerns include the ability to regenerate foresrs to pre-harvest stand conditions, remore tourism concerns, implications for moose populations, and required information on caribou biology and habitat. The forest industry and other stakeholders have been actively involved with the OMNR in attempting to address these concerns, so that caribou habitat requirements are met while ensuring the maintenance of a viable timbet industry, other forest uses and the forest ecosystem.

Key words: *Rangifer tarandus caribou*, forest management planning, forestry, logging, ecosystem management.

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Introduction

Woodland caribou occur in low densities and a dispersed distribution across all of northern Ontario, within the northern portion of the boreal forest (Rowe, 1972). Some isolated or remnant populations still exist along the islands and shoreline of Lake Superior. In northwestern Ontario, the OMNR has been involved in the development of a woodland caribou habitat management strategy for the past several years. The objective of this strategy is to maintain current woodland caribou range occupancy in northwestern Ontario by sustaining a suitable landscape for the provision of year-round caribou habitat needs. This initiative was undertaken because of the progressive loss of caribou range and habitat over the past century - woodland caribou range has gradually but steadily receded northward since the late 1800's (Darby et al., 1989; Cumming & Beange, 1993). While many factors are likely involved in this range recession, recent range loss appears to coincide directly with the habitat disruption and human disturbance associated with the northward expansion of timber harvesting in the boreal forest. Progress on the development of habitat management guidelines for Ontario, and on the development of a habitat management strategy, have been reported at previous sessions of the North American Caribou Conference (Racey *et al.*, 1991, Racey & Armstrong, 1996).

The forest industry and the OMNR have been gradually implementing this strategy. The practical realities of planning and field implementation focused attention on further issues and questions requiring resolution, within an adaptive management framework. The intent of this paper is to summarize the current status of caribou habitat management within Ontario, outlining major challenges and issues that have arisen, and how they are being dealt with.

Background

The northward recession of woodland caribou range within Ontario has been well documented (Darby *et al.*, 1989; Cumming & Beange, 1993). The current southern limit of continuous caribou range now closely approximates the northern limit of timber management operations in northern Ontario. There is a great variation in topography, drainage, soil conditions, climate and fire patterns between northeastern and northwestern Ontario. Due to this variation, there is substantially greater overlap between the southern limit of caribou range and the area of licensed and actively managed FMU's in northwestern Ontario than in northeastern Ontario (Fig. 1). Because of this situation, the development of a caribou habitat management strategy to integrate caribou habitat needs with those of the forest industry has been focused primarily in northwestern Ontario. Greater emphasis has recently been placed on caribou management in northeastern Ontario, addressing many of the same issues being addressed to the west.

Woodland caribou have been the subject of research and management interests since the 1960's, although that interest has been sporadic and not focused on the development of management plans for the species. Woodland caribou studies essentially began with Simkin's (1965) preliminary report on caribou in Ontario and the habitat studies of Ahti & Hepburn (1976). A considerable amount of woodland caribou research, focused on caribou that summered on the islands of Lake Nipigon, was conducted throughout the 1980's (Cumming & Beange, 1987). Ontario began development of a provincial caribou policy and provincial habitat guidelines in the mid-1980's. There is as yet no provincial caribou policy in place, although a draft policy and draft habitat management guidelines

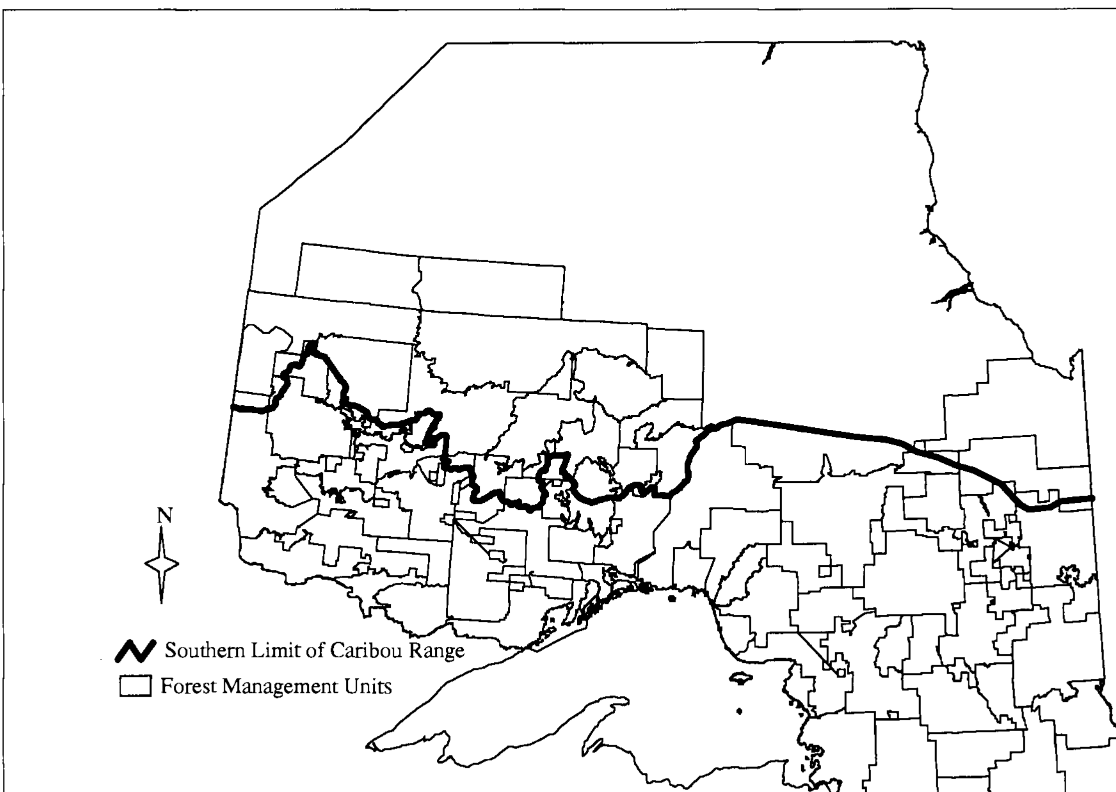

Fig. 1. The southern limit of continuous woodland caribou range in northern Ontario in relation to designated Forest Management Units.

have been developed (OMNR, 1994a), and background information compiled (Darby *et al.*, 1989).

Much of the early information on woodland caribou in Ontario resulted incidentally from surveys of moose. More intensive inventory efforts, focused specifically on woodland caribou distribution and seasonal habitat use, generally began in forested areas during the late 1980's and have continued through the 1990's. Earlier work occurred on caribou in the Hudson Bay Lowlands during the 1970's and 1980's (e.g. Thompson & Abraham, 1994). There is a much more comprehensive inventory and data base for woodland caribou in northern Ontario now than there was even a decade ago (e.g. Smith, Miller & Associates, 1995a & 1995b), although much more needs to be done. There was no consistent or coordinated attempt to address caribou habitat needs within Forest Management Plans until the late 1980's and early 1990's. Habitat inventory information was limited or lacking, and there was no corporate direction on how to address caribou habitat needs. Local staff did attempt to address specific known caribou habitat values with what they considered to be appropriate protective prescriptions; in many cases these were unsuccessful (eg. Brousseau, 1979).

At the same time that there was increasing interest in addressing woodland caribou needs within Forest Management Plans, changes were occurring within the timber management planning process to better ensure integration and environmental protection. After several years of hearings and input, the report on the Class Environmental Assessment for Timber Management on Crown Lands in Ontario was delivered, with a total of 115 terms and conditions (Ontario Environmental Assessment Board, 1994). Later in 1994, the Crown Forest Sustainability Act was enacted to "provide for the sustainability of Crown forests", where sustainability was defined as long-term forest health (Government of Ontario, 1994). One of the principles identified for forest management planning was that forest practices should, where feasible, "emulate natural disturbances and landscape patterns". These two events were followed by the development of a new Forest Management Planning Manual for Ontario (OMNR, 1996), and a number of associated manuals and guidelines. These were developed to ensure that forest planning and operations are conducted in a manner that attempts to sustain the forest ecosystem. Woodland caribou needs were specifically addressed in the Forest Operations and Silviculture Manual (OMNR, 1995), which provided for woodland caribou habitat guidelines to be applied where "traditional forest management practices are likely to reduce permanently the amount of suitable habitat for woodland caribou and their population in that particular district". All of these developments took place against the broader international backdrop of international agreements to conserve biodiversity, movement in both the public and private sectors towards ecosystem-based approaches to resource management, and progress on the environmental certification of the forest industry (e.g. Canadian Council of Forest Ministers, 1995).

The caribou habitat management approach is a significant departure from past management practices within caribou range, which saw the broad designation of moose as the featured ungulate species, and the application of the moose habitat management guidelines (OMNR, 1988). Ontario's "Management Guidelines for Woodland Caribou Habitat" (OMNR, 1994a) have the objective of sustaining a suitable landscape for the provision of year-round caribou habitat needs. Caribou habitat must be managed on a very large temporal and spatial scale, spanning the entire rotation age of the forest and across the entire FMU. Very generally, the caribou habitat guidelines require that the forest be managed at the broad landscape level, while still considering site-specific habitat needs. Thus, currently used winter habitat, calving sites and travel corridors are identified and protected within a broader forest mosaic. This mosaic consists of large blocks of mature, undisturbed habitat that can provide a combination of winter and summer habitat, escape cover, and areas of low moose and wolf densities, as well as adjacent blocks of young, regenerating (harvested or burnt) habitat that can provide future caribou habitat. This mosaic pattern is intended to crudely emulate the natural disturbance patterns that result from wildfire, rather than the more progressive, continuous cutting of smaller harvest blocks often associated with traditional timber harvesting. While it is not appropriate to specify rigid minimum or maximum sizes for these deferred and harvested blocks, they would generally be in the range of 100 square km; however this is not a continuous clear-cut. It is also necessary to integrate plans so that caribou habitat needs are considered across several adjacent FMU's. As well as providing for suitable habitat, the caribou habitat management guidelines are intended to maintain a predator-prey balance on the landscape similar to that which occurred before timber harvesting. The objective is to not significantly enhance the quality of moose habitat, which could lead to increasing numbers of moose, corresponding increases in gray wolf (*Canis lupus*) densities, and finally, increased predation levels on caribou by wolves. The rationale and basis for these guidelines have been described in detail by Racey *et al.* (1991).

The Northwest Region of the OMNR has been developing a regional caribou habitat strategy. Although no provincial policy and approved guidelines are yet in place, resource managers believed it was necessary to either begin to consider caribou habitat needs within forest management plans, or accept that there would be the further predictable and permanent loss of caribou habitat, and a corresponding continued recession of caribou range northward. Progress on the initiation of this strategy was reported at the last North American Caribou Conference (Racey & Armstrong, 1996). In that paper we reported on the initiation of the strategy, major issues raised through public consultation, and steps that were being taken to address these issues. The balance of this paper will report on further progress that has been made as the strategy has been implemented, and as we have attempted to integrate caribou habitat requirements with the forest management planning cycle and forest industry constraints.

Current status and issues regarding implementation of the caribou habitat strategy

Timber management implementation

Caribou habitat mosaics have been developed for each actively managed FMU within caribou range in northwestern Ontario. In most cases, these mosaics were developed jointly by OMNR biologists and foresters, and company foresters, although the degree of involvement of company representatives varied. These mosaics identify the general leave and disturbance blocks across the landscape, and the projected period of harvesting (20 year harvest periods) throughout the rotation age of the forest. Plans for ten FMU's that were approved during the 1994-97 period have considered caribou habitat needs during their development, and plans for the remaining three units within caribou range will be finalized in 1998.

The Northwest Region of the OMNR issued "Interim Direction" in 1994 to guide forest managers in considering caribou habitat needs until the final regional strategy and/or guidelines are approved and in place (OMNR, 1994b). This directed resource managers to manage for woodland caribou as "locally featured species" in FMU's within caribou range, and to manage in such a way so as to avoid adversely affecting caribou habitat. Harvest areas were allocated with a caribou habitat mosaic in mind (i.e. within the larger harvest or "disturbance" blocks), and with specific caribou habitat guidelines applied for the protection of winter habitat, calving sites and travel corridors. Moose habitat is not specifically managed north of the caribou line, except in local areas where there is high potential for moose production and very limited capability for caribou habitat. Harvest blocks are larger than under the moose guidelines, and are consolidated within larger "disturbance blocks" consistent with the overall caribou mosaic. Timber allocations avoid large deferral or "leave" areas within the mosaics, which provide for current and/or future caribou habitat. The "Interim Direction" was issued to ensure that current high value caribou habitat and future caribou habitat management opportunities were maintained. In all FMU's, the caribou mosaic has been considered but there has been variability in the degree to which it has been actively applied. In some cases, the mosaic formed a background check to ensure that the harvest pattern was consistent with the mosaic. In some other units the caribou mosaic is being more directly applied, with strategic decisions on harvest areas, access networks, and unharvested areas being made on the basis of the mosaic.

Interest in woodland caribou has increased recently in northeastern Ontario, where proposed logging areas are beginning to overlap more with areas of known caribou occurrence. A caribou habitat strategy is currently under development for northeastern Ontario. Habitat conditions differ markedly between northeastern and northwestern Ontario, and it is likely that the final habitat management strategies will be considerably different for the two regions.

Wood supply

Potential impacts of the caribou management strategy, and in particular the application of the caribou habitat mosaic, were the most commonly raised concerns from the forest industry. A study was undertaken to compare available wood supply under a caribou mosaic approach to that under a more traditional timber harvesting approach (i.e. application of moose habitat guidelines within a progressive cut approach) (Aldridge, 1995). There were negative impacts of the caribou guidelines on available wood supply over the first rotation period of the forest: i) a reduction of approximately 23% in the sustainable conifer harvest as compared to the benchmark scenario, and ii) an increase in the distribution of balsam fir (*Abies balsamea*) mixedwood forest units over time due to increased (deferral) mortality and natural succession (Aldridge, 1995). The benchmark case considered land base reductions due to riparian reserves and expected quantities of inoperable areas.

These results must be carefully interpreted. Current management direction to more closely emulate natural disturbance patterns (e.g. Government of Ontario, 1994), and to adopt an ecosystem-based approach to resource management, will clearly place spatial and temporal constraints on the landscape even in the absence of caribou management. Aldridge (1995) concluded that the wood volume reduction that can be attributed specifically to caribou management will be less than the 23% indicated by this study. These results suggest wood supply losses can be reduced by careful analysis and refinement of caribou habitat mosaic options. In fact, participants in this study concluded that "thoughtful mosaic development can be one of the most significant steps in mitigating any reduction in wood supply, provided the mosaic is still being driven by the biology of woodland caribou" (Aldridge, 1995). This experience has been affirmed by experience in other FMU's, which has shown that the impacts can be substantially reduced by careful and thoughtful placement of mosaic blocks and harvest schedules, while also considering landscape characteristics such as landforms, disturbance history, and forest unit distribution (J. Mackenzie, pers. comm.). Wood supply impacts will clearly vary with the age class structure and species composition of the forest, with greater impacts in older-aged forests and forests with a heavy preponderance of shorter-lived species. Deferring harvest areas for an extended period beyond the normal operable life-span of the stand results in reduced stand volumes as trees decay and die. Wood supply impacts also appear to increase in FMU's which have a longer history of harvesting and access development; there are fewer options for the deferral of large habitat tracts, and mature trees that were not cut during the same period as the rest of the harvest block are not available to harvest during the deferral period (J. Mackenzie, pers. comm.).

Wood supply impacts have also been examined from a regional perspective (McKenney & Nippers, 1996). Implementing a form of spatial adjacency requirements, such as with the caribou mosaic, was estimated to decrease the wood harvest values by 16-32% of the "unconstrained" value. There were also implications to longer term wood supply; harvest targets did not appear to be achievable beyond 50-60 years without any constraints, and beyond 30 years with caribou habitat constraints. Intensive silviculture, although expensive, was recognized as a key to reaching harvest targets.

In both studies, the reduction in projected available wood supply was likely an over-estimate. The benchmark case was determined aspatially, where every stand in the FMU could be theoretically considered for harvest at any time regardless of spatial and operational constraints such as access, adjacent stands or minimum area.

Road access costs

The forest industry has also raised concerns about access development costs (Racey & Armstrong, 1996). The spatial element of the caribou mosaic requires that road development programs be accelerated to bypass some deferred blocks of mature timber and to access identified harvest blocks. The concern is that this may have an associated increased cost, further compounded by the fact that road construction costs cannot be subsidized by harvesting wood from leave blocks that the road must bypass. There were further concerns related to road maintenance costs - a larger primary road network may be required than under a traditional harvesting pattern, although roads within identified future winter habitat blocks will likely be abandoned and regenerated soon after harvest. Road access costs remain a significant issue with the forest industry, but as yet there have been no detailed projections or estimates of additional costs that may be incurred by the application of the caribou mosaic. The regional analysis of wood supply tradeoffs suggested that road costs may not differ greatly among various management scenarios (McKenney & Nippers, 1996). The actual costs will depend on the way in which the caribou guidelines are implemented regionally. If portions of the region were harvested more heavily in some decades, with wood flow agreements between companies, then road costs would not necessarily be higher. However, road costs will likely be higher if companies are restricted to obtaining their entire wood volume from within their own management units.

Silviculture and forestry

Considerable use has been made of the Forest Ecosystem Classification system to aid in identifying and regenerating high value caribou habitat (Racey *et al.*, 1989; Morash & Racey, 1990). Two issues have been raised regarding the ability of resource managers to successfully regenerate winter caribou habitat: i) the regeneration of lichen in second growth forests, and ii) evidence of caribou re-use of second growth managed forests as winter habitat. Lichen sampling at a number of mature stands, cutovers and burns showed that cutovers that formerly supported lichen-rich forest are likely to regenerate to similar conditions (Harris, 1992). Residual *Cladina* spp. fragments often survive in the cutover after harvesting, and biomass recovery may actually be more rapid after logging than after a fire due to the presence of this residual lichen. Caribou use of a second growth logged forest has been documented approximately 40 years after harvest (Racey *et al.*, 1996).

A number of additional silvicultural issues remain to be addressed. A significant concern relates to the potential increase in the hardwood component, at the landscape level, after logging. A significant increase in the proportion of hardwood and mixedwood stands may decrease the quality of caribou habitat and increase the suitability for moose production, ultimately leading to changes in the predator-prey balance. This is of special concern along the southern limit of caribou range, where moose densities may be higher and where there will be less opportunity for caribou to re-colonize young stands that are currently unsuitable. In some instances herbicide treatments will likely be necessary to control hardwood regeneration. Efforts can also be made to modify harvesting and silvicultural practices to control hardwoods in other ways. The harvesting or "highgrading" of conifers within mixedwood stands is also of similar concern because of the potential for conversion to hardwoods.

Remote tourism impacts

Some concerns have also been raised by the remote tourism industry. Some outfitters perceive that implementation of the caribou habitat guidelines will have impacts in two major areas - larger cut sizes and the increased development of road networks. The concern about cut size relates to the potential negative aesthetic impact of larger cuts on remote tourism guests. A Remote Tourism Decision Support Model was used to conduct a preliminary evaluation of this concern, comparing the aesthetic implications of implementing moose and caribou habitat guidelines (Line & Racey, 1997). Preliminary results indicated that the evidence of logging itself has the major impact on tourist aesthetics and user preferences, with little difference between the moose and caribou guidelines. Remote tourism clients would clearly prefer outposts with no evidence of logging. Thus it appears that some criticisms by the tourism industry may reflect more general concerns about logging, rather than concerns specifically about caribou habitat management. In this study large shoreline buffers, such as those that could be used around calving lakes, were effective in minimizing the negative perceptions of logging activity. Over the rotation age of the entire forest, the caribou guidelines may actually have slightly less effect upon aesthetics than the moose guidelines, primarily because logging would occur in a more restricted time period, and then not occur for an extended period of time.

Another tourism issue raised was the potential for accelerated development of an access road network, and the possible earlier construction of logging roads near remote tourism facilities. There is a related impression that the caribou mosaic is now forcing roads into previously remote areas. On the short time scale, this may be true. In other situations, remote tourism facilities within a harvest deferral block may maintain their remote status much longer than under a conventional logging strategy. However, all licensed FMU's are intended to be accessed and harvested by the forest industry over time, so the net effect of the caribou guidelines may be to accelerate access to some specific portions of the unit earlier than under a more traditional "progressive road construction and harvest" scenario. This issue ultimately points out the need for strategic access road planning for each FMU, to ensure that access roads are planned properly to have the least impact on the tourism industry and other forest uses, over the entire rotation age of the forest.

Moose management implications

One of the objectives of the caribou management strategy is to reduce the enhancement of moose habitat potential after logging, in order to avoid increases in predator numbers. The intent is to not enhance habitat for moose to the degree that would occur with application of the moose habitat guidelines (OMNR, 1988). This objective has been interpreted by some members of the public, including some hunters, as managing "against moose", with the perceived goal of a reduction or even the elimination of moose populations. Resource managers generally believe that moose habitat potential will still increase after logging even under the caribou guidelines, although the increase will not be as great as if the moose habitat guidelines had been applied.

Knowledge base

Gaps in knowledge base identified during public consultation included incomplete information on woodland caribou populations, habitat use and predator-prey relationships. In response to these concerns, and to provide more detailed information to Forest Management Plans, a radio-collaring project was undertaken across northwestern Ontario. Fifteen woodland caribou were captured and equipped with ARGOS satellite collars during 1995 and 1996. This study is continuing, and further animals are being captured and fitted with collars. The project included university research partners to broaden its scientific basis and applications (Hillis *et al.*, 1998). A considerable amount of information directly relevant to forest management planning has already resulted from this study, and is being applied. The large-scale movements of caribou observed in this study have reinforced the need to consider caribou management at the landscape level, rather than the stand or working circle level.

Increased emphasis is being placed upon habitat inventory and distribution surveys , including winter habitat surveys and summer calving site surveys (Timmermann, 1993a & 1993b). Woodland caribou continue to be the species with the highest priority information needs for forest management planning across the northwest.

A comprehensive bibliography of caribou related information for northern Ontario, with emphasis on northeastern Ontario, has been developed (Smith, Miller & Associates, 1995a & 1995b).

Public education and awareness of caribou occurrence and biology continues to be an area where more effort is required. There has been a gradually increasing public awareness of the presence of woodland caribou in northwestern Ontario, and of their specialized life history and habitat requirements. Forest industry staff have become much more familiar with caribou habitat requirements as they have attempted to address caribou habitat concerns in forest management planning, incorporate caribou mosaics into harvest allocation decisions, and deal with operational harvest and silvicultural issues related to caribou management. Woodland caribou have featured prominently in forest management planning open houses, another mechanism for increasing public awareness and understanding.

Stakeholder advisory panel

There continues to be both some misunderstanding and some concern about the basis for and application of the caribou habitat management strategy. At the same time, there has been no public consensus on the best approach to caribou management; for example, some stakeholders clearly want caribou to be protected but have concerns with the management strategy, while others have less concern about caribou conservation but are very concerned about specific aspects of the strategy that could impact upon their use of the forest (see Racey *et al.*, 1996).

An advisory panel was established to review the strategy and make recommendations on improvements and implementation. This panel had regional representation from all major forest client groups, including both the pulp and paper and the lumber industry, tourist outfitters, anglers and hunters, environmentalists, naturalists, trappers, labour and local citizens. Their discussions and recommendations took place within the context of three "givens":

i) maintenance of caribou populations within current range;

ii) maintenance of viable forest-based industries; and

iii) consideration of the principles of ecological sustainability and forest health.

A series of four facilitated workshops was held at various locations across northwestern Ontario during 1995 and 1996.

While this group could not achieve consensus, they did make a number of very valuable recommendations in their final report (Greig & Duinker, 1997). Of particular significance were recommendations on the structure of a regional caribou management strategy. These included components on communications and education, increased knowledge and awareness, decision-making protocols, habitat management, other (non-habitat) management considerations, and adequate support for implementation. This report will play an important role in the future development of the caribou strategy.

A giant experiment?

A recurring criticism of any proposal to manage caribou habitat is that this is in effect a "giant experiment" that has not been tested before, and the success of which will not be known for several decades. This same criticism can similarly be directed at other past approaches to wildlife habitat management within the forest management planning process, such as application of moose habitat guidelines. It can also be argued that past management efforts, namely sequential logging and application of moose habitat guidelines to provide a fragmented habitat, have also been an experiment with a clear result - the loss of caribou from previously occupied range.

This dilemma was highlighted eloquently by Sample (1994) in an essay on the challenges of sustaining forest ecosystems: "... we don't yet - and may never - have the scientific knowledge to maintain or restore all the important pieces of a complex forest ecosystem... 'adaptive management' means we are all part of an immense, high stakes experiment, the outcome of which will remain unknown for the foreseeable future ...".

The criticism of a "giant experiment" can not be completely refuted to the satisfaction of those concerned. As for other forest management guidelines, this management strategy has been based upon a substantial foundation of scientific literature and a knowledge of local (i.e. Ontario) caribou biology. However the reality is that it will be several decades before the success of the caribou management program can be completely assessed. What is important is to monitor and evaluate shorter-term results within an adaptive management framework, so that refinements and improvements can be made to the program as new information is obtained. This is the only reasonable option to consider where timber harvesting is currently underway within caribou range - take action now, and modify as scientific knowledge and management information improves.

Conclusion and future direction

The issues associated with implementation of the caribou habitat management strategy in northwestern Ontario are many. However, significant progress is being made in many areas, and caribou habitat needs are being given more rigorous consideration in forest management planning and operations.

Resource management within Ontario is being undertaken more and more within an ecosystem management context. Caribou habitat management will continue to be important, but habitat needs will be addressed within a broader ecosystem framework that attempts to emulate natural disturbance patterns. This approach is very consistent with the caribou mosaic approach. Spatial and temporal constraints on timber harvesting can be expected to result from any application of ecosystem management approaches, whether or not caribou needs are specifically addressed.

A caribou strategy is still seen as very important, to address and integrate the variety of related habitat and non-habitat issues that affect caribou. Efforts must continue to be made to find ways to address the concerns of and reduce the impacts on the forest industry and other users, without loss of caribou range. For example, greater involvement of the forest industry in the initial stages of mosaic development will help to reduce wood supply impacts.

Woodland caribou are a key component of the fauna of the northern boreal forest in Ontario, and maintenance of caribou populations and range is critical to any biodiversity conservation strategy in the region. There will continue to be challenges to implementing any caribou strategy that requires significant changes to traditional timber harvesting practices. However, Ontario resource managers believe it is feasible to achieve the objective of maintaining caribou within their currently occupied range within the managed forest.

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The Northeast Region Standing Committee on Woodland Caribou (NERSC): an example of a co-operative management partnership

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Abstract: This paper describes the history and current status of NERSC (Northeast Region Standing Committee on Woodland Caribou), a government/industry partnership established to address issues related to industrial developmenr and the conservation of woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberra. In mid 1991, NERSC was established with broad participation from the oil and gas and forestry indusrries and relevant government agencies. Its ptimary role has been as an advisory body to the government through the regional environmental resource management committee. Since its inception, it has become an open forum for the annual review of industrial operating guidelines based on adaptive management. NERSC has been highly successful at attracting financial support from various sponsors and co-ordinating appropriate research and monitoring programs. Key achievements include: 1) greatly enhanced understanding of problems, issues and positions among its diverse membership related ro resource development and caribou management; 2) greatly enhanced delineation of imporrant caribou habitats, and improved understanding of population status and limiting factors; 3) modified and more effective land use straregies; and 4) a recognized collaborative partnership.

Key words: *Rangifer tarandus caribou*, oil and gas industry, forestry, industrial development, environmental impacts, mitigation.

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Introduction

The distribution of woodland caribou (*Rangifer tarandus caribou*) in North America has shrunk substantially since European settlement (Bergerud, 1974). Various causes have been suggested and debated, but it appears likely that human activities such as logging, agriculture, infrastructural development and settlement have generally been contributing factors. In Alberta, sport hunting for caribou was ended in 1981 due to concerns that the population was declining. Extensive oil and gas development throughout the 1980s, along with major commitments of timber, heightened concern and created an environment in which government agencies felt obliged to adopt a more restrictive posture towards regulatory approvals.

The primary emphasis was on reducing mid- to late-winter disturbance by placing timing restrictions on industrial activities in known caribou ranges. Other measures included limiting the usability of new seismic lines for public or predator travel by "rolling back" woody debris and reducing snowplowing, line widths, lines of sight, etc. Industrial operators typically saw these restrictions as onerous and costly, resulting in numerous disagreements. In 1991, the Alberta Government approved a "Procedural Guide for Oil and Gas Activity on Caribou Range" (Information Letter 91.17) which established a policy framework allowing for a more constructive approach. Its most important principles were:

1. Industrial development could occur on caribou range, provided that the integrity of the habitat was maintained to support its use by caribou.
2. Government and industry should co-operate in finding and applying solutions which satisfactorily addressed the concerns of both parties. In particular, regionally-based committees should be established to provide a forum for moving forward.

Formation of NERSC

Following a series of preparatory meetings and discussions in 1991, NERSC (Northeast Region Standing Committee on Woodland Caribou) was formally established with a five-year mandate to be an advisory body to the regional environmental resource management committee. Its original members represented eight oil and gas companies, one forestry company and six government agencies. Its objectives were:

1) to foster co-operation between government and industry.
2) to share information on environmental and industrial needs.
3) to identify issues, define problems, and seek resolution.
4) to recommend effective and practical operational guidelines.
5) to develop area-specific plans to achieve caribou conservation while meeting the needs of industry.
6) to identify and address research and information priorities.

NERSC is co-chaired by one industry representative and one government (wildlife agency) representative. Typically, it has met twice per year. Its central focus has been on considering advice from various subcommittees and making recommendations regarding operational guidelines for the upcoming winter field season. Decision-making is by consensus, and recommendations are brought forward to the government environmental resource managers' committee for adoption and implementation.

Achievements

NERSC has been considered a significant success by its participants in three particular areas: 1) research and information acquisition; 2) communication and information sharing; 3) co-operation and improved understanding among its members.

1) Research

The most important issue for NERSC has always been the search for effective, efficient operational guidelines. The rules in place prior to 1993 had focused on terminating industrial activity in identified caribou ranges after January 15 in order to minimize mid- to late-winter disturbance. Debate on the reasonableness of this approach demonstrated that new information from field research would be required to justify changes. Work of this type, in turn, would cost a significant amount of money. NERSC established a funding subcommittee to gather and manage funds, and a research subcommittee to priorize and oversee research activities. Since its inception, NERSC has been able to attract a total of $1,200,000 for research related to woodland caribou. The source of these contributions has been roughly: industry (54%); Alberta government (16%); NSERC and other funding agencies (30%); non-governent organizations (<1%).

Major research initiatives have included: 1) a study of caribou behaviour in response to disturbance from simulated seismic exploration (Bradshaw, 1995); 2) habitat selection by caribou, as determined by radio-telemetry (Bradshaw *et al.*, 1995); 3) an examination of population structure and status in relation to different landscape types (Stuart-Smith *et al.*, 1997). In addition, work is currently underway on habitat use by moose (*Alces alces*), wolves (*Canis lupus*) and caribou in relation to roads and seismic lines in caribou range.

Taken together, these and other information-gathering efforts have resulted in: much more precise caribou range maps for northeastern Alberta; a better understanding of disturbance effects and population status; a significant relaxation of timing restrictions (to March 1).

2) Communication

NERSC has made a point of keeping its members and all other interested parties informed of its activities and achievements. It produces an annual newsletter, an occasional research newsletter, and has produced two pamphlets, an internet home page, and three videos for general public use. Presentations and posters have been provided at conferences and other functions, and information sessions have been held with senior company and government officials. NERSC meetings have been open to non-members, and membership itself has expanded to include representation from the horticultural peat industry and several additional energy and forestry companies.

3) Co-operation
The most significant achievement of NERSC is that it has provided a forum for co-operative problem solving for government and industry. In its five-year history, NERSC has seen the number of conflicts greatly diminished and replaced by a significant level of trust and openness amongst its members. Discussion has been candid and problems have usually been addressed directly. Most members have been impressed by the commitment which has been demonstrated by the whole membership in continually moving towards workable solutions. At the end of its five-year mandate earlier in 1996, the membership agreed that NERSC had been a substantial success and that it should be continued to the end of 1999.

Challenges

Even though NERSC has so far been seen as a positive effort, it has not been without difficulties. These include:

1) Time commitment
NERSC relies on consensus decision-making and requires thorough consultation and communication between many individuals representing numerous agencies and interests. This requires what frequently seems to be an inordinate amount of time to get things done. Although this can be a source of frustration, it has to be kept in perspective. The alternative would likely be a similar amount of time engaged in repetitive conflicts without the benefit of new information or productive discussion. Most NERSC members seem to have reached similar conclusions, since they frequently display a surprising level of commitment to the whole endeavour.

2) Compliance
NERSC has focused on developing practical, effective operating guidelines to accomodate the needs of woodland caribou with those of industry. Even though all members are involved on an annual basis in reviewing and ratifying these guidelines, not all companies have demonstrated an equal commitment to applying them conscientiously at all times. This has strained the fabric of NERSC from time to time, but it has also brought out one of its strengths. NERSC is an advisory body with no power to enforce compliance. However, peer pressure from within its tanks has frequently been successful in bringing things back into line and maintaining a level playing field for all operators. From a government perspective, this has been one of the more surprising and gratifying features of the whole experiment.

3) Access management
Access management was recognized as a priority even before NERSC's establishment. More access encourages more poaching and aboriginal hunting, more vehicle collisions and more disturbance. Although the guidelines call for effective access management as a key component of industrial operations in caribou range, it has never been easy or straightforward to achieve this goal. Native and non-native members of the public typically resent restrictions on their use of Crown land, and frequently ignore signs, gates and other access management measures. In addition, there is a real reluctance to create new rules and restrictions, particularly if strong public support cannot be demonstrated. NERSC has not found a simple solution, (it is not alone in this regard), but it has now recognized this as its most pressing challenge.

4) Funding
Although its ability to fund and conduct research has been one of NERSC's most notable successes, it is now at a point where its members, particularly on the industrial side, are expressing a growing reluctance to continue contributing money at previous levels. The typical concern is that NERSC might become simply a source of funds for graduate students and other researchers, and that research must bear some clear relation to solving the problems of the NERSC membership. These are recognized as legitimate concerns, and steps are being taken to ensure that the research program, and its required funding, are understood and supported by the members.

New directions

1) Research program
Several new developments are changing the research program. First, it has recently been amalgamated with the research program of the Northwest Region

Standing Committee, so that there will be a co-ordinated approach and more efficient use of resources across the boreal caribou range of Alberta. Second, a co-ordinator has been hired under an industrial post-Doctoral fellowship program to: i) co-ordinate the amalgamated research programs; ii) conduct research; iii) manage the research budget; and iv) become a central source of information regarding the research program and its budget.

It is too early to tell how this will work out, but these measures were adopted to address several concerns, including: potential duplication of effort between two regions; confusion regarding status of individual projects or of the overall direction of the whole program; and excessive demands on a few individuals to manage large budgets "in their spare time."

2) Community participation

In response to the five-year review by NERSC of its objectives, access management was identified as a priority area which had not been successfully addressed. To meet this challenge, a new subcommittee has been created with a mandate to explore ways of developing direct involvement in NERSC by aboriginal communities and other stakeholders. This initiative has just now started, so it is impossible to provide more details. It is likely that any successful expansion of NERSC beyond its traditional membership (government and industry) will fundamentally change it in ways that cannot be predicted. It is also likely (and desirable) that stakeholders from the general public will be interested in more than access management.

Summary

In summary, the 5-year NERSC experiment has achieved some significant successes, especially in developing understanding between government and industry and in developing co-operative approaches to solving problems. Following a review of its mandate, the members agreed that it had been substantially worthwhile, and felt that it was worth continuing for another five years.

There have been stresses and strains, but the overall conclusion is that this partnership approach has proven highly beneficial to its members, especially in contrast to the confrontational approach which preceded it.

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Developing a woodland caribou habitat mosaic on the Ogoki-Nakina North Forests of northwestern Ontario

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Abstract: The Ogoki-North Nakina Forests consist of (10 638 km^2) unroaded boreal forest approximately 400 km northeast of Thundet Bay, Ontario (lat 50°- 51°31'N, long 86°30'- 89°W). Woodland caribou (*Rangifer tarandus caribou*) inhabit discrete portions within these forests based on minimal current and past historical data. As part of the Forest Management Planning process, for the period 1997-2097, a woodland caribou habitat mosaic has been developed to cootdinate present and furure foresr management activities with the retention and development of current and furure woodland caribou habitat. Several criteria including, past fire history, forest structute, age, species composition, proximity to current road access and location of existing and potential caribou habitat, helped identify and delineate 50 mosaic harvest blocks. Each harvest block will be logged in one of five 20 year periods over a 100 year rotation (1997-2097). The harvest blocks have been developed to simulate a pattern of past wildfire history in an area that has not been subjected to past forest management activities, while managing for woodland caribou, a locally featured species.

Key words: forest management planning, harvest blocks, Canada.

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Introduction

The Ogoki-Nakina North Forest (10 638 km^2 of largely unroaded boreal forest) is located 400 km northeast of Thunder Bay in the northwest region of Ontario (Fig. 1). Sustainable Forest Licences (SFL) for both forests have recently been awarded to Long Lake Forest Products Ltd. Mature and over mature coniferous species, primarily black spruce (*Picea mariana* Mill), and jackpine (*Pinus banksiana* Lamb) occupy 87% of the productive forest land base. Both species will supply fibre to a spruce/pine/fir dimensional lumber mill in Longlac and a "Small Wood Maximizer" mill in Nakina Ontario.

The Ogoki Forest was first established in 1974 and was licenced to Kimberly Clark Forest Products Inc. as a Forest Management Unit. The first 20 year management plan (1986-2006) was prepared in accordance with the Timber Management Planning Manual for Crown Lands in Ontario (OMNR, 1985).

The Nakina North Forest was originally part of the Nakina Forest established in 1985 and licenced

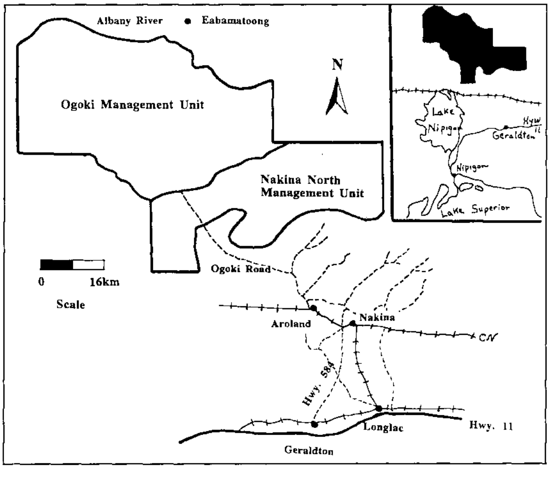

Fig. 1. Location of the Ogoki- Nakina North Forests in northwestern Ontario.

to Kimberly Clark Forest Products Inc. under a Forest Management Agreement (FMA). A SFL was issued to Long Lake Forest Products in March 1996 and the current unit contains 382 132 ha of land and water.

Long Lake Forest Products Ltd. is currently preparing a Forest Management Plan for both the Ogoki and Nakina North Forest in accordance with the new Forest Management Planning Manual for Ontario's Crown Forests (OMNR, 1996). The plan will be rewritten and updated every five years for subsequent 20 year periods. Included under signed terms and conditions is a comprehensive renewal and maintenance program.

Both moose (*Alces alces*) and woodland caribou are commonly found within the area (Whitlaw *et al.*, 1993; Darby *et al.*, 1989). Moose densities are considered low (< 0.10 per km^2), and woodland caribou densities are estimated at 0.06 per km2 or lower based on density estimates in the nearby Wabikimi Wilderness Park (Bergerud, 1989). The Ogoki-Nakina North Forests are located in the northern portion of the commercial forest which also includes the southern portion of the present-day continuous caribou distribution.

This paper describes the methods used to develop a caribou habitat mosaic on the Ogoki-Nakina North Forests for the period 1997-2017. The objective is to develop and coordinate present and future forest management activities with the retention and development of current and future woodland caribou habitat.

Forest description

Both forests are located within the arctic watershed and contain approximately 11-12% water. Productive forest land consists of 893 812 ha, while the balance is classified as non-forested land (120 877 ha) and non-productive forest land (123 598 ha). Major waterbodies drain north to James Bay through the Ogoki-Albany river systems and create formidable barriers to road construction and access. Both units are located in the Central Plateau (B8) section of the Boreal Forest Region (Rowe, 1972) within Hill's Site Region 3w and 2w (Hills, 1959). They are considered part of a natural wildfire-driven ecosystem characterized by short, hot summers and long, cold, dry winters. Current forest conditions are believed to be similar to historic forest conditions as minimal fire suppression and logging activities have been carried out in the past. Predominant tree species are black spruce (±74%), jackpine (±15%) and trembling aspen (*Populus tremuloides* Michx) (±10%). White birch (*Betula papyrifera* Marsh), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill), eastern white cedar (*Thuja occidentalis* L.) and tamarack (*Larix laricina* (Du Roi) K. Koch) are also found intermittently throughout these forests. Forest age composition is predominantly mature (70-120 years) to overmature (120+years) stands of predominantly coniferous forest originating from large even-age wildfire ranging in size from several hundred to 100 000 hectares.

The growing season generally lasts from 145-155 days with a mean frost-free period of 70-80 days (Chapman & Thomas, 1968). Mean annual precipitation is 737 mm which includes an average annual snowfall of 2660 mm (Environment Canada, 1973).

Geologically, the area lies in the northeast portion of the Precambrian shield with bare and partially bare bedrock exhibiting low to moderate relief (Ontario Geological Survey, 1991). The most common surficial deposit is a ground moraine of variable depth with a discontinuous layer of bouldery silty sand till overlying the bedrock (Cooper, 1983). Local patches of silty sand lacustrine plain deposits and pockets of organic soil are common in low lying areas. Glacial fluvial kame deposits with some outwash deposits form the bulk of both major moraines; the Augutua and Nipigon Moraine (Prest, 1963; Cooper, 1983) located on these forests.

Past and current use - a regional perspective

Historically the area was settled by the ancestors of local native people who developed through a number of hunting, gathering, fishing and trading cultures (Bray & Epp, 1984). In the late 1700s the Hudsons Bay Company established posts on Wasi and Eabamet lakes based on the fur trade. Trapping for beaver (*Castor canadensis*), mink (*Mustela vison*), marten (*Martes americana*), otter (*Lutra canadensis*), fisher (*Martes pennanti*), lynx (*Lynx canadensis*), weasel (*Mustela* spp.), gray wolf (*Canis lupus*) and red fox (*Vulpes fulva*) is still active in these forests and contributes to the local native economy. In addition a native commercial fishery is based on the Albany River along the northern boarder and on Ara and Met lakes along the forest's southern boundary. Remote tourism actvities offer fly-in angling and hunting opportunities. The area currently boasts 119 main base tourism lodges, remote outpost camps and land use permits that contribute to the local economy. In addition several parks including Sedgman Provincial Park, Wabikimi Park and the Albany River Waterways Park provide high quality remote fly-in fishing and canoeing opportunities.

Road access to the the southern boundary of the Ogoki Forest and to portions of the Nakina North Forest is currently restricted to the Ogoki road which terminates at the Ogoki River (Fig. 1).

Woodland caribou habitat mosaic
Woodland caribou in this area are managed as a locally featured species (OMNR, 1994) for the purposes of Timber Management Planning. The caribou habitat/forest mosaic (Racey *et al.*, 1991) is the basic approach currently suggested for all Forest Management Units within caribou range. Ecosystem management designed to mimic the habitat resulting from large naturally occurring fire is the current habitat management focus. Ontario timber management guidelines for the provision of woodland caribou habitat (OMNR, 1994) assume that logging can replace fire as a means of regenerating winter habitat and re-establish terrestrial lichens (*Cladina* spp.) in boreal forest cutovers (Harris, 1992; Racey *et al.*, 1996). Allocation of harvest areas over a 100 year rotation are to be concentrated within what would become a large disturbance to provide future habitat blocks (+40 years), while cuts will avoid large deferral blocks of currently identified high value seasonal caribou habitats (Timmermann, 1993a; 1993b).

Specific guidelines for management of calving sites, travel corridors and protection of wintering areas are described (OMNR, 1994). Critical/core caribou wintering areas or "virtual refuges" (Cumming, 1996) are to be avoided in Timber Management Plan allocations and road corridors. In addition an uncut buffer should be considered around large or contiguous, clearly defined areas of wintering habitat (Cumming, 1992; Cumming & Beange, 1993). Caribou habitat management prescriptions will minimize edge habitat and develop patterns of cutting that do not favour moose as a means of controlling wolf numbers.

Methods

The development of the caribou habitat mosaic for the Ogoki- Nakina North Forest was consistent with those outlined in Instructions for Developing Caribou Habitat Mosaics (Young, 1995) and Ontario Timber Management Guidelines For The Provision Of Woodland Caribou Habitat (OMNR, 1994).

The following five steps were used in developing the mosaic:

Data collection
All available data relating to woodland caribou and their habitat use was compiled. This included caribou seasonal observations (both recent and historical), identification of current and potential future caribou habitat (Timmermann, 1993a), current and suspected calving sites (Timmermann, 1993b) and existing travel corridors or migration routes. These data were collected from recent Ontario Ministry of Natural Resource aerial caribou surveys, current and past reported sightings from tourist operators and their clientele, caribou information collected during past moose aerial surveys, and file reports and plans (e.g. OMNR, 1983) that made reference to woodland caribou and their location within these forests.

Other sources used to help identify potential areas of caribou habitat were NOEGTS (Northern Ontario Engineering Geology and Terrain Study) maps in combination with NWOFEC (Northwestern Ontario Forest Ecosystem Classification) guide (Ontario Geological Survey, 1991; Sims *et al* , 1989). All sources were helpful in identifying land forms, soil types, forest age, structure, and composition, and vegetative cover, that are commonly associated with woodland caribou habitat.

Forest disturbance history and patterns
Recorded wildfire size (1500 to 130 000 ha) and distribution pattern from 1928 to the present was obtained from the Ontario Ministry of Natural Resources Regional Fire Centre in Thunder Bay.

Large areas of even aged forest exist and these areas were used to develop a forest unit eligibility map based on Forest Resource Inventory (FRI). An attempt was made to map these areas on the assumption that their size and pattern would reflect the pre-suppression fire history. Criterion for stand inclusion was that the ages between stands could not vary by more than 20 years. This period was consistent with the Timber Management Guidelines for the Provision of Caribou Habitat (OMNR, 1994) that requires a mosaic block to be harvested within a 20 year time frame. We believe this criterion could potentially create a 20 year variation between age classes within that mosaic block as a result of younger stands within the block being harvested towards the end of the 20 year time frame. Isolated stands of spruce lowland (site class 3) did not have to meet the above criteria to be included in the fire area. This was done to reflect those stands that may have been bypassed during a fire and helped explain the sometimes substantial difference in age between these isolated lowland sites and surrounding upland sites. Another approach used to determine fire size and pattern was to identify those features that act as natural fire breaks such as water, wetland ecosites, forest unit types (lowland black spruce), and topographic features. We believe these features assist in establishing mosaic block boundaries that closely emulate natural fire patterns.

Forest eligibility and maturity criteria

Maturity Class maps were used to identify stands based on forest unit and age class and placed into one of four maturity classes. They are: Juvenile, Maturing, Prime Product, and Declining. This breakdown helps identify forest areas where mature and over-mature wood exists and thus delineates preferred forest development areas within the mosaic. Such a maturity class map is also useful for identifying areas that may be potential preferred winter caribou habitat such as coniferous-dominated V30 sites (Sims *et al.,* 1989). Eligibility maps were created to identify current and future stands that are considered eligible for commercial harvest and each eligibility map was broken down by forest unit at a stand level.

Other forest values

During mosaic development consideration was also given to other existing forest values. These include areas that could receive some Area Of Concern (AOC) protection that may preclude Forest Management Operations (e.g. remote tourism, parks, and native values). Although these values are not considered a major priority in mosaic development at the landscape level, they do require some consideration in as far as the potential impacts that the mosaic may have on values at the operational level (e.g. mosaic blocks containing many high value tourism lakes).

Other considerations

Several additional key points were considered such as: whether the mosaic development was consistent with the Forest Management Plan objective for woodland caribou as developed for the Ogoki-Nakina North 1997-2017 Forest Management Plan. The objective for woodland caribou is as follows: "To manage for the maintenance of woodland caribou range and habitat through habitat maintenance and species range conservation" (Armstrong, 1997). To help achieve this objective it was important to ensure that the mosaic provided good habitat (preferred & suitable) distribution throughout the forest over time, especially at the southern portion of current caribou range. Here caribou have the opportunity to remain so they can repopulate areas that become eligible as suitable habitat. Distribution of habitat was determined by entering the FRI information from each mosaic block into the Strategic Forest Management Model (OMNR, 1995) and applying the Northwest Region wildlife matrix to determine the type of woodland caribou habitat (preferred/marginal) present, if any and its location within the mosaic.

Considerations were given towards identifying economic and logistical limitations during mosaic development. It is important to ensure that the access road development program associated with the mosaic is within the economic capabilities of the Company, and that forest units within mosaic blocks allow for a balance of summer and winter operating areas. Although these considerations were not a major priority, they were considered to help achieve an operable mosaic. In addition we examined the pattern of planned harvest blocks after 40 years to evaluate the protection of currenrly known habitat, remaining habitat and travel corridor linkages between uncut and logged mosaic blocks. The final consideration was to develop a mosaic that complemented caribou mosaics developed on the adjacent forests of Armstrong, Auden, and Nakina FMUs.

Results and discussion

A total of 50 mosaic harvest blocks to be logged in one of five-20 year periods over a 100 year rotation (1997-2097) were delineated (Fig. 2). Watershed boundaries were used to delineate the majority of harvest blocks while the balance used past fire boundaries. The disturbance cut pattern (mean size 20-25 000 ha.) was uniformly distributed, providing a balance of both summer and winter operating areas. Block configuration was southwest to northeast, consistent with prevailing winds and previous fire history. Only several large lakes had more than one block eligible for harvest in a similar time period; thus minimizing disturbance impact. Cut patterns were designed to impact only portions of individual traplines within each 20 year period. The objective being to provide a range of age classes within each trapline to accommodate the habitat requirements of a wide variety of furbearers and other

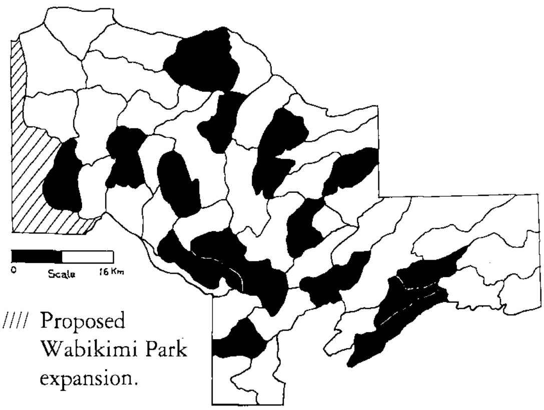

Fig. 2. Location of 50 mosaic harvest blocks within the Ogoki-Nakina North Forests of northwestern Ontario. Shaded blocks represents the pattern of forest logging disturbance after 40 years.

wildlife. Examination of planned forest disturbance suggests a solid pattern of travel corridor linkages remained between seasonal caribou habitats after 40 years. In addition tourism and park values were identified as areas of concern and were withdrawn from harvest eligibility.

The impact of disturbance on wood supply was minimized by strategically locating individual mosaic blocks.Every effort was made, however to identify mature and overmature wood in eligible blocks. In some cases old wood available on a deferred block was left and considered a lost opportunity and in its place younger-aged wood was considered eligible for harvest before reaching maximum yield potential.

The mosaic pattern requires an extensive road network to access the initial 20 year cut blocks. A higher initial road cost is partially compensated by both a short and long- term wood flow pattern from these designated cut blocks. In addition, attempts were made to design road locations that minimize impacts on deferral blocks, allow for long- term extraction use and provide management flexibility. Finally, mosaic block design recognized established mosaic patterns on adjacent southern forests and attempted to reduce disturbance impact along mutual boundaries.

It is believed that the Ogoki-Nakina North Forests are somewhat unique in providing an opportunity to apply a caribou habitat mosaic. The applied methodology allowed flexibility in considering other objectives including a sustainable supply of wood and other socio-economic benefits associated with tourism and wildlife values. However, this approach may not be directly applicable to other forests where caribou are currently found; hence flexibility, innovation and modifications will likely be needed to meet specific resource-based objectives.

Advantages of the mosaic approach include facilitating a long-term planning and application approach to the entire management unit over a 100 year rotation. This replaces past practices which only included those areas falling under a 20 year allocation and a 5 year cutting cycle. Current known seasonal presence of woodland caribou was largely left undisturbed in the first 40 years of planned logging, while provision was made to create future habitat by mimicking the pattern of large naturally occurring wildfires. The responsibility of harvesting and regenerating 100 years from now is assumed by the sustainable forest licence (SFL) holder. Periodic assessment and incorporation of new information through adaptive management will be required to ensure biological and economic objectives are achieved. We believe this ecosystem based approach will allow for both a long-term sustainable wood supply while providing a continuous supply of woodland caribou habitat.

Some concerns however remain and will need to be addressed. These include reduced flexibility to manage for a sustained yield because the harvest level for each mosaic block is determined by the need to manage caribou in large blocks and not necessarily on forest characteristics. Large cut blocks are a sensitive issue and may produce a negative impact in the marketing of forest products. In addition there is less incentive to practice intensive silviculture because those areas treated intensively will not be available for harvesting when they reach their maximum growth and yield potential (i.e. 60 years of age). This is a direct result of the 100 year cycle or rotation age dictated by the woodland caribou habitat mosaic.

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Experimental log hauling through a traditional caribou wintering area

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Abstract: A 3-year field experiment (fall 1990-spring 1993) showed that woodland caribou (*Rangifer tarandus caribou*) altered their dispersion when logs were hauled through rheir traditional wintering area. Unlike observations in control years 1 and 3, radio-collated caribou that had returned to the study area before the road was plowed on January 6 of the experimental year 2, moved away 8–60 km after logging activities began. Seasonal migration to Lake Nipigon islands usually peaked in April, but by February 22 of year 2, 4 of the 6 had returned. The islands provide summer refuge from predarion, but not when the lake is frozen. Tracks in snow showed that some caribou remained but changed locations. They used ateas near the toad preferentially in year 1, early year 2, and year 3, but moved away 2–5 km aftet the road was plowed in year 2. In a nearby undisturbed control area, no such changes occurred. Caribou and moose partitioned habitat on a small scale; tracks showed gray wolf (*Canis lupus*) remote from caribou but close to moose tracks. No predation on caribou was observed wirhin the wintering area; 2 kills were found ourside it. Due to the possibility of displacing caribou from winter refugia to places with higher predation risk, log hauling through important caribou winter habitat should be minimized.

Key words: *Rangifer tarandus caribou*, disturbance, moose, gray wolf, predation.

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Introduction

Increasing concern for the viability of remnant woodland caribou (*Rangifer tarandus caribou*) herds along the southern limits of their range in North America has led to recommendations for more restrictive forest harvesting practices where these caribou still occur (e.g., Freddy, 1979; Bloomfield, 1980; Ritcey, 1988). In Ontario, where the geographic range of caribou has been dramatically reduced over the last hundred years (Fig. 1), similar concern has been expressed (DeVos & Peterson, 1951; Cringan, 1957; Darby *et al*, 1989; Racey *et al.,* 1991; Cumming & Beange, 1993). The widespread caribou declines have traditionally been attributed to habitat disturbance or direct mortality factors. A third factor, disturbance of caribou themselves by human activities, has been less thoroughly investigated. Several studies have examined effects of human disturbance on barren-ground caribou mostly in connection with oil pipeline construction (e.g. Klein, 1979; Cameron & Whitten, 1980; Fancy, 1983; Curatolo & Murphy, 1986), but the relevance of these studies to woodland caribou is questionable. Relatively few studies have concentrated on disturbance of woodland caribou.

Those that have been reported have proven somewhat contradictory. Most have concerned caribou in Newfoundland. Bergerud (1974b) maintained that caribou have no aversion to human developments, roads, or railroads, but Northcott (1985) reported that caribou avoided development areas in Newfoundland, and their movements were disrupted by vehicular traffic during a construction period; caribou returned to pre-construction locations after the development was completed. Hill (1985) found caribou in Newfoundland more alert and less inclined to intake energy while construction of a hydroelectric development was in progress, though they eventually became sensitized to the construction. Mercer *et al.* (1985) concluded that the distribution of caribou on the Avalon Peninsula, Fogo Island, and Random Island relative to the road networks implied avoidance of these structures. He pointed out that despite large numbers of caribou, only 1 has ever been recorded killed by vehicles on Newfoundland highways compared with 200-300

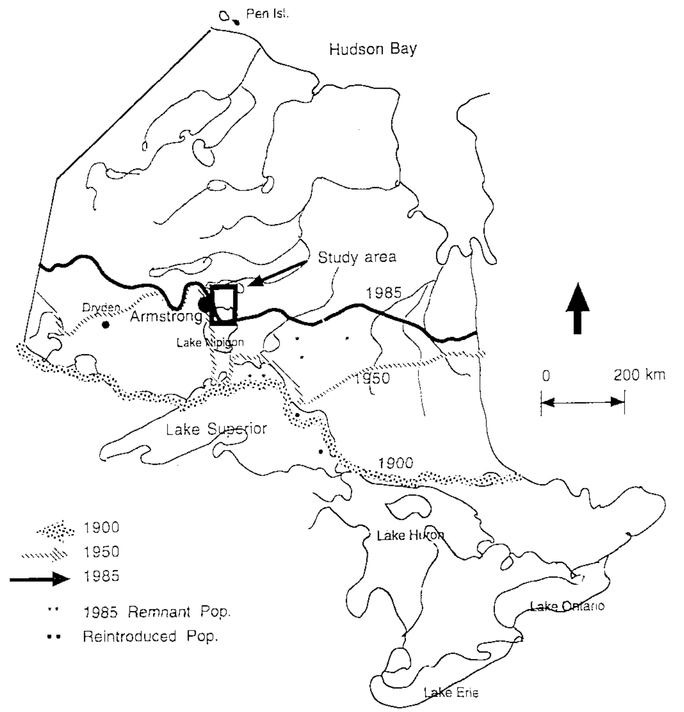


Fig. 1. Study area in relation to the historic lines of continuous distribution for woodland caribou in Ontario (after Darby & Duquette, 1986).

moose (*Alces alces*) killed annually. He suggested that caribou may avoid the roads. Mercer *et al.* (1985) also drew attention to the fact that centres of year-round ranges for all caribou herds, especially calving grounds, are at maximum distances from roads and population centres, and that distributions of several herds have changed with the placement of high use roads and railways within their ranges. Bergerud (1974b) suggested that a road could be a barrier if vehicular activity was perceived continuously; perhaps developments and road traffic have increased in Newfoundland since Bergerud (1974b) made his observations. Mercer *et al.* (1985) reported that both flushing and flight distances have been reduced on the Avalon Peninsula since the 1960's.

In British Columbia, Johnson *et al.* (1977) found that mountain caribou near Kootenay Pass became habituated to the presence of highway traffic and continued to use traditional routes, but Simpson (1985) discovered that mountain caribou in southern British Columbia avoided single snowmobile trails and left areas where recreational snowmobiling was extensive, probably due to the presence of human scent and large group movements.

Based on contemporary knowledge, the Ontario Ministry of Natural Resources (OMNR) viewed with concern plans by a local forest company, Buchanan Forest Products Limited (BFPL), to haul logs through a known caribou wintering area while the caribou were present (the cutting could not be carried out at any other time of year). To answer some of the questions regarding possible effects on caribou, a research partnership was formed in 1990 among OMNR, BPFL, and Lakehead University .

The major goal of the three-year study was to examine the direct and indirect effects of log hauling on caribou use of this traditional wintering area. The hypothesis to be tested was that transporting machinery and logs through a traditional woodland caribou wintering area would cause caribou to leave, or to modify their movements and dispersion within the wintering area in measurable ways. We identified 2 null-hypotheses: (1) caribou will not measurably alter their occupancy, dispersion, or movements when logs are hauled through their traditional wintering area; (2) caribou will alter these parameters coincident with log hauling, but by chance - the changes will be caused by concomitant alterations in other environmental influences, most likely in view of previous studies, wolf presence (e.g., Simkin, 1965; Bergerud, 1974a; Bergerud, 1985a; Bergerud, 1985b; Elliott, 1985; Page, 1985; Edmonds, 1988; Archibald, 1989; Bergerud, 1989; Elliott, 1989; Gasaway, 1989; Hayes *et al.,* 1989; Seip, 1991), or snow depths (e.g., Formozov, 1946; Pruitt, 1959; Bergerud, 1974; Lent, 1979; Darby & Pruitt, 1984; Edmonds & Bloomfield, 1985; Fancy & White, 1985; Simpson *et al*, 1985; Vandal & Barrette, 1985).

Study area

The study required several related study areas, surveyed at varying intensities. Overall Study Area (2500 km²) included all forested land within a radius of 32 km from the Armstrong airport (200 km north of Thunder Bay, Ontario) and islands in the north half of Lake Nipigon (north of 50 degrees latitude), which lies 20-70 km east of the Prime

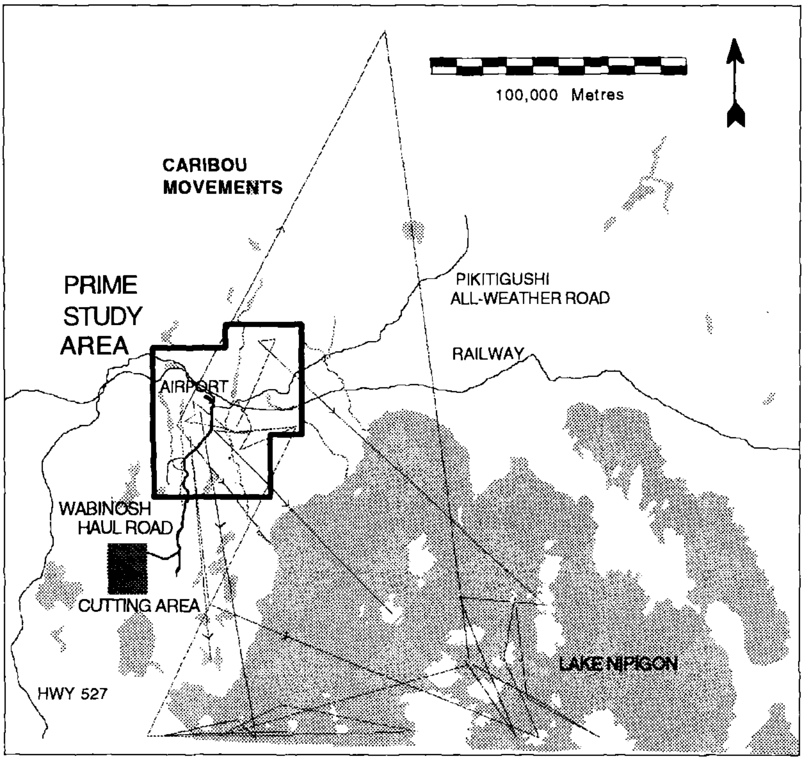


Fig. 2. Movement of radio-collared caribou during the winter of experimental log hauling from Dec. 10 until Apr. 17. For date details see Table 3.

cm). Wildfires have left a mosaic of stands, primarily black spruce (*Picea mariana*) and jack pine, (*Pinus banksiana*) with a few mixed stands including trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). Mosses, such as *Pleurozium schreberi* cover much of the forest floor, but patches of ground lichens, e.g., *Cladonia mitis, C. rangiferina,* and *C. alpestris,* grow under poorly stocked stands of jack pines on sand flats and under scattered spruce on rock outcrops. Tree lichens, e. g., *Usnea comosa* and *U. dasypoga,* are common but not especially abundant (Ahti & Hepburn 1967). Ground access is provided by an east-west railway, highway 527 from Thunder Bay, the all-weather Pikitigushi Road running north from the railway, and the seasonal (experimental) Wabinosh Road running south. The forest has been cut back some 10+ m from the railway and highway, but along other roads it grows within about 3–7 m.

Study Area (Fig. 2). In the Overall Study Area, sand, gravel and till thinly cover the Archean granitic uplands, typical of the heavily glaciated Precambrian shield. Summer temperatures are cool (mean daily temperature 16 °C), winters cold (mean daily January temperature -20 °C). Total precipitation (750 mm/year) and snow depths are moderate (highest weekly average depth during the study 76

A Prime Study Area, centered on Armstrong airport and Jojo Lake, encompassed 280 km², 14 km wide from Vallee Lake on the west to Mount St. John on the east and 20 km long from Mt. St. John

Table 1. Design of log-hauling experiment: yeats 1, 3 served as controls; in year 2 logs were experimentally hauled through a traditional caribou winrering area during January 14-March 10.

Period	Before Dec 11	Dec 11-Jan 5	Jan 6-7	Jan 14-Mar 10	Mar 11-April 30
Year 1	Control period	Control period	Control period	Control period	Control period
Year 2	Control period	Control period	Road plowed	Log hauling experiment carried out	No log hauling
Year 3	Control period	Control period	Control period	Control period	Control period
Possible human disturbance in year 2	Snowmobiles		Snow plow	Large machines trucks, private moving in, vehicles	Private vehicles only

on the south to Whitesand Lake on the north. In this area deep but poor sands support widely spaced jack pine with a ground cover rich in lichens (Antoniak & Cumming, 1998). A Northern Extension of this Prime Study Area was bordered by Big Lake on the west and Pikitigushi Lake on the east, covering an additional area of approximately 800 km^2. A Southern Extension, approximately 400 km^2, included Waweig, Wabinosh and Castle Lakes.

Methods

Experimental design

Since the nearest potential control area was 25 km distant (Wabakimi Provincial Park), a location that differed in soils and landform, we turned to a control in time rather than space. Year 1 of the experiment constituted a control year during which activities of caribou were mapped throughout their winter occupation of the study area while the road remained closed and little disturbance occurred (Table 1). Year 2 was the experimental year during which caribou activities were recorded before, during and after a period when trucks hauled logs through the caribou wintering area. Year 3 provided a second control year during which the road was not plowed and disturbance was minimized. However, the picture was changed when field work during the first winter revealed a second (at least partially segregated) aggregation of caribou only 6 km north of the disturbance area. This second aggregation provided a suitable control in space and was added to the study as such.

Field data collection

Capture techniques followed methods reported by Cumming & Beange (1987). Caribou were captured by crews of up to 6 men and 1 or 2 dogs driving them from islands into the water where they were approached by boat, lassoed, and tagged. Fourteen caribou (one cow in 1990; 1 bull, 6 cows, and 6 calves in 1991) were fitted with battery powered radio transmitter collars (adults) or solar ear tags (calves), from Advanced Telemetry Systems, running at 164 Mh.

High level winter flights to search for caribou covered the entire study area (or the area being used by the animals actively transmitting, if smaller); we did not search for missing signals beyond the borders of the study area, but reception range from high altitudes covered a substantial surrounding band. Aircraft included a Cessna 185, a DeHaviland Turbo-beaver, and an Aeronca Champion. Altitudes ranged from ca. 1800 to 6000 m above ground level (AGL). We used a transect width of 10 km at 1 800 to 3 000 m AGL, wider at higher altitudes. Twin directional yagi antennas were attached to the wing struts, angled outward and downward (as per Gilmer *et al.,* 1981). We flew weekly at times of likely significant movement (i.e. migration times, disturbance times) and at intervals of 1-3 weeks in mid-season when movements were expected to be fewer. Wherever possible, caribou that were roughly "found" during high level telemetry were located as exactly as possible, by "dropping lower" and circling, while switching from one antenna to the other to "zero in" on the animals. Practice trials demonstrated that transmitters could be located within a radius of about 200-500 m.

Radio transmissions were also monitored during low level transect flights to look for tracks in snow. A Lotek scanner was connected to a small (20 cm) whip antenna, which scanned the 14 frequencies (all VHF in the 164 MHz range) of collared or tagged animals, and fed the audio beeper into the aircraft intercom. With a detection range (at that altitude, with just a whip antenna) of only about 2 km, any collared caribou were noted and recorded as to location. This was a supplement to, not a replacement for, high level telemetry searches using twin yagi antennae.

The main tools for mapping tracks in the Prime Study Area and Extension Area were fixed wing aircraft, using methods described by Cumming & Beange (1987). Except in year 3 when lack of aircraft and personnel reduced effort, flights were made at 1-2 week intervals, from before the freeze-up of Lake Nipigon (late November or December) to whenever the caribou left their winter ranges to return to their summer calving grounds, always before ice-out. North-south transects flown at 300-600 m (AGL) aimed at total coverage of the Prime Study Area. For the Extension Areas, transect width was 3 km, at a higher altitude (600 to 1200 m AGL) to ensure transect coverage. A Champion 7EC provided excellent visibility on both sides for two people, a pilot/spotter and a spotter/recorder, seated fore and aft. The air speed of 90 km/hr to 155 km/hr provided sufficient time for careful inspection of tracks. One observer spotted to the right, the other to the left, and communicated via a two way intercom. Data recorded on a 1:50 000 scale topographic maps, included live caribou, caribou tracks, caribou beds, cratering, moose, moose tracks, moose beds, wolves, wolf tracks, vehicle tracks, and snowshoe tracks. Where helpful and possible (e.g. on lakes) landings were made to confirm track types. Tracks were also examined on the ground where accessible, e.g. along the roads in the airport area.

In view of the null-hypothesis that caribou might move due to changes in wolf behaviour, we recorded tracks of wolves as well as caribou. Suspecting that moose dispersion and movements might influence wolf behaviour which in turn might affect caribou dispersion, we recorded moose tracks along with caribou and wolf tracks. Three types of track records were recorded: individual, aggregate and linear. Individual tracks were recorded as discrete caribou, moose, or wolf tracks. However, in many places tracks were too numerous to be recorded individually. In these places, track aggregates were recorded as caribou, moose, or wolf tracks, with a line drawn around the perimeter of the aggregate, a practice that has become common in studies of moose (e.g., McNicol & Gilbert, 1980). Linear tracks were drawn as lines, with direction noted by an arrow where possible (e.g. after ground truthing, or where the animal was seen making the track).

The priorities for winter aerial surveys were first, the Prime Study Area; second, the North and South Extension Areas; third, the Overall Study Area. Temperature, wind, and sun were recorded on days of flights or ground surveys.

Ground surveys

Although the most important means of collecting data was by surveys with aircraft, we also examined the Wabinosh Road, the Pikitigushi Road, and snow machine trails on the ground to verify tracks spotted from the air, as to location, species, and completeness.

Tracks under heavy canopy cover were examined on snowshoes where they lay close to a road.

To examine the null-hypothesis that snow depths would affect caribou movements, we measured snow depth and consistency throughout the study. But the remote location of the study area made any intensive (e.g., weekly) investigation of snow conditions impossible. Instead we dug snow pits late in each winter; in this northern location where snow melts rarely occur, snow pits in late winter record the entire snow history to that date each year. A National Research Council snow kit was used to measure snow depths, hardness and density. Plots were located in clear-cuts 7 km south on the Wabinosh Road, and under jack pine stands used by the caribou as winter habitat about 1 km south of the Armstrong airport. Under the jack pines, two pits per visit were dug; one directly beneath tree cover (1 meter from the bole), and one in a small "open" (unstocked) space midway between trees. Two pits per outing were dug in the open clear-cuts.

To supplement these data, snow depth information was obtained from the OMNR snow station at Flat Lake, near the centre of the study area. The station is located in a trembling aspen stand to measure intermediate conditions between those in open areas and those under conifers. At each location, 10 measuring rods were placed in position before snowfall and mean snow depths for the station were recorded each Monday morning throughout the winter. Due to the complexities of measuring snow hardness and density, they were reported in only 3 classes: A - no crust, B - light crust, C - crust heavy enough to hold a man on snowshoes.

To document the nature of any perceived disturbance from the logging trucks we attempted to record traffic on the experimental road. Traffic counters were placed on the Wabinosh Road in year 2, and on the Wabinosh and Pikitigushi Roads in year 3. However, these counters did not distinguish types of vehicles. On the other hand, movements recorded by BFPL (Robinson & Bodie, 1992) identified all types of forest harvesting equipment. Since these data were judged superior they were reported here.

Important also for evaluation of the second null-hypothesis were records of caribou killed by wolves or as a result of deep snow. Reception of a "mortality signal" (rapid beat) initiated a search by aircraft, followed by ground search (using a scanner and yagi directional antenna) to recover the collar or tag, and to identify means of death if possible.

GIS and statistical analyses

Results from mapping tracks were first examined manually. Subsequently, they were digitized into a Macintosh computer running a rastor based Geographic Information System (GIS) called Map Factory . Original mapping error was estimated to be within 100-1000 m for telemetry locations, 30-100 m for low level mapping of tracks in the Prime Study Area, and 30-300 m in the extensive study areas. Due to the frequency of caribou aggregates in this small, heavily used wintering area, analysis of tracks as points (Cumming *et al.,* 1996) was not possible. Instead, the rastor pixel size was set at 30 m and the computer counted numbers of pixels

Table 2. Chronological time chart of traffic on haul road during experiment.

Date Year 2	Equipment movement	Personal vehicle travel - implied by number of shifts*
Jan 06	Snowplow opens Wabinosh Road	1
Jan 07	Grading begins, feller buncher floated in	5
Jan 08-13	Grapple skidder, delimber, bulldozer floated in	7
Jan 15	Haul trucks begin, sand truck begins sanding road; loader, front end loader floated in	13 25 haul trucks Monday-Friday until January 16, haul in progress 24 hrs.
Jan 17	Loader, haul bulldozer, front end loader floated out; sand truck moves out	10 No hauling until Jan 23
Jan 23	2 loaders, front end loader, haul bulldozer floated in; sand truck driven in; haul trucks begin again	13 Hauling in progress once more.
Feb 01-11	Five slashers floated in	15-21
Feb 21	Cutting ceases	18
Feb 29 -Mar 1	Skidding, grading cease 4 slashers, grapple skidder floated out	14-12
Mar 02	Delimbing ceases	10
Mar 04	Slashing ceases, delimber floated out	7
Mar 06 - 10	Slasher, feller buncher, 2 bulldozers floated out; grader, sand truck, front end loader out	Haul operation personnel only
Mar 11	2 loaders floated out Haul trucks finish	Haul operations cease

From: Robinson, L. & B. Bodie, 1992.
* Since no accomodation was available at the cutting location, workers used personal vehicles to go on and off shift.

showing presence or absence of tracks. Observed track frequencies were then compared using chi-square. Spatial relations among caribou, moose and wolves were examined by establishing 900 m buffers (the closest to 1 km that Map Factory could easily handle) around each species and counting numbers of pixels within the buffer showing fresh tracks of other species.

Results

Disturbance during year 1 consisted of a few snowmobiles on special trails and along the Wabinosh haul road, mainly during the early winter when snow depths were not excessive. The early part of year 2 was similar. On January 6 of year 2, the road was plowed and on January 7 company workers began to move in heavy equipment (Table 2). The haul consisted of 25 trucks hauling 24 hours/day, Monday - Friday. The sounds produced by the harvesting equipment used in the actual logging operation could not be heard by humans from the caribou wintering area, as they were too far south; however, large trucks and other pieces of equipment could be heard for several kilometers, depending on temperature and wind, and these passed right through the occupied area. Among the sounds produced by these trucks low frequencies predominated. The highest frequencies recorded fell below 10 000 Hz (Hyer, 1997). In addition to this work-related traffic, some people living nearby took advantage of the plowed road for winter outings, but they were not counted.

Telemetry data

All 14 of the caribou fitted with radio transmitters on western islands of Lake Nipigon were relocated in or near the Prime Study Area during year 2. However, only 6 of these caribou actually returned close to the haul road prior to the experimental hauling in year 2. All 6 left again after initiation of logging activities (Fig. 2). Caribou 1 moved far north before returning to Lake Nipigon islands. Caribou 2 moved to the control area, then to the islands.

Table 3. Locations of radio collared caribou during 2 winters.

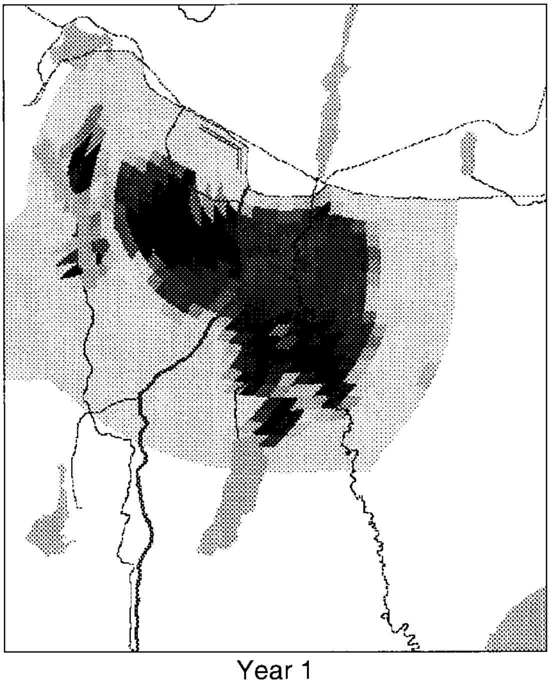
		Caribou collar frequency					
Year	Date	cow 90	310	354	533	253	333
Year2	Dec. 10/91		W L.NIp	W L.NIp	W L.NIp		W L.NIp
pre-	Dec 19/91	Expt. area	Expt. area	Expt. area	Expt. area	E. Expt. area	W L.NIp
haul	Dec 28/91	E. Expt. area	Expt. area	Expt. area	Expt. area	Expt. area	
period	Jan 4/92	E. Expt. area		Expt. area	Expt. area		
hauling	Jan 7/92	Expt. area	Expt. area	Expt. area	Expt. area		
period	Jan 14/92		Expt. area	E. Expt. area	E. Expt. area	Control area	
	Jan 24/93			E. Expt. area	E. Expt. area		
	Feb 22/92	Islands		Expt. area	Islands	Islands	Islands
	Mar 1/92			Expt. area	W L.NIp	Islands	Islands
	Mar 10/92	Islands		Expt. area	Islands		Islands
post-haul	Mar 30/92	Islands		Expt. area	Islands		Islands
period	Apr 17,18/92	Islands		Islands	W shore	Islands	Islands
Year3	Oct 22/92	Islands	Islands	Islands	Islands		Islands
pre-haul	Dec 22/92	Islands	Islands	Islands	Islands		Islands
hauling	Jan 7/93	Expt. area					
period	Jan 14/93	Expt. area					
	Jan 19/93	Expt. area	Control area	Control area		Islands	Islands
	Jan 27/93	Expt. area	Control area	Control area		Islands	Islands
	Feb 4/93	Expt. area	Control area	Control area			
	Mar 3/93	Expt. area	Control area	Control area			
post-haul	Mar 18/93		Expt. area				
period	Apr 1/93	Expt. area	NW L. Nip	Control area	Islands		Islands

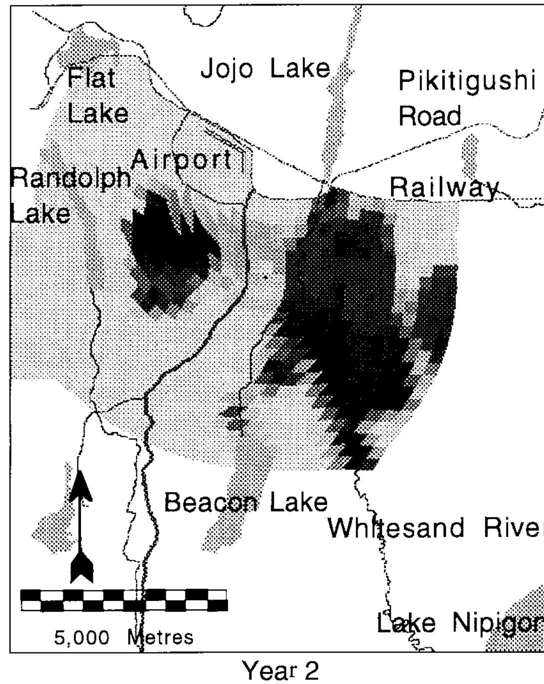
Note - abbreviations indicate the following:
Expr. area - the experimental area south of the railway within 8 km of the road on which logs were hauled.
Control area - the undisturbed winter area north of the airport near Jojo Lake.
Islands - the islands of Lake Nipigon used as calving and summer habitat.
E., NE. Expt. area - within the prime study area but beyond 8 km from the haul road.
W., NW L. Nip - on the indicated shores of Lake Nipigon where they are usually found enroute to or from calving or wintering areas.

Caribou 3 moved to a location 2-8 km east of the experimental area, then to the west shore of Lake Nipigon (a common staging location on the way to the wintering area), then to the islands constituting summer habitat. Caribou 4, 5, and 6 moved almost directly to the islands. Four of the 6 caribou returned to Lake Nipigon islands before February 22 (Table 3), an exceptional early date, for a previous study during a period when the haul road was not open in winter, found that spring movement from the Armstrong area began in early March and reached a peak in April (Cumming & Beange, 1987).

Mapping tracks

Maps of tracks in the Prime Study Area showed caribou close to the haul road during the pre-haul, and hauling periods of year 1 (tracks were not recorded for the post-haul period of the first year). Caribou returned to much the same areas in year 2, leaving many tracks close to the road during the pre-haul period (Fig. 3). On the day when the road was plowed, many linear tracks were recorded oriented at right angles to the road. Caribou tracks continued to be found in the Prime Study Area, even though all collared animals had left, but they were found spaced away from the road > 900 m during the haul period of year 2. Except for one small aggregation of tracks 300 m from the road, caribou continued to use only areas remote (>900 m) from the haul road through the post-haul period of year 2. In year 3, caribou arrived later than in previous years, but did return to areas near the unplowed road and continued to track these places throughout the winter (Fig. 3). The fewer tracks recorded in year 3 could have been due to reduced effort due to problems with aircraft availability.





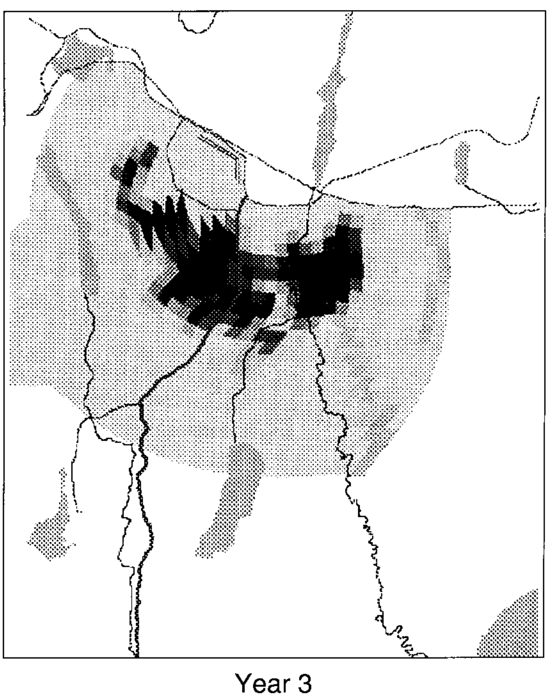


Fig. 3. "Contour" maps of track densities showing proportions of pixels wirh caribou tracks during the mid-winter period (Jan 7–Mar 11) wven logs were hauled in year 2. The darker the area, the denser the tracks. The very light gray outer area indicates the extent of the prime study area. Conrour width 300 m.

"Contour" maps of caribou tracks showed proportions of occupied computer cells concentrated in 3 preferred areas in year 1: the area directly south of the airport, from the haul road to 2400 m west; an area 1200-5400 m east of the haul road along the outlet from Beacon Lake; and an area 2100-9900 m east of the road along the Whitesand River (Fig. 3). The same area west of the haul road continued to be used during year 2, except for a strip 600 m wide adjacent to the haul road which was used only lightly. The caribou virtually abandoned this stretch by late winter. Areas east of the haul road were occupied later in years 2 and 3. In year 2, caribou tracks showed little use of the area within 900 m of the haul road once logging began; some moved closer to the railway tracks. In the post-haul period largest track aggregations were located 2-3 km from the road. Caribou began to use the area along the Beacon Lake outlet in early winter, but discontinued its use during logging. In contrast, they continued to leave tracks in the Whitesands River area, far-

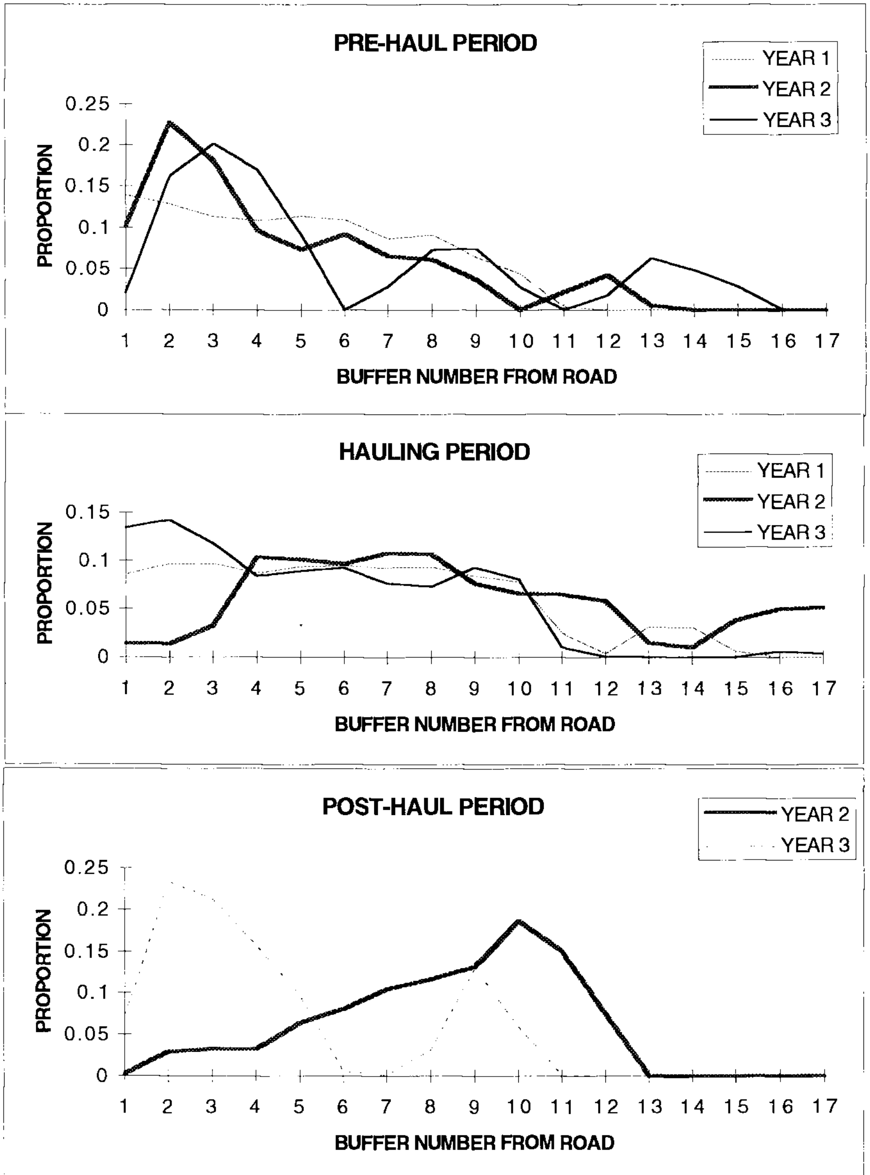


Fig. 4. Proportions of 300x300 m cells showing presence of caribou for 3 winters in buffers numbered east and west from the Wabinosh Road.

ther from the haul road, even into late winter. In year 3, caribou used the area west of the haul road in ways similar to year 1 throughout the winter. However east of that road, the Beacon Lake area was used very lightly, and caribou left tracks in only a northern section of the Whitesands River area, a section that was not favoured in years 1 or 2. Most caribou left both eastern areas by late winter in year 3.

Proportions of occupied computer cells were graphed using data from 300 m buffer zones east and west of the road. During year 1, the control year, caribou tracks were found on the road or close to the road throughout the winter; presence of tracks decreased with distance from the road (Fig. 4). In year 2, the hauling year, only small proportions of tracked cells were located within 1200 m of the road. During year 3, a pattern similar to year 1 was re-established. Chi-square tests showed significant differences among years for each of the 3 important periods of the experiment - before January 6 (pre-haul), January 7 - March 11 (hauling in year 2), and after March 11 (post-haul) (Table 4). No significant differences in caribou dispersion appeared between the pre-haul and hauling periods of year 1, but highly significant differences were found before and after the experimental hauling in year 2. These differences indicated that caribou changed their dispersion patterns about the time the road was plowed. A similar significant difference in year 3 probably arose from the later return of many caribou to the prime study that year, making the early period different from the period after the main body arrived. Post-haul dispersions did not differ significantly from the experimental hauling period in year

Table 4. Chi-square values and probabilities for proportions of cells occupied by caribou or caribou tracks in 1-9 300 m GIS buffers from "the Wabinosh Road, near Armstrong, Ontario. Six east-west rows of cells" were chosen to avoid influences of north and south habitat changes. In "year 2, trucks hauled logs through the caribou wintering area. Years" "1,3 were controls."

Test results	Winter periods and years		
	Comparison of pre-haul periods over all 3 years	Comparison of hauling periods over all 3 years	Comparison of post-haul periods over years 2,3
Chi-square	39.31	31.66	88.2
Probability	0.006	0.047	<0.001
	Pre-haul periods - c. f. years 1,2	Haul periods - c. f. years 1,2	
Chi-square	13.79	19.13	
Probability	0.183	0.039	
	Pre-haul period c. f. haul period in year 1	Pre-haul period c. f. haul period in year 2	Pre-haul period c. f. haul period in year 3
Chi-square	5.5	50.92	27.32
Probability	0.856	<0.001	0.002
	Haul period c. f. post-haul period in year 2	Haul period c. f. post-haul period in year 3	
Chi-square	16.63	27.16	
Probability	0.083	0.003	

1) All 3-year comparisons showed significant differences (including others not shown).
2) Dispersion in the periods before and during the first (control year), bur it did during the experimental year.
3) The hauling period did not differ significantly from the post-haul period in year 2, but did in year 3.
4) Pre-haul dispersion did not differ berween years 1, 2, but during the hauling period it did.

2. This lack of significant suggests that the more remote (from the road) dispersions established by caribou during the haul period of year 2 carried through into the post-haul period. In contrast, track locations did differ significantly between the hauling and post-hauling periods of year 3, perhaps due to the change from normally heavy track densities during the January 6 - March 11 period to reduced densities in the post-haul period as caribou began to move toward summer locations. Comparisons of pre-haul periods between years showed no significant differences between years 1 and 2, but similar comparisons for the hauling period did show a significant difference, supporting the idea that the change did not occur until hauling began.

At the control area in year 1, ttacks indicated ingress of caribou along a water course from a start at least 10 km north. Similar movements were tracked in each succeeding year suggesting that this might be a traditional travel route. At the same times, radio-telemetry showed that some caribou also moved there from the Lake Nipigon islands. Thus, the caribou in the Control Area appeared to come from at least 2 widely spaced summer locations. During winter, tracks of caribou in the Control Area showed similar patterns for all 3 years (Fig. 5). The only obvious shift in track dispersion unique to year 2 constituted a filling-in of what had previously been an unoccupied strip near the northern end. Thus track locations of caribou in the control area changed little during the experimental year 2 compared with other years.

Possible alternative explanations

Moose tracks were not usually found near locations of caribou tracks (Fig. 6). A small exception occur-

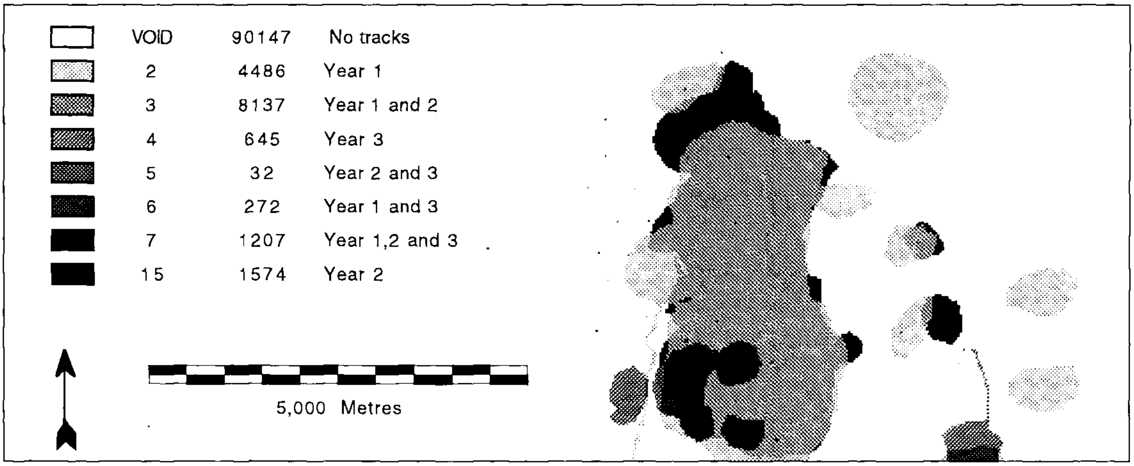


Fig. 5. Locations of caribou tracks at the control area (north of the railway and west of the Pikitigushi Road) during 3 winters. Note that the largest single area was that used by caribou in both year 1 and year 2 (light grey). Year 2 (black) was uniquely used in only a few small places. Thus changes from year to year were small. Column 2 indicates grey scale of category. Column 3 provides a pixel count indicating area.

Table 5. Association of wolves with moose and caribou as indicated by numbers of pixels showing wolf presence within 900 m buffers of prey species.

Year	Prey species	Wolves	No wolves	Totals	% used by wolves	Chi-square	Probability
1	moose	3099	8134	11233	27.6		
	caribou	986	42883	43869	2.2		
	Total	4085	51017	55102	7.4	8366.7	$P<0.001$
2	moose	11382	4580	15962	71.3		
	caribou	4064	41159	45223	9.0		
	Total	15446	45739	61185	25.2	24279.9	$P<0.001$
3	moose	1362	11064	12426	11.0		
	caribou	2503	21294	23797	10.5		
	Total	3865	32358	36223	10.6	1.679	$P=0.1951$

red in year 2, when a southwestward extension of caribou tracks remote from the haul road coincided with a northward shift in moose tracks producing a small area near Randoph Lake where caribou and moose tracks overlapped, the only such place in the 3-year study. East of the haul road, caribou and moose were occasionally recorded in the same location, but in different years. Apart from snowmobile trails followed by wolves in portions of both the Prime Study Area and the Control Area, wolf tracks were found close to those of moose. Few wolf tracks were observed at any time during the course of the study in the parts of the Prime Study Area tracked by caribou, but they were frequently found in other parts where the moose tracks were located. Distances to nearest wolf were significantly greater for caribou than for moose in years 1, 2, but not significantly different in year 3 (Table 5). Both aerial and ground investigations located moose tracks and wolf tracks, but not caribou tracks, in and around the cutting area 2.8 km to the south.

In three winters of intensive flying, only 2 caribou were found fed on by wolves. The first caribou, #233, died 100 m from a snowmobile trail between Jojo and Whitesand Lakes sometime between Jan. 7 and Jan. 24, 1992. Interviews with a local hunter/trapper led to suspicion that the animal might have been shot, and the remains scavenged by wolves. Support for this belief, in addition to the impression gained from the interview and the proximity of the snowmobile trail, came from caribou #293, the calf of caribou #233, which was not killed

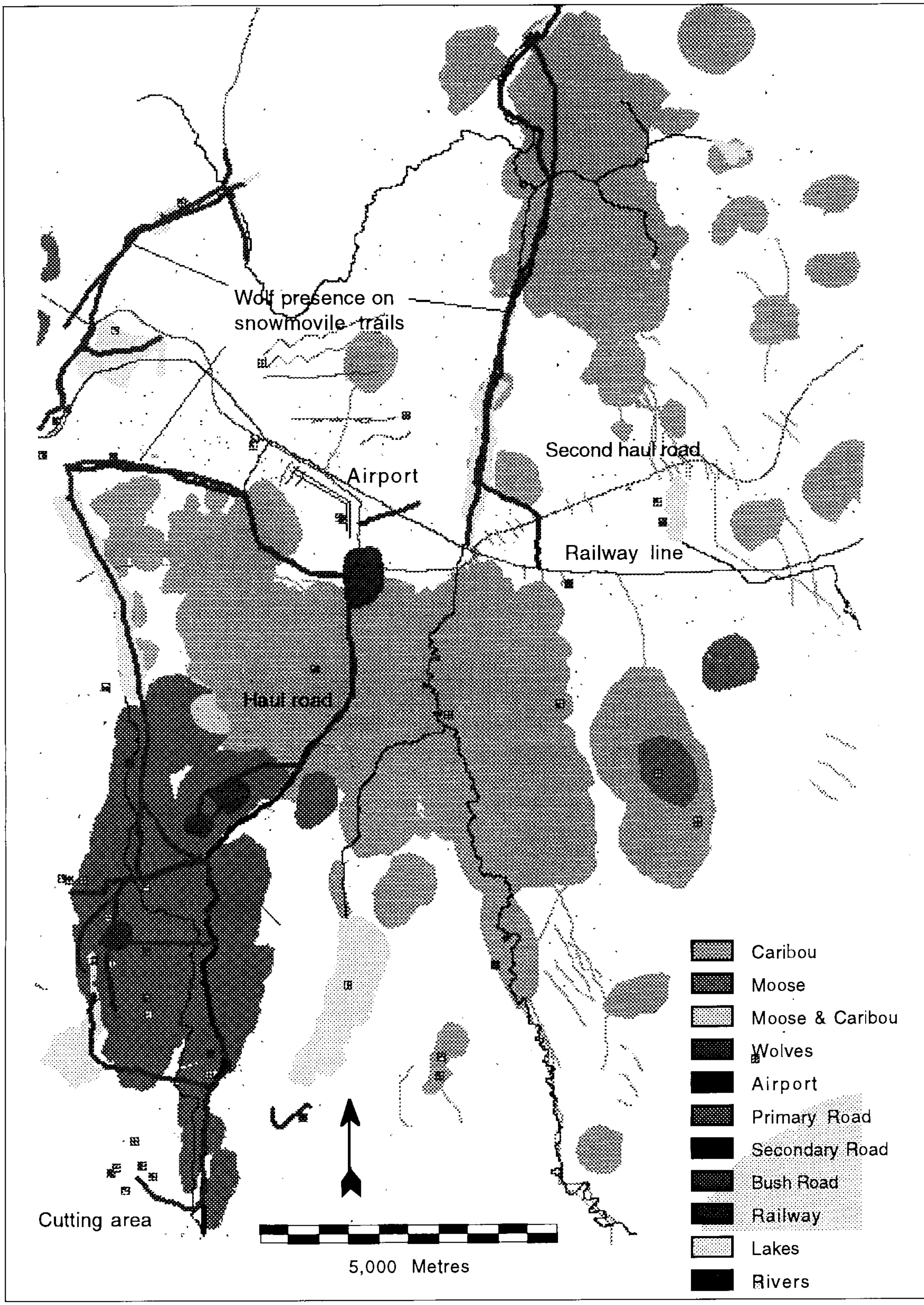


Fig. 6. Three years' combined track data showing habitat partitioning by caribou and moose, with wolves, traveling roads and snowmobile tracks, mostly associated with moose rather than caribou.

but lived till the end of the study. If wolves had been doing the killing, the calf would likely have been killed first.

The only other dead caribou was found on Dec. 22, 1992, on the travel route used by caribou approaching the Control Area from the north. Unsafe ice conditions made landing to verify the identification impossible, but the carcass lying on its back with intestines removed, out strongly suggested a wolf kill.

Not a single instance was observed of wolves, or wolf tracks, following live caribou or caribou tracks, although some wolf tracks may have been missed, as Jackson (1990) suggested after a previous winter of ground surveys in the area. Wolf tracks were frequently found within 3 km of caribou tracks in the airport area, yet we never observed any tendency for wolves to depart from human and moose trails to follow caribou.

In contrast, wolves and wolf tracks were recorded closely associated with live moose and moose tracks on many occasions (Fig. 6). During the 3 years, wolves were seen on 3 fresh moose kills in the Prime Study Area, but always at locations remote from areas occupied by caribou.

Snow pits showed slightly deeper snow in year 2 (mean open depth on 16 March of 64 cm) than in years 1 (60 cm) and 3 (50 cm, Table 6). Further, records from the OMNR snow station at Flat Lake showed greater snow depths in year 2 also (maximum depth 76 cm, compared with 63 in year 1 and 59 in year 2). To find if the second year depth was unusual in the area, OMNR records for 1989 were also examined; these depths equaled or exceeded (maximum 79 cm) snow depths in year 2 (Table 6).

The heaviest crusts were in year 1 when some layers of pure ice resulted from a brief rainfall; crusts were lightest in year 3. Densities also averaged consistently highest in year 1. Stardom (1975) determined critical levels (i.e. levels that initiated emigration from an area) for woodland caribou. Snow depths at the study area never exceeded Stardom's (1975) critical snow depth level of 65 cm. The snow hardness threshold was exceeded in up to 4 layers during year 1, but rarely in the other years. Lowest density thresholds were exceeded in 2 snow pits in year 1, and 1 snow pit in year 2.

Discussion

An experiment requires changing some aspect of a situation and comparing consequences with an unchanged control. But establishing control areas for operational-size field experiments involving wildlife is notoriously difficult (Walters & Holling, 1990). Even the most carefully chosen controls in nearby, apparently comparable, areas can differ significantly from treatment areas in ways unrelated to the treatments (Cumming, 1989). For this reason, the experiment was set up with controls in time rather than space. We examined the status quo, changed the vehicular traffic pattern and observed consequences; then we allowed traffic to return to its original, minimally disturbing condition, once more observing results. This control worked well. Caribou showed behaviour in year 2 different from either of the other 2 years. The discovery of a previously unknown additional caribou wintering area north of the railway tracks, provided an opportunity to add a spatial control as well. The changes found in the experimental area were not observed in the control area. Therefore the evidence seems substantial that the change in caribou behaviour occurred only at the time of log hauling and only near the road on which the logs were hauled. Further, during the experimental period of year 2, the 6 radio-collared caribou all left the experimental area; fresh rrack aggregates of remaining caribou could be found only beyond 2-5 km from the haul road. Caribou dispersions differed significantly between periods of log hauling and no hauling. No similar changes were observed in the control area, nor near the contiguously used railway and all weather road. Null-hypothesis #1 that there would be no change was disproved, and the hypothesis at least to some degree supported.

The most likely alternative explanation for changes in caribou dispersion and movements was the presence of wolves. Presumably, caribou harassed by wolves would be sensitive to changes in behaviour or abundance of the latter and might have moved out during year 2 for that reason coincident with the log hauling. Yet results indicated that wolves did not in any year spend appreciable time in areas occupied by the caribou, rather their tracks were found in areas frequented by moose, and these areas were usually spaced some distance from those used by caribou. The small over-lap between areas showing tracks of caribou and moose in year 2 appeared to result from independent changes in dispersion by each species that brought them closer together. In the most intensively used and observed areas near the Wabinosh Road wolf tracks were virtually absent. Furthermore, no evidence suggested that

Table 6. Snow depths from the Ministry of Narural Resources snow station at Flat Lake, Ontario, and from" snow pits dug in this study. Data for rhe log hauling experimental year are shown in bold.

Years			1989-90	1990-91	1991-92	1992-93
Snow depths recorded by OMNR personnel at Flat Lake snow station						
Week 13-14	"(includes January 6,7)"					
Average depth (cm)			57	47	59	55
Crust			A	A	C	B
Week 22-23	(includes March 11)					
Average depth (cm)			66	57	71	57
Crust			C	C	C	B
Entire winter						
First recorded snow depth			6-Nov	26-Nov	4-Nov	9-Nov
No. of weeks snow depth >65 cm			8	0	10	0
Greatest depth (cm)			79	63	76	59
Last recorded snow depth			23-Apr	15-Apr	25-May	12-Apr
Snowpit data						
Dates				16-Mar	(Mar 11) Apr 8	11-Mar
Snow depth						
Open locations	Snowpit 1			60	(68) 58	48
	Snowpit 2			58	79	53
Forested location	Snowpit 1			61	55	55
	Snowpit 2			60		50
Comparable OMNR reported depths		Dates		11/18-Mar	9/16-Mar	8/15-Mar
		Depths		57/ 46	71/73	57/59
Snow hardness						
Open location	Snowpit 1	Mean g/sq. cm.		230	(54) 74	38
		Max. g/ sq.cm.		750	(78) 100	75
		No layers>80		4	(0) 2	0
	Snowpit 2	Mean g/sq. cm.		1814	47	8
		Max. g/ sq.cm.		6500	70	10
		No layers>80		4	0	0
Forested location	Snowpit 1	Mean g/sq. cm.		233	35	29
		Max. g/ sq.cm.		600	67	65
		No layers>80		3	0	0
	Snowpit 2	Mean g/sq. cm.		1771	n/a	12
		Max. g/ sq.cm.		7000	n/a	35
		No layers>80		1	n/a	0
Mean density per snow pit						
Open locations	Snowpit 1			0.22	0.30	0.12
	Snowpit 2			0.26	0.16	0.11
Forested locations	Snowpit 1			0.25	0.13	0.16
	Snowpit 2			0.12	n/a	0.12

1) Road was plowed and log hauling began on January 6,7, 1991-92. Hauling ceased March 11.
2) 65 cm was found to be a critical snow depth for caribou in Manitoba (Stardom, 1975).
3) A crust is very light, B medium, C heavy enough to hold a man on showshoes.

wolf abundance or behaviour had changed noticeably. Therefore, the results make impact of wolves an unlikely alternative explanation for caribou movements.

Snow depths were greater in year 2, than in either the previous or subsequent year, supporting the null-hypothesis that caribou might have moved in year 2 because of the snow. However, depths never exceeded critical thresholds that initiate movement for caribou in Manitoba (Stardom, 1975). Nor could they be considered unusual for the study area; similar snow depths were recorded at Flat Lake the year before the study began, and were reported previously in the general area by Cumming and Beange (1987). Likewise, changes in snow consistency did not appear to be a factor since heaviest crusts, hardness values, and densities, factors that might make digging in snow more difficult and so spur caribou to move, were most adverse in year 1, not in year 2. Furthermore, similar behavioral changes were not detected among caribou at the northern control area during year 2 where snow depths could be presumed to be similar to those in the nearby study area (they were not measured because of inaccessibility). Thus all evidence suggested that differences in snow conditions would not likely explain the experimental results.

Other factors not measured might have affected the caribou. Although habitat change due to fire occurred some 5 km distant during the summer of 1991, none occurred in the occupied winter range. No other habitat changes that could have accounted for the caribou movements were recorded. No changes in poaching or native hunting were noted. Snowmobiles showed disturbance potential by displacing caribou up to 200-300 m. Furthermore, Klein (1971) reported snowmobile disturbance of reindeer (*Rangifer tarandus tarandus*) in Scandinavia, stating that if approached too closely the reindeer may panic and become unmanageable. But in this study the snowmobiles stayed on roads and established trails where their effects on caribou seemed similar to but less than impact from roads. Apart from log hauling, the human activity most likely to have affected results was use of the haul road by private vehicles. We considered use of private vehicles during the hauling period as part of the overall impact of the hauling operation. But use of private vehicles after the hauling period in year 2 might have extended the length of disturbance time. We concluded that in this instance, hauling logs through a caribou wintering area caused caribou to change their behaviour by shifting their winter dispersion from areas near the road to locations farther from the haul road, some returning all the way to summer habitat. Jackson (1990) reported similar movements of caribou from the same wintering area during December 1989, a time when trucks were also hauling logs.

Long term effects of the log hauling could not be determined from this study. Possible habituation was suggested by the continued presence of caribou in the area despite the presence of the railway and permanent all-weather roads. Further, the return of caribou to the Prime Study Area the third year suggested some degree of resilience after disturbance. If the road were traveled every winter, the observed displacement of caribou might decline or the caribou continue to occupy more remote areas in a way similar to caribou in the control area. Although small groups of caribou some time cross the Pikitigushi Road where they are sighted by local people and truckers, our aerial surveys showed major concentrations 2-3 km remote from the road, perhaps avoiding it in a way similar to caribou in Newfoundland (Mercer *et al.,* 1985). Bergerud (1974b) suggested that caribou might exhibit adaptive modification to human activities when food or weather were the primary influences on their behaviour. Perhaps that could happen here if hauling continued. Still this possibility is not reason for complacency about the impacts of roads on caribou. The number of caribou that became habituated to disturbance aftet several winters of displacement from favoured winter refugia might be considerable fewer than the number of caribou originally displaced.

Without disputing the validity of either or both of the major theories attempting to explain caribou declines, we speculate that a third possibility - severe or chronic disturbance to caribou - might also cause range reduction or population decline. When caribou occupy traditional winter habitats, they may be very sensitive to predation, or to the perceived risk of predation. Consequently, they may also be extremely sensitive to sights and sounds that are unfamiliar, sounds that may cover the approach of wolves. Therefore, habituation such as that reported in British Columbia (Johnson & Todd, 1977) and Newfoundland (Hill, 1985) may be more likely where predators on winter range are rare or nonexistent. Where predators are present, caribou may abandon, temporarily or permanently, otherwise suitable winter habitat if stressed chronically by noise or other stimuli (e.g. sight, smell) that may put them on "predator alert". They would also be less likely to move adjacent to disturbance areas during their normal patterns of winter habitat use. Thus, they may be forced into habitats with increased metabolic demand, decreased quality or quantity of food, and increased susceptibility to predation. Caribou displacement from wintering areas may result from various agents: humans, predators, climate, fires; the fact of displacement may be more important than the absolute effect of a single cause.

Management implications

It might be argued that shifts in winter location would be of little consequence for management of animals as notable for their wandering as caribou, but suitable wintering areas may not be in unlimited supply (Cumming *et al.,* 1996). This suggestion is supported by a comparison of the population estimates by Simkin (1965) with contemporary estimates of population potential by Ahti & Hepburn (1967). Caribou numbers in the Hudson Bay Lowland regions amounted to only 19% and 32% of their estimated carrying capacity. But in the Nipigon-Superior and Central Regions they reached 80% and 50% of their habitat potentials. Habitat loss in the former case presumably would be of little consequence, but in the forest loss of winter habitat through logging or disturbance might result in decreased caribou numbers. The mechanism could be simple food shortage, but it seems more likely to involve the need for winter refugia from predation. Even within the study area, movements of caribou and moose during the time of log hauling brought the two species together, possibly increasing predation risk for the caribou. The finding of caribou killed or scavenged by wolves outside the major wintering areas suggests that immunity to predation may not extend beyond the traditional winter range boundaries. Movements of radio-collared caribou support this suggestion. The caribou that moved to the control area might have been equally safe once there, but the 2 collared caribou that traveled north, probably into areas with more moose and wolves, would likely face higher predation risks as a result. Caribou that returned to Lake Nipigon islands did so in the face of poor winter habitat conditions and increased wolf presence (Bergerud *et al.,* 1990). A caribou found killed by wolves near one ofı the islands during the winter of 1989 (Beange, pers. comm.) provided supporting evidence. Cumming & Beange (1993) suggested that the best explanation for disappearance of caribou bands in Ontario was displacement by logging from their wintering areas that forced them into places with reduced protection from wolves, poaching, and accidents. The results of this study suggest that displacement of caribou by winter traffic might have similar effects.

The observation of recreational driving on the logging road suggests possible consequences for roads through caribou wintering areas beyond direct disturbance. The presence of more roads may provide better access for wolves; more vehicles increase the risk of caribou being killed in road accidents; more people heighten the risk that some may be poachers. Even when caribou are not displaced, the presence of roads may increase all usual hazards.

The multiple increased risks to caribou from the use of winter roads, whether for logging or otherwise, argues for a complete ban on roads through caribou wintering areas. In Ontario caribou have been threatened by human activities throughout this century. Now even small bands are important to retain linkages for genetic exchange. Increased mortality due to displacement from favoured wintering areas should be avoided. However, a complete ban may not always be possible e.g., in places where roads have already been built; in these cases, winter use of roads should be reduced as much as possible. In summary, management action should aim at minimizing location of roads through caribou wintering areas, and restricting winter where there are such roads.

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Brief communication

Incorporating spatial scale into ecological studies of *Rangifer*

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Key words: methodology, study area.

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Spatial scale is integral to description in ecology, including the ecology of *Rangifer.* Increasingly, we are aware that observations in ecology may be fundamentally altered, or even reversed, as a result of seemingly trivial changes in scale (Wiens, 1989). Scale has been labelled by some as the unifying feature of ecology (Allen & Hoekstra, 1992).

Particularly important are changes in the bounds of the study area (i.e., the extent) or the size of individual sampling unit (i.e., the grain). As an example, consider species associations. Such pair-wise relationships, as between caribou and moose, are typically conducted by noting the presence or absence of species in a quadrat. The results may be scale-dependent: the choice of grain, in the form of quadrat size, can dictate the direction of species associations, i.e., whether positive or negative (e.g., Schaefer & Messier, 1994).

Similarly, the choice of extent may strongly affect study conclusions. Suppose, for instance, that an animal selects strongly for a particular resource type, such as forest (Fig. 1). A study covering a large extent may indeed detect this pattern, whereas a study conducted using a smaller extent will likely conclude that no such pattern of selection exists (Fig. 1).

Unfortunately, current decisions regarding grain and extent in studies of caribou ecology are typically relegated to whim.

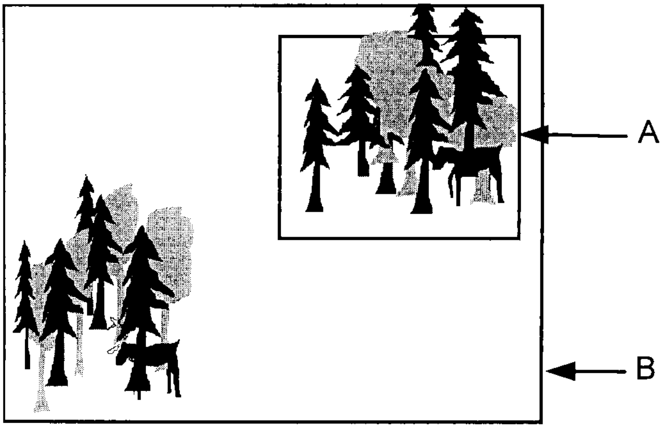

Fig. 1. Hypothetical habitat selection by an ungulate studied using small (A) and large (B) study areas.

An organism-centred approach represents a rigorous methodology for incorporating scale. For example, in the study of caribou resource selection, a natural hierarchy of scales exists, from choice of home range to choice of plant species (e.g., Schaefer & Messier, 1995). An equally useful approach is to apply the techniques of spatial pattern analysis. Largely the domain of plant ecologists, these simple methods, such as paired-quadrat variance (Fig. 2), can indicate scales of pattern for further study (Ludwig & Reynolds, 1988).

Caribou carry out their ecological functions simultaneously on many scales. This implies that no one scale of study is universally appropriate. At the same time, larger scales may offer constraints,

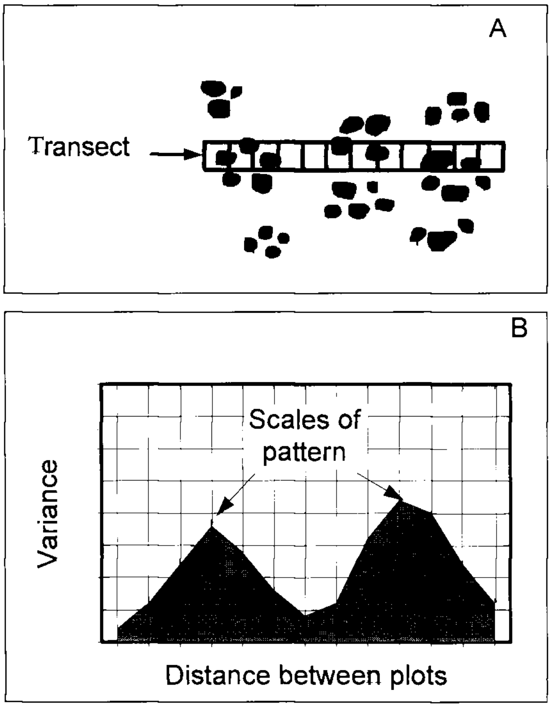

Fig. 2. Spatial pattern analysis of a hypothetical organism using paired-quadrat analysis (Ludwig & Reynolds, 1988). (A) Organism abundance is quantified using a set of contiguous quadrats. (B) Variance between pairs of quadrats is calculated and plotted as a function of inter-quadrat distance; peaks in the graph represent the scales of the clumped pattern.

and lower scales, explanations, for any scale of interest (Allen & Hoekstra, 1992). This suggests that a minimum of three scales is needed in research. For example, in the study of population dynamics, one might examine patterns on the levels of sub-population, population, and meta-population (Wells & Richmond, 1995). Fuller understanding of caribou ecology may come from descriptions that employ a hierarchy of spatial scales.

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Abstract

Autumn foraging dynamics of woodland caribou in experimentally manipulated habitat

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Abstract: Unlike other North American cervids, woodland caribou (*Rangifer tarandus caribou*) in the Selkirk ecosystem do not forage on browse. Therefore, during autumn as forbs become senescent and deciduous shrubs defoliare, caribou foraging decisions are narrowed. Shallow snow depths preclude a diet shift to arboreal lichen (*Ascomycetes*) in standing trees, as is observed in lare winter. The objecrive of this research was to determine the importance of the two principal forage irems previously reported in autumn diets: (1) arboreal lichen on windthrown trees and (2) the evergreen shrub myrtle boxwood (*Pachistima myrsinites*). Foraging ttials were conducted with three tame woodland caribou in six 5000 m^2 pens experimentally manipulated to either remove all windthrown trees and myrrle boxwood or retain extant myrtle boxwood and add "windthrown" trees by felling trees. Additionally, the pen design was such that half was in an old-growth stand of western red cedar (*Thuja plicata*)/ wesrern hemlock (*Tsuga heterophylla*) and half was in an adjacenr clear-cut.

Arboreal lichen, as a result of a large bite size, had the greatest influence on intake tate. Caribou in pens with lichen bearing windthrown trees had significantly higher intake rates ($P<0.006$) and significantly lower ($P<0.01$) eating bite rate (exclusive of search time between plants). Foraging bite rate (inclusive of search time between plants) did not differ ($P<0.20$) due ro treatment. Intake rates ($P<0.005$) and foraging bite rates ($P<0.03$) of caribou were significantly greater in timbered portions of pens. Search time was significantly greater ($P<0.005$) in clear-cut portions of pens. In the timbered portion of treatment pens, lichen comprised 34% of the total bites and 67% of the dry matter intake and arboreal lichen from windthrown ttees comprised 27% of the total bites and 52% of the dry matter intake. These data suggest that arboreal lichen is an important dietary component earlier in autumn than previously reported and extends the period that woodland caribou subsist primarily or solely on arboreal lichen 30-60 days in high snowpack ecosysrems of wesrern North America.

Tame caribou aurumn diets were comprised of <1% myrtle boxwood, in apparent conflict with observations of wild caribou in timbered habitats with myrtle boxwood. However, in these trials >95% of the myrtle boxwood occurred in the clear-cut porrion of trial pens, and forages in clear-cuts have been reported to have significantly higher levels of secondary plant compounds. Total phenolics in myrtle boxwood samples collected from the clear-cut portion of trial pens and from clear-cuts in British Columbia were 3-times grearer than levels in myrtle boxwood samples collected from old-growth stands in British Columbia. In addition, snow depths underneath the forest canopy never covered the primary forage species. I hypothesize that these woodland caribou foraged very little on myrtle boxwood because of (1) the availability of other forage species, and (2) the high level of phenolics present in myrrle boxwood during these trials.

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Workshop: Conserving woodland caribou in the managed forest

A workshop was held August 19 to foster discussion and debate on issues related to conservation of woodland caribou in the managed forest. Six panelists were invited to make brief presentations on their points of view on this subject. They were Don Thomas (Canadian Wildlife Service); Hartley Multimaki (Buchanan Forest Products); Colin Edey (NOVA Corporation); Jerry English (Ontario Ministry of Natural Resources - retired); Dale Seip (British Columbia Ministry of Forests) and Harold Cumming (Lakehead University - retired).

Following some questions and discussion with members of the audience, a "mini-debate" was set up between Don Thomas and Dale Seip to discuss in more detail the roles of the coarse vs. fine filter approaches in dealing with woodland caribou. The coarse filter implies a focus on protecting natural processes and other attributes of the whole ecosystem as a means of achieving a range of conservation goals. The fine filter approach focuses on managing individual species or addressing specific environmental concerns. There had initially been an intent to run several such debates, and to invite audience participation in them, but this plan was altered due to time constraints and substantial agreement among the panellists regarding most points.

The main points emerging from the workshop were summarized as:

1. Caribou should be conserved. (This may seem obvious, but it should not be assumed that everyone will always agree with this.)

2. The focus of caribou conservation efforts should be on maintaining or managing habitat. (Primarily, this will mean maintaining the integrity of the habitat to support caribou.)

3. An ecosystem or landscape approach should be adopted, as a backdrop for conserving caribou, and also for conserving the full range of biodiversity on the landscape.

4. There will always be a need for fine filter approaches, both for caribou, and for the multitude of other species on the landscape.

5. Effective conservation initiatives require the involvement and support of the broader community, including all relevant economic interests.

Discussion / Identification of Information Gaps

A. The ecosystem approach was seen as a commonsense strategy for conserving natural systems through maintaining or mimicking natural processes. However, there is a need for ecosystem-level research:
-to define ranges of natural variability and to refine our ability to establish acceptable treatments.
-to explore and more fully understand the implications of various spatial and temporal scales.
-to provide better and more flexible treatment options.

B. There was a clear recognition that the coarse filter approach will never be sufficient. Research will always be needed to continue monitoring various species for undesirable effects of management, and to better understand linkages between various ecosystem components.

C. We must acknowledge limitations to landscape approaches. For example, roads and other developments are in place and will continue to be developed; these fundamentally alter the landscape. We must be realistic in what can be achieved. Monitoring and study of the implications of these artificial elements will be required.

D. Management implies underlying assumptions and objectives.
- Our research and management should acknowledge "givens" such as timber allocations and other human uses.

-Our objectives should be explicit, and they should enjoy the support of the broader community.
-We must incorporate community and economic interests in developing strategies which can actually be implemented. The partnership approach was recommended as a means for doing this.

In summary, the challenge here is to deal with social and economic self-interests explicitly and place them in a context of larger conservation goals. This is needed to overcome fear and natural resistance to change.

This report was prepared by George Hamilton (Alberta Environmental Protection), Katherine Parker (University of Northern British Columbia) and Bill Dalton (Ontario Ministry of Natural Resources).

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