

*Special communication*

## The need for the management of wolves — an open letter

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**Abstract:** The Southern Mountain and Boreal Woodland Caribou are facing extinction from increased predation, predominantly wolves (*Canis lupus*) and coyotes (*Canis latrans*). These predators are increasing as moose (*Alces alces*) and deer (*Odocoileus* spp.) expand their range north with climate change. Mitigation endeavors will not be sufficient; there are too many predators. The critical habitat for caribou is the low predation risk habitat they select at calving: It is not old growth forests and climax lichens. The southern boundary of caribou in North America is not based on the presence of lichens but on reduced mammalian diversity. Caribou are just as adaptable as other cervids in their use of broadleaf seed plant as forage. Without predator management these woodland caribou will go extinct in our life time.

**Key words:** adaptive management, balance of nature, critical habitat, caribou extinction, density dependent, population regulation, wolf predation.

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### Introduction

A major ecological question that has been debated for 50 years is: are ecosystems structured from top-down (predator driven) or bottom-up (food limited) processes (Hairston *et al.*, 1960; Hunter & Price, 1992)? Top-down systems can vary widely from sea mammals such as sea otters (*Enhydra lutris*) to ground nesting birds. The sea otter causes an elegantly documented trophic cascade through sea urchins (*Strongylocentrotus* spp.) down to kelp beds (Estes & Duggins, 1995). Ground nesting waterfowl and gallinaceous birds are not limited by food resources but are regulated by top-down nest predation caused by a suite of predators, mainly skunks (*Mephitis mephitis*), red foxes (*Vulpes vulpes*) and crows (*Corvus brachyrhynchos*) (Bergerud, 1988; 1990; Sargeant *et al.*, 1993). Management decisions depend on understanding which structure is operational.

Discussions on top-down or bottom-up have been recently been rekindled with the introduction of wolves (*Canis lupus*) to Yellowstone National Park and Idaho in 1995 (Estes, 1995; Kay, 1995; 1998). The elk/wapiti (*Cervus elaphus*) population in Yellow-

stone prior to introduction were basically limited by a density-dependent shortage of food (Singer *et al.*, 1997) but now is declining from wolf predation (Crête, 1999; White & Garrott, 2005). All three states, Wyoming, Idaho, and Montana, are litigating the federal government to get the wolf delisted so they can start wolf management to maintain their stocks of big-game.

We conducted a 30 year study (1974 to 2004) of two caribou (*Rangifer tarandus*) populations, one in Pukaskwa National Park (PNP) and the other on the Slate Islands in Ontario, relative to these two paradigms of top-down or bottom-up. (Bergerud *et al.*, this conference). In Pukaskwa National Park, there was an intact predator-prey system including caribou, moose (*Alces alces*), wolves, bears (*Ursus americanus*), and lynx (*Lynx canadensis*). On the Slate Islands, our experimental area, there were no major predators of caribou. The PNP population was regulated top-down by predation and existed at an extremely low density of 0.06 caribou per km<sup>2</sup> whereas the population on the Slate Islands averaged 7-8 animals/km<sup>2</sup> over the

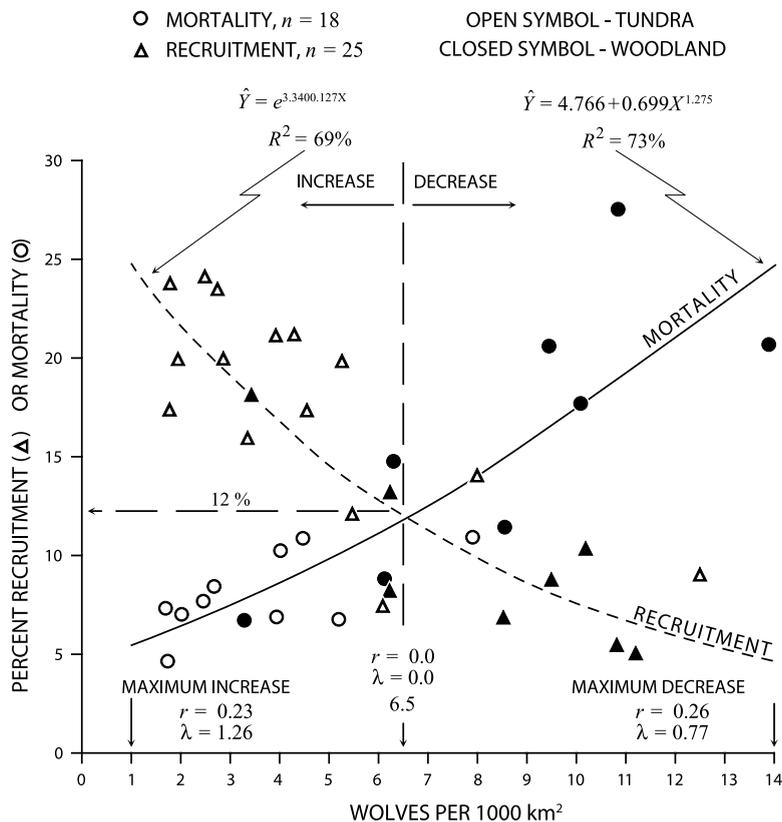


Fig. 1. The recruitment of caribou based mostly on the percentage of calves at 6 or 10-12 months-of-age, and adult mortality, both parameters regressed against the density of wolves. This figure is a modification of a figure in Bergerud & Elliott, 1986. The figure included all the studies in North America as of 1986 that had provided data on all three parameters, recruitment, adult mortality (mostly females) and wolf densities.

30 years (100X greater than in PNP). In the absence of predators, these island caribou were regulated from the bottom-up by a shortage of summer foods and the flora was impacted, resulting in some floral extinctions. The extremely low density of only 0.06 caribou per km<sup>2</sup> in PNP is normal for caribou populations coexisting with wolves (Bergerud, 1992a: Fig. 1, p. 1011). The top-down predator driven ecosystem of caribou in PNP also applies in Canada to moose, elk, and black-tailed deer (*Odocoileus bemonius*) that are in ecosystems with normal complements of wolves and bears (Bergerud, 1974; Bergerud *et al.*, 1983; Bergerud *et al.*, 1984; Messier & Crete, 1985; Farnell & McDonald, 1986; Seip, 1992; Messier 1994; Hatter & Janz 1994; Bergerud & Elliott, 1998; Hayes *et al.*, 2003).

Of all the predator driven ecosystems of cervids, the threat of extinction is most eminent for the southern mountain and boreal woodland caribou ecotypes, both classified as threatened (COSEWIC 2002, Table 11). These herds are declining primarily from predation by wolves plus some mortality from

bears. From west to east the equations for continued persistence are not encouraging -- in British Columbia the total of the southern mountain ecotype is down from 2145 (1992-97) to 1540 caribou (2002-04) and four herds number only 3, 4, 6, and 14 individuals (Wittmer *et al.*, 2005). In Alberta, the range has become fragmented and average recruitment recently was 17 calves/100 females, despite high pregnancy rates (McLoughlin *et al.*, 2003). That low calf survival is less than the needed to maintain numbers - 12-15% calves or 22-25 calves per 100 females at 10-12 months-of-age to replace the natural mortality of females (Bergerud, 1992a; Bergerud & Elliott 1998). In Saskatchewan, populations are going down,  $\lambda=0.95$  (Rettie *et al.*, 1998). The range is retreating in Ontario (Schaefer, 2003) as southern groups disappear; in Labrador the Red Wine herd is now less than 100 animals (Schmelzer *et al.*, 2004); in southern Quebec, there may be only 3000 caribou left (Courtois *et al.*, 2003), and in Newfoundland, herds are in rapid decline from coyotes (*Canis latrans*) and bear predation (G. Mercer and R. Otto, pers. comm.). In Gaspé, the

problem for the endangered relic herd is also coyotes and bear predation (Crête & Desrosiers, 1995). In Gaspé, these predators have been reduced and there is a plan in place to continue adaptive management (Crête *et al.*, 1994). Do we have to wait until the herds are listed as endangered to manage predators?

Woodland herds can be expected to decline when wolf densities exceed 6.5 wolves/1000 km<sup>2</sup> (Fig. 1). Thomas (1995) reported a similar estimate of only 5 to 8 wolves/1000 km<sup>2</sup> that seriously impacted woodland herds. Wolf populations are increasing because moose are spreading north with climate change with wolves on their heels - now some woodland caribou populations face wolf numbers greater than 7-8/1000 km<sup>2</sup>. These wolves commonly switch from moose to caribou in the winter especially when deep snow increases the difficulties of killing moose (Mech *et al.*, 1998).

I do not agree with one option expressed at this conference that we not try and save these southern vulnerable herds. Not only can extinction be avoided but with pulsed reductions of predators, both predator and prey can prosper. In the Muskwa region of British Columbia, both elk and moose were decreasing from 1982 to 1985. 505 wolves were removed in 1984, 1985, and 1987; by 1988-89, the total elk plus moose populations in the region had increased from 23 000 to 33 000 animals. Further five cohorts of caribou and Stone's Sheep during and just after the removal had recruitment > than 25 young per 100 females; hence these populations also increased. Wolves then emigrated into the vacant wolf territories and reached densities of 20 wolves/1000 km<sup>2</sup> by 1990 (Bergerud & Elliott, 1998). Because these ungulate systems are not food limited, **with management we could have it all - densities of caribou of 1 per km<sup>2</sup> and more wolves**; without management, we will have extinctions and fewer wolves. We know the problem, yet continue to spend large sums on research that could be used for adaptive management (*sensu* Walters & Hilborn, 1978). We should be counting and radio tracking wolf populations. The problem is not the habitat, it is predation; habitat per se does not kill caribou. The Slate Island study documented the wide tolerance levels of caribou for disturbed habitats and meager lichen supplies, but also showed their wide use of herbaceous and deciduous forage; they are a very tolerant adaptable species (see also Cringan, 1956 and Bergerud, 1977).

### The northward march of extinction

The northern demise of woodland caribou in the Lake States started in the middle of the 1800s (Fig. 2) (Cringan, 1956; 1957; Fashingbauer, 1965). The common cliché is that this decline resulted from

habitat disturbance (fire and logging and human disturbance); the altered deciduous forest that lacked lichens were not suitable and coupled with disturbance, the animals shifted further north. These ideas are in error. The animals did not move north. The animals remained and declined because of increased mortality. Cow caribou show philopatry to their calving habitat and do not shift, **when they can't be found they have died**.

There was a rise in temperatures when the "The Little-Ice-Age" ended in the 1850s. This warming trend coincided with the opening of the coniferous canopy by logging, facilitating deciduous succession. The range of both moose and later white-tailed deer (*O. virginianus*) expanded north. Riis (1938) stated that there were no deer in the caribou range in Minnesota in 1860. By 1900, the deer were common north to the Canadian border and the Minnesota caribou were gone. The deer brought the brain worm disease fatal to caribou (i.e., *Paraelaphostrongylus tenuis*; Bergerud & Mercer, 1989; Bergerud, 1992b) and both the deer and the moose provided an increase in prey biomass that supported a larger wolf population. It was increased mortality that caused the caribou extinction, and warming temperatures were a factor in the expansion north of the two other cervid species.

Baker (1983) argued that caribou in the 1800s may have only populated northern Michigan and Wisconsin during the autumn, winter, and early spring. The latest spring record for Michigan is March 2 and April 18 in Wisconsin. Caribou in northern Minnesota were also seen only in the fall and winter (Fashingbauer, 1965). The last stronghold of the herd in Minnesota was on the muskeg north of Red Lake. The old leads from that muskeg went directly north to the shore of Lake-of-the-Woods (Bergerud, 1992b), where the caribou had previously calved on the islands. In Wisconsin, the caribou probably calved on the Apostle Islands. In Michigan, Isle Royale was a strong hold but the animals were gone by 1926 (Dustin, 1946 in Cringan, 1956). Other islands in Michigan occupied included High, Beaver and Drummond (Burt, 1946; Cringan, 1956). Hence, the caribou decline during this period resulted from increased mortality from hunting, predation, and disease that took place in the period when water safety was not available. The spring and summer strategy of remaining near water escape habitat remained successful.

In our study, the PNP population had adequate summer survival because of its proximity to water safety in Lake Superior. It also resided in an undisturbed wilderness park with abundant winter lichen food, but the caribou were susceptible to winter wolf predation when land fast ice formed on Lake Superior in the winter. This undisturbed wilderness (balance

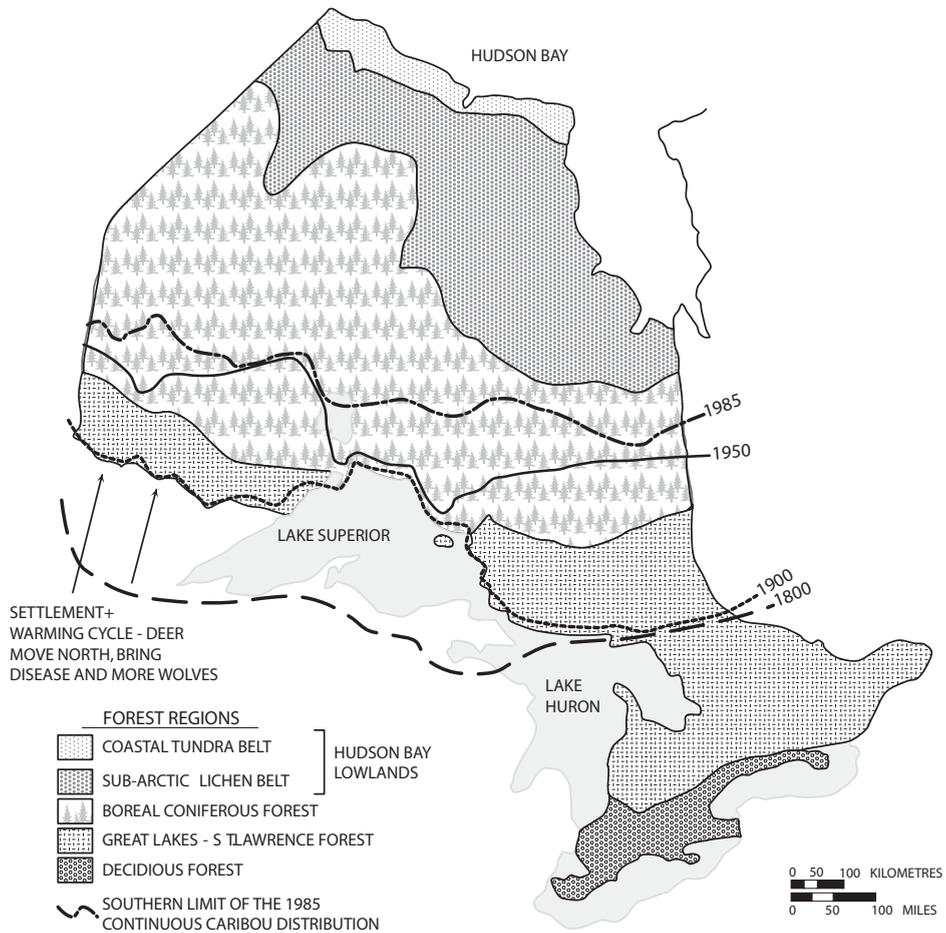


Fig. 2. The line of continuous distribution has moved northward since the end of the Little Ice Age as moose and deer moved north increasing the mortality of caribou through predation and disease. Hunting also contributed to the decline of caribou.

of nature view) and the abundant lichens were not sufficient to maintain numbers. The Slate Island population has persisted for 50+ years on an island archipelago in the absence of predators by foraging primarily on deciduous/herbaceous forage and ground hemlock; the presence of extensive lichens was not necessary for their persistence. In recent years these caribou have persisted despite considerable disturbance from power boats, canoeists, and kayakers.

But the late 1800s scenario is here again, as logging is hastening secondary succession. Temperatures are rising, accelerating the growth of deciduous species more favorable to moose and deer. The density of wolves is increasing and leading to predation rates greater than the equilibrium needed for recruitment to balance mortality for caribou (Fig. 1). The southern mountain and boreal woodland caribou will go extinct south of 60°N in our time unless we are prepared to manage wolf populations and find a solution to the *P. tenuis* disease.

### Fragmentation of the Ontario caribou distribution

*“Because of forest fires, timber operations and spruce budworm infestations much of the climax forest was removed and replaced by forests ... favourable to moose and deer. Consequently moose and deer increased, while caribou become confined to islands of suitable habitat, each island being surrounded by newly-created moose and deer range... the higher population of wolves now supported by moose and deer in the peripheral range may have an adverse effect on the caribou populations”* (Simkin, 1965, p. 46). Everything that goes around comes around.

Fragmentation of the southern distribution of woodland caribou commenced in the mid 1800s in northern-central Minnesota, Wisconsin and Michigan, and has now reached midway across Ontario (Fig. 2). This range loss has repeatedly been attributed to forest harvest, wildfires, and settlement. This over simplification explains little. For the population to disappear, mor-

tality has to exceed recruitment. The problem is not the summer critical range; the fidelity of calving near water bodies results in satisfactory recruitment (>15%, Bergerud, 1974; 1992a). Simkin (1965) documented 40 years ago in his research on the islands at Irregular Lakes that 86% of the cows were accompanied by calves in three summers; that calf survival was better than the enclosure study of pregnant females in the Yukon discussed at this conference (Farnell *et al.*, this conference). Islands are enclosures in the growing season but become predator traps when ice forms. Cumming & Beange (1987) reported a recruitment of 21 per cent calves in the Lake Nipigon herd where males also used the islands. But when lakes freeze and the animals aggregate, this survival advantage disappears. The mortality sequence is complex: initially, the forest canopy is opened (logging + land-clearing + fires), summer temperatures can increase (end of The Little Ice Age-1850), deciduous forage increases, white-tail deer and moose expand their range and, then the wolf population increases; the mortality of caribou from disease, predation and hunting exceeds the high summer calf increments. Gradually, all the females and their female progeny that recognize a safe calving location and show philopatry are gone, and a summer critical range is left vacant. Vors *et al.* (in press) calculated that in central Ontario, the time sequence from the time an area is logged until the caribou disappear is now about 20 years. With global warming it may be sooner.

When a tradition is lost the range is fragmented. It is the "burned-out" marsh theory of Albert Hochbaum (1955): when all the locally reared ducks that first saw their natal marsh from the air are killed by local hunters before they disperse, the breeding homing tradition to that marsh is lost. When the last females are killed that calve on the shore and islands of Lake Nipigon, Ontario, the tradition will be lost and the line of continuous occupation will be retreat further north. Lost traditions are near-impossible to rebuild.

## Critical habitat

The Federal Species At Risk Act requires that critical habitat be identified. It is generally accepted that the calving grounds of the migratory barren-ground herds are the critical habitat (review Russell *et al.*, 2002). However some still do not recognize that the key value of that habitat is reduced predation risk rather than optimal foraging. The critical habitat of the montane (southern mountain) and boreal woodland populations (the sedentary ecotype) is also the habitat used for calving to reduce predation risk for their neonates. The calving locations for this ecotype

are the anchors to their annual ranges and philopatry is strong (Shoesmith & Storey, 1977; Hatler, 1986; Brown *et al.*, 1986; Edmonds, 1988; Cummings & Beange, 1987; Schaefer *et al.*, 2000). The spacing of the females at calving represents the maximum spread of each "herd" and the concept of being rare (Bergerud, 1990). This distribution represents the key density-dependent component in the regulation of the herd by predation. Herds with densities above  $D_s$  (the stabilizing density) should decline from predation until the surviving females are sufficiently spaced due to philopatry that densities are less than  $D_s$  and predation pressures are reduced and recruitment equals mortality, population extinction is avoided (Bergerud, 1992a). This spacing strategy has evolved at the fitness level of the individual female but supports the persistence of the group (population).

This wide spacing of the females complicates a description of what is critical habitat, but normally the basic component is that water is available for escape. Water is the great equalizer and its value known in traditional knowledge. A Labrador hunter from Hopedale, described why deer (caribou) calve "*in mossy places and nearly always near water... with the wolves around the only chance these little ones get to have a rest is they head for water... they go in about two or three feet and the wolf can't do nothing because the wolf's legs are shorter than the deer*" (Brice-Bennett, 1977, p.161). On August 14, 1779, Captain Cartwright noted along the Labrador coast "*When pursued in the summer time they (deer) always make for the nearest water, in which no land animal has the least chance with them*" (Townsend, 1911). Large lakes with many islands, such as Lake Nipigon, Trout Lake, and Lac St Joseph in Ontario should be listed as critical habitat. The small islands in these lakes are absolutely safe; wolves are not prepared to swim between islands that don't have moose, only to have the females and calves that are living near the shore of the island swim to another island (Bergerud *et al.*, 1990). More lakes further north will have to be added to the list as temperatures advance and these lakes are free of ice in May/June. For montane animals, the critical habitat would commonly be the high alpine ridges used to space away from moose and wolves below, but these alpine ridges are not nearly as safe as shoreline retreats.

Old growth forest and lichens stands are not critical habitat. The southern limit of caribou is not based on lichen abundance. In the last glacial period, as the Laurentide Ice sheet retracted 12 000 to 10 000 ybp the caribou spread north from the Appalachian Mountains, where they had persisted during the ice age, moving into mixed conifer and hardwoods and jack pine/spruce forests. They did not generally inhabit either taiga or tundra lichen ranges; only 5 of

**Table 1.** Comparison of moose densities in Ontario 1974-85 *vs.* 2001 and management goals for Ontario Wildlife Management Units as projected in 2001 that still have a continuous caribou distribution (Fig. 3). Files provided the author from OMNR files, Thunder Bay office in 2006<sup>5</sup>.

WMU Area		Moose per km <sup>2</sup>			% change estimated	Wolves per 1000 km <sup>2</sup>	
No.	km <sup>2</sup> x 1000	74-85	01	Goal	2001 to Goal	2001	Goal <sup>1</sup>
1A	78.9)			0.04	0	5.3	5.3
1C	93.0)	0.003	0.08	0.08	0	6.4	6.4
1D	111.3)			0.004	0	4.3	4.3
2 <sup>2</sup>	7.0	0.08	0.13	0.25	92	<b>7.8</b>	<b>11.0<sup>3</sup></b>
16A	14.3)		0.04	0.06	50	5.3	5.9
16B	8.4)	0.05	0.11	0.15	36	7.2	<b>8.3</b>
16C <sup>4</sup>	9.8)		0.10	0.16	60	7	<b>8.6</b>
17	27.8	0.05	0.04	0.06	50	5.3	5.9
18A	7.8)		0.11	0.17	54	7.3	<b>8.9</b>
18B	11.1)	0.07	0.03	0.04	33	5.1	5.3
19	9.6)		0.18	0.19	6	9.1	9.4
24	18.6	0.07	0.11	0.13	18	7.2	7.8
25	38.6	0.01	0.04	0.05	25	5.3	5.6
26	25.9	0.02	0.05	0.05	0	5.6	5.6

<sup>1</sup> calculated from:  $Y=4.239+27.217x$ , wolf densities regressed on moose densities (see Bergerud *et al.* this conference, Fig. 10), this equation is conservative since the caribou biomass is not included.

<sup>2</sup> Includes Woodland Caribou Provincial Park.

<sup>3</sup> **In bold:** wolf densities that will cause the decline of caribou.

<sup>4</sup> Includes a portion of Wabakimi Provincial Park.

<sup>5</sup> In February 2007, OMNR supplied me with their latest targets (2003). These targets (goals) were essentially the same as their goals in 2001 except moose had been censused in WMU 1C at 3369 (0.04/km<sup>2</sup>) rather than rough estimate in 2001 of 7000 animals. The philosophy remained unchanged 2001 to 2003 of setting targets based on maximum moose projections without consideration of the impact that more moose would have wolf numbers and the negative spin-off to caribou.

21 fossil locations were in the taiga/tundra (Bergerud & Luttich, 2003). In the late Holocene, 4000 to 500 ybp, they were south again residing in forests of pine and northern hardwoods (Faunmap, 1994, Bergerud & Luttich, 2003). The southern boundary was not old growth forests and not lichen dependent but determined by the abundance of spermatophytic species that supported deer, moose, and elk populations. These cervids, in turn, sustain a suite of predators: mountain lions (*Felis concolor*), wolves, and bears that were too abundant for caribou to persist (top-down not bottom-up). **The diversity of mammal species set the southern limit for the distribution of caribou and not the abundance of lichens.**

We have wasted so much time measuring lichen abundance for a bottom-up answer to the low caribou numbers. I overlooked lynx predation in Newfoundland for years (Bergerud, 1971) measuring lichens, because I had been taught that predation did not regulate population numbers (Errington, 1946; Errington, 1967).

Caribou are constantly switching winter lichen ranges. They adapted long ago to rotating their range use from overgrazing and trampling, from the loss of habitat from forest fires and the changing snow cover. Further, they can maintain their numbers and physical condition foraging on earlier lichen successions, evergreen shrubs, ground hemlock, horsetail, winter greens, etc. (Bergerud & Nolan, 1970; Bergerud, 1972; Miller, 1976; Bergerud review, 1977; Luick review, 1977). In this study, caribou on the Slate Islands maintained densities greater than 4/km<sup>2</sup> for the past 60+ years without meaningful amounts of terrestrial and few arboreal lichens and inhabiting what was originally a relatively young forest (Cringan, 1956). True, animals on the Slate Islands were at times in poor physical condition in the fall, but that was not due to the quality of the food but due the extreme densities of animals. On the Slate Island, the fecal nitrogen (FN) in three years was 40% higher in May and early June than for five other herds in North America - the mean FN for females on the Slate Islands was 3.38±0.117%,

and for males  $3.53 \pm 0.111\%$ , compared to  $1.81 \pm 0.079\%$  for females and  $2.20 \pm 0.067\%$  for males in five other herds (Bergerud, 1996: Table 1 p. 96.)

When the last female is killed by wolves in the lichen-rich undisturbed Pukaskwa National Park -- and time is short as the remaining animals may number less than 10 -- the herd will be gone. The caribou on Michipicoten residing in a **hardwood forest** may be the last relic herd in northeastern Ontario - but the island is now a park and if a wolf reaches the island, would control be allowed? Can we finally reject the closely held view that caribou are wilderness animals that require climax forests and lichens, and saving such habitats is the panacea for persistence? This climax-lichen theory has hindered our understanding of the adaptability of the species for the past 50 years.

## The Balance of Nature

When caribou biologists attempt to reduce wolf populations to increase caribou stocks, they are blamed for intruding into the Balance of Nature, a community of animals that has evolved together where the community is greater than the sum of the individual species and there is a system of checks and balances that prevents extinction. Charles Elton, the father of ecology (Elton, 1924; 1927) said "*it is assumed that an undisturbed animal community lives in a certain harmony ... the balance of nature. The picture has the advantage of being an intelligible and apparently logical result of natural selection in producing the best possible world for each species. It has the disadvantage of being untrue*" (Connell & Sousa (1983) quoting Elton). Connell & Sousa (1983), in their extensive review of the stability and persistence of a wide variety of animal populations from protozoans to rodents, concluded that the evidence in the past 50 years upholds Elton's description. The Balance of Nature is not a scientific hypothesis, since there is no disproof that the advocates will accept. It is a closely held idea that is not testable. The Balance of Nature advocates, as a last argument blame imbalances between predator and prey as an artifact of man's intrusion.

The most widely quoted balance of nature example in wildlife management is the interaction of wolves and moose on Isle Royale, Michigan (Mech, 1966). The moose have not gone extinct and there was evidence of territorial self regulation in the wolf population. However, Isle Royale is an experimentally unnatural area, as is the Slate Islands. The artifacts of that study were that there was little opportunity for egress-ingress of the wolves, the major pathway by which they adjust their numbers, and that there were no bears on the island, a major predator of moose. Van Ballenberghe *et al.* (1975) challenged the belief of self regulation

by showing that wolf numbers were based on prey biomass not territorial exclusion. Keith (1983) and then Fuller (1989) showed that in an open system, wolves are constantly dispersing, and we now calculate wolf numbers on the basis of prey biomass equations.

In the period 1959 to 1974, there appeared to be an equilibrium between wolves and moose on Isle Royale (Mech, 1966, Peterson, 1977). But since that time, the equilibrium has been lost. Wolves developed canine parvovirus (CPV) in 1980 or 1981 and crashed (Peterson *et al.*, 1998) and in the 1990s, there was a four fold increase in moose (see Fig. 1 in Wilmers *et al.*, 2006). Pimm (1991), in a penetrating discussion of the Balance of Nature, argues that assumed equilibriums between predator and prey commonly disappear in long term investigations. In the 1990s, McLaren & Peterson (1994) documented that the growth rings of balsam fir (*Abies balsamea*) on Isle Royale had depressed growth in periods when wolves were rare - these authors postulated a wolf-induced trophic cascade (wolves>moose>fir)- top-down.

The concept that wolves and caribou evolved together and therefore will continue to coexist is not valid. The Faunmap's (1994) tabulation of mammalian fossils in the United States south of Canada from 40 000 to 10 000 ybp shows 22 fossil locations of wolves west of 98W lat. and only three east where the woodland caribou persisted during the Wisconsin ice age. From 30 000 to 10 000 ybp, the eastern woodland caribou persisted only in the Appalachian Mountains (Bergerud & Luttich 2003, and in press). Other common species of mammals in the Appalachians during these years were the Jefferson ground sloth (*Megalonyx jeffersonii* (4 records), tapirs, *Tapirus* (9 records), *Mylobus*, the long-nosed peccary (11 records), and *Platygonus compressus*, the flathead peccary (7 fossils). The most common predator was the black bear (6 records). No wolf fossils from 40 000 to 10 000 have been found in those mountains. The fossil record besides the species listed includes armadillos, prairie ground squirrels, skunks, and jaguars (Churcher *et al.*, 1989; Faunmap, 1994). This was not the boreal community where caribou and wolves interact today and are supposed to have evolved their balance of nature.

The Herculean study of the fossil mammal fauna of the Late Quaternary at 2945 sites in the United States (Faunmap, 1994) was published in *Science* by 20 distinguished investigators (Graham *et al.*, 1996). They summarized that the record of fossil mammals supported the Gleasonian community model rather than the Clementsian community model that stresses competitive interaction. The Gleasonian model assumes that species respond to environmental changes in accordance with individual tolerance with varying rates of range shift. These authors concluded (page

1601) "modern community patterns emerged only in the last few thousand years and many late Pleistocene communities do not have modern analogs." Hence, each species through individual selection evolves its own distinct behavior/habitat strategies to persist, but they are not guaranteed to avoid extinction. Each species walks its own road down through time - there is no balance of nature.

### Adaptive management of wolves

Will we leave the fate of woodland caribou to mitigation of habitat/disturbance questions, or will we reduce the natural mortality rate of caribou by wolf reductions? Mitigation endeavors in lieu of wolf reduction will not succeed if the cause of the declining population is too many wolves. Mitigation recommendations commonly call for reducing road net works/seismic lines, access for wolves, reducing and or redistributing logging, oil development, and etcetera. These problems didn't exist in Pukaskwa National Park. Furthermore, the PNP population had satisfactory summer survival. Yet, those caribou are facing extinction from predation even though in the 1990s only two wolf packs existed relatively close to the caribou along the coast.

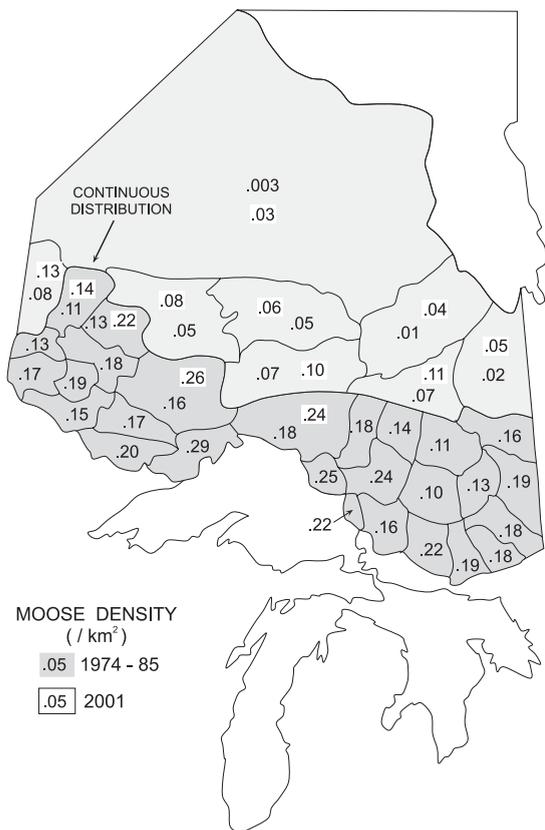
Nor should we blame human development for the supposed advantages they have given wolves. Caribou are better able in coping with development than wolves. The Central Arctic Herd grew from 5000 in 1977 to 27 000 in 1999 as the oil field developed (Russell *et al.* eds., 2002). The adjacent controversial Porcupine Herd calving in a wildness wildlife refuge where there has been no economic development grew from  $\approx$  100 000 to 178 000 by 1989 and then declined to 123 000 by 2001, experiencing heavy predation of young of the year (Griffith, 2002). We live in the age of the industrial revolution with its footprint everywhere and the depletion of the earth's resources. Intrusion into the predator-prey system cannot be avoided if we want prey persistence and diversity which will also benefit the predators. Mitigation without predator reductions will not work. Wolves are a highly intelligent species with prey switching part of its *modus operandi*; too many moose equals too many wolves and too few caribou.

Caribou/predator management will work. The woodland herds in the Yukon are the most successfully managed in North America. They have been increasing as a result of intense management (COSEWIC, 2002). The caribou herds are counted reasonably accurately and recruitment is measured annually. Moose recruitment and numbers are constantly monitored. Wolves are censused and radio tracked. In recent years, some wolf populations have been both reduced and fertility control experimented with (Hayes *et al.*, 2003). At this conference, Farnell *et al.*

and Adams *et al.* reported on a management endeavor where pregnant females were captured and held in an enclosure in which predators were excluded until their calves were three weeks of age. Surveys in the fall showed 74-76% of the former captive calves still alive compared to a survival of calves born in the wild exposed to predation of 13 to 32%. This is the ultimate experiment that should convince even the most die-hard skeptic on the huge loss of calves of the montane ecotype in their first summer to predators (Bergerud *et al.*, 1984). The monitoring of caribou herds in British Columbia and Alberta has improved in recent years and they are moving towards management. Elsewhere in Canada, there are no plans to manage wolves. Most jurisdictions do not even monitor caribou numbers and recruitment (Labrador is an exception).

In Ontario, home to the Slate Islands and the PNP populations, there is no caribou management. The Ontario Ministry of Natural Resources does not count caribou herds or measure recruitment, nor does it census or radio track wolves. The Department's ungulate management program is directed at increasing moose. Woodland Caribou Park and Wabakmi Provincial Park are the southern corner-stones of the continuous distribution of caribou in Ontario, yet the goal of the biologists in 2001 for Wildlife Management Units (WMU 2 and WMU 16c) that contain these parks established for caribou, is to increase the moose populations by 92% and 60% (Table 1), see Fig. 3. Their moose strategy, if successful, will eliminate the caribou. Moose densities of 0.25 and 0.16/km<sup>2</sup> are far too high. The goal should be to *decrease* these moose populations so the caribou can increase. This technique is now being tested in British Columbia (D. Seip, *pers. comm.*). The behaviour of caribou in both Woodland Caribou Park and Wabakmi Park is to calve on islands (Simkin, 1965; Cumming & Beange, 1987; Bergerud *et al.*, 1990; Racey & Armstrong, 1998). The island calving strategy will continue to provide satisfactory summer calf survival, but after the lakes freeze, wolves will commonly switch from moose to caribou when snow depths increase. Global warming will increase the duration of water for escape in the spring but in the winter, ice will be reduced and slush will reduce escape advantages. This predation will lead to further fragmentation of the continuous distribution in Ontario.

Darby & Duquette (1986) listed 9 mitigating points to maintain Ontario caribou (pages 91-92). Point 8 "implement predator control if wolf predation rates on caribou increase. This is likely to occur if moose or deer densities increase following cutting." Now global warming is increasing the spread of these cervid species faster than 20 years ago. Point 9 stated "discourage moose and deer populations from increasing in or adjacent to caribou



**Fig. 3.** The line of continuous caribou in 1985 (Darby & Duquette, 1986) bisected the boreal coniferous forest (Fig. 2) but also bisected the moose range with moose densities greater than 0.10/km<sup>2</sup> south of the discontinues distribution of caribou and the continuous distribution north of the line. Only relic herds are still found south of the line that have special escape habitat such as PNP with the Lake Superior coast and the herds on islands in Lake Superior, i.e. Slate Islands, Pic Island and Michipicoten Island (Bergerud, 1989). The moose have increased north of the line between 1985 and 2001 and wolves are predicted to exceed 6.5/km<sup>2</sup> causing herds to decline in WMUs that now have more than 0.10 moose/km<sup>2</sup>. Densities are based on OMNR statistics from the Thunder Bay office provided to me in 1989 and in 2006.

range. Application of herbicides to cutovers may do this while encouraging conifer regeneration." These comments were made 20 years ago and still no one is listening, nor do many care. In Ontario, environmental groups will probably never support wolf management and instead will argue for the mitigation of disturbance factors. This argument will not save the caribou. There is no hunter clientele to argue for management, as is the case for elk in Yellowstone Park. Nor

will the creation of more parks be helpful, which is the World Wildlife Fund's solution to the caribou conservation conundrum (Petersen *et al.*, 1998). The Park solution means wolves cannot be managed and the rationale is based on the faulty bottom-up premise that caribou require old growth habitat with undisturbed lichens. The phenomenal success of the caribou on Pic Island (Ferguson, 1982; Ferguson *et al.*, 1988), the Slate Islands and Michipicoten Island, and their demise in the lichen rich wilderness of Pukaskwa National Park give a different insight. There is no caribou conservation conundrum, only a lack of political will.

## References

- Adams, L., Garnell, R., Oakley, M., Roffler, G. H., & McLelland, J. 2006. The *Chisana caribou recovery project: a modeling assessment of the utility of captive rearing as a management tool for at-risk caribou*. Abstract: 11th North American Caribou Conference, Jasper, Alberta.
- Baker, R. H. 1983. *Michigan Mammals*. Michigan State University Press.
- Bergerud, A. T. 1971. The Population Dynamics of Newfoundland Caribou. – *Wildl. Monogr.* No. 25.
- Bergerud, A. T. 1972. Food habits of Newfoundland caribou. – *J. Wildl. Manage.* 36: 913-923.
- Bergerud, A. T. 1974. Decline of caribou in North America following settlement. – *J. Wildl. Manage.* 38: 757-770.
- Bergerud, A. T. 1977. Diets for caribou. – In: M. Rechcigl (ed.). *CRC Handbook, Series in Nutrition and Food, Section D: Diets, Culture Media, Food Supplements* Vol. 1. CRC Press, Cleveland, Ohio, pp. 243-266.
- Bergerud, A. T. 1988. Population ecology of North American Grouse. – In: A. T. Bergerud & M. W. Gratson (eds.). *Adaptive Strategies and Population Ecology of Northern Grouse*. Univ. Minnesota Press, Minneapolis, pp. 473-577.
- Bergerud, A. T. 1989. *The Abundance, Distribution and Behaviour of Caribou in Pukaskwa National Park, 1972-1988*. Unpubl. Report Pukaskwa National Park, Ontario. 143pp.
- Bergerud, A. T. 1990. Rareness as an antipredator strategy to reduce predation risk. – *Proc. International Congress. of Game Biologists* 21: 15-25.
- Bergerud, A. T. 1992a. Rareness as an antipredator risk for moose and caribou. – In: D.R. McCullough & R. H. Barrett, (eds.). *Wildlife 2001 Populations*: Elsevier Applied Science, New York, pp. 1008-1021.
- Bergerud, A. T. 1992b. *Factors limiting the reintroduction of caribou to Voyageurs National Park, Minnesota and a habitat suitability model*. Bergerud and Associates, Fulford Harbour, B. C. 136 pp.
- Bergerud, A. T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? – *Rangifer Special Issue* No. 9: 95-116.

- Bergerud, A. T., Butler, H. E. & Miller, D. R. 1984. Antipredator tactics of calving caribou: dispersion in mountains. – *Can. J. Zool.* 62: 1566-1575.
- Bergerud, A. T. & Elliott, J. 1986. Dynamics of caribou and wolves in northern British Columbia. – *Can. J. Zool.* 64: 1515-1529
- Bergerud, A. T. & Elliott, J. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. – *Can. J. Zool.* 76: 1551-1569.
- Bergerud, A. T., Ferguson, R. & Butler H. E. 1990. Spring migration and dispersion of woodland caribou at calving. – *Anim. Behav.* 39: 360-368.
- Bergerud, A. T. & Luttich, S. N. 2003. Predation risk and optimal foraging trade-off in the demography and spacing of the George River Herd, 1958 to 1993. – *Rangifer* Special Issue No. 14: 169-191.
- Bergerud, A. T. & Mercer, E. 1989. Caribou introductions in eastern North America. – *Wildl. Soc. Bull.* 17: 111-120
- Bergerud, A. T. & Nolan, M. 1970. Food habits of hand-reared caribou (*Rangifer tarandus*) in Newfoundland. – *Oikos* 21: 348-350.
- Bergerud, A. T., Wyett, W. & Snider, D. B. 1983. The role of wolf predation in limiting a moose population. – *J. Wildl. Manage.* 47: 977-988.
- Brice-Bennett, C. 1977. Land use in the Nain and Hopedale regions. – In: Brice-Bennett C. (ed.). *Our Foot Prints Are Everywhere*. Labrador Inuit Association, Ottawa, pp. 97-204.
- Brown W. K., Huot, J., Lamothe, P., Luttich, S., Paré, P., St-Martin, G. & Theberge, J. B. 1986. The distribution and movement of four woodland caribou herds in Quebec and Labrador. – *Rangifer* Special Issue No. 1: 43-49.
- Burt, W. H. 1946. *The Mammals of Michigan*. Univ. Mich. Press, Ann Arbor.
- Churcher, C. S., Parmalee, P. W., Bell, G. L. & Lamb, J. P. 1989. Caribou from the late Pleistocene of north-western Alabama. – *Can. J. Zool.* 67: 1210-1216
- Connell, J. H. & Sousa, P. 1983. On the evidence needed to judge ecological stability or persistence. – *Am. Nat.* 121: 789-824.
- COSEWIC. 2002. *COSEWIC assessment and update status report on the woodland caribou Rangifer tarandus caribou in Canada*. Committee on the Status of Endangered Wildlife in Canada in Canada, Ottawa. 98pp.
- Courtois, R., Quillet, J.-P., Gingras, A., Dussault, C., Breton, L. & Maltais, J. 2003. Historical changes and current distribution of caribou, *Rangifer tarandus*, in Quebec. – *Can. Field Nat.* 117: 399-414.
- Crête, M. 1999. The distribution of deer biomass in North America supports the hypothesis of exploitation ecosystems. – *Ecology Letters* 2: 223-227.
- Crête, M., Barette, C., Boulanger, R., Ferron, J., Fournier, N., Huot, J., Huot, M., Lamoureux, J., Leveque, J. & Ross, H. 1994. *National recovery plan for Gaspésie caribou*. RENEW Rept. No. 9. Recovery of Nationally Endangered Wildlife Committee, Ottawa. 18pp.
- Crête, M. & Desrosiers, A. 1995. Range extension of coyotes, *Canis latrans*, threatens a remnant herd of caribou, *Rangifer tarandus* in southeastern Quebec. – *Can. Field Nat.* 109: 227-235.
- Cringan, A. T. 1956. *Some aspects of the biology of caribou and a study of the woodland caribou range of the Slate Islands, Lake Superior, Ontario*. M.A. thesis, Univ. of Toronto.
- Cringan, A. T. 1957. History, food habits and range requirements of the woodland caribou of continental North America. – *Trans. N. Am. Wildl. Conf.* 22: 485-501.
- Cumming, H. G. & Beange D. B. 1987. Dispersion and movements of woodland caribou near Lake Nipigon, Ontario. – *J. Wildl. Manage.* 51: 67-79.
- Darby, W. R. & Duquette, L. S. 1986. Woodland caribou and forestry in Northern, Canada. – *Rangifer* Special Issue No. 1: 87-93.
- Edmonds, E. J. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. – *Can. J. Zool.* 66: 817-826.
- Elton, C. 1924. Periodic fluctuations in number of animals: Their causes and effects. – *J. Exper. Biol.* 2: 119-163.
- Elton, C. 1927. *Animal Ecology*. London: Sidgwick and Jackson.
- Estes, J. A. 1995. Top-level carnivores and ecosystem effects: Questions and approaches. – In: Jones, C. G. & J. H. Lawton, (eds.). *Linking Species and Ecosystems*. Chapman and Hall, New York, New York, pp. 151-158.
- Ester, J. A. & Duggins, D. O. 1995. Sea otters and kelp forests in Alaska : generality and variation in community ecological paradigm. – *Ecol. Monogr.* 65: 75-100.
- Errington, P. L. 1946. Predation and vertebrate populations. – *Quart. Res. Biol.* 21: 144-177.
- Errington, P. L. 1967. *Of Predation and Life*. Iowa State Univ. Press, Ames, Iowa.
- Farnell, R. & McDonald, J. 1986. *The demography of Yukon's Finlayson Caribou Herd 1982-1987*. Progress Rept. Yukon Renewable Resources, Whitehorse, 54pp.
- Farnell, R., Oakley, M., Adams, L. G., McLelland, J. & Roffler, G. H. 2006. *Captivity protocol and efficacy of a field application to raise recruitment of a declining woodland caribou population*. Abstract: 11th North American Caribou Conference, Jasper, Alberta.
- Fashingbauer, B. A. 1965. The woodland caribou in Minnesota... – In: *Big Game in Minnesota*. Minn. Dept. of Conservation, St. Paul, Minnesota Tech. Bull. 9, pp. 133-166.
- Faunmap. 1994. *A Data Base Documenting Late Quaternary Distributions of Mammal Species in the United States*. Illinois State Museum, Scientific Papers 25 (1 and 2) (3 compilers, and 14 collaborators).
- Ferguson, S. H. 1982. *Why are Caribou on Pic Island?* M.Sc. thesis, University of Victoria, British Columbia.
- Ferguson, S. H., Bergerud, A. T. & Ferguson, R. 1988. Predation risk and habitat selection in the persistence of remnant caribou population. – *Oecologia* 76: 236-245

- Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. – *Wildl. Monogr.* No. 105.
- Graham, R. W. *et al.* (20 authors). 1996. Spatial response of mammals to late Quaternary environmental fluctuations. – *Science* 272: 1601-1606.
- Griffith, B. 2002. The Porcupine Herd, – *In: Arctic Refuge Coastal Plain Terrestrial Wildlife Research Summaries*. U.S. Dept of Commerce, Springfield, Va., Biological Science report USGS/BRD/BSP 2001-002, pp. 8-37.
- Hairston, N. G., Smith, F. E. & Slobodkin, L. B. 1960. Community structure, population control and competition. – *Am. Nat.* 194: 421-425.
- Hatler, D. F. 1986. *Studies of radio-collared caribou in the Spatsizi Wilderness Park area*. Report 3, British Columbia Spatsize Association for Biological Research, Smithers. British Columbia.
- Hatter, I. & Janz, D. W. 1994. The apparent demographic changes in black-tailed deer associated with wolf control in northern Vancouver Island, Canada. – *Can. J. Zool.* 72: 878-884.
- Hayes, R. D., Farnell, R., Ward, R. M. P., Carey, J., Dehn, M. & Kuzyk G. W. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. – *Wildl. Monogr.* No. 152.
- Hochbaum, H. A. 1955. *Travels and Traditions of Waterfowl*. Univ. of Minnesota Press, Minneapolis.
- Hunter, M. D., & Price, P. W. 1992. Playing chutes and ladders: bottom-up or top-down forces in natural communities. – *Ecology* 72: 724-732.
- Kay, C. E. 1995. An alternative interpretation of the historical evidence relating to the abundance of wolves in the Yellowstone ecosystem. – *In: L.N. Carbyn, S.H. Fritts & D. R. Seip (eds.). Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute, Occasional Publication 35, pp. 77-84.
- Kay, C. E. 1998. Are ecosystems structured from the top-down or bottom-up: a new look at an old debate. – *Wilson Soc. Bull.* 28: 484-498.
- Keith, L. B. 1983. Population dynamics of wolves. – *In: L. Carbyn (ed.). Wolves in Canada and Alaska: Their Status, Biology, and Management*. *Can. Wildl. Serv. Rept Ser.* 45: 66-77
- Luick, J. R. 1977. Diets for captive reindeer. – *In: M. Rechcigl (ed.). CRC Handbook Series in Nutrition and Food. Sect D. Diets, Culture, Media, Food Supplements*. Vol. I. CRC Press, Cleveland, Ohio, pp. 279-294.
- Mech, L. D. 1966. *The Wolves of Isle Royale*. US. National Park Service, Fauna of the National Parks Series, No. 7, Washington, D.C.
- Mech, L. D., Adams, L. G. Meier, T. J., Burch, J. W., & Dale, B. W. 1998. *The Wolves of Denali*. 1998. University of Minnesota Press, Minneapolis.
- Messier, F. 1994. Ungulate population models with predation: a case study with North American moose. – *Ecology* 75: 478-488.
- Messier, F. & Crête, M. 1985. Moose-wolf dynamics and the natural regulation of moose populations. – *Oecologia* 65: 503-512.
- McLaren, B. E. & Peterson, R. O. 1994. Wolves, moose, and tree rings on Isle Royale. – *Science* 266: 1555-1558
- McLoughlin, P. D., Dzus, E., Wynes, B. & Boutin, S. 2003. Declines in populations of woodland caribou. – *J. Wildl. Manage.* 67: 755-761.
- Miller, D. R. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 3: taiga winter range relations and diet. – *Can. Wildl. Serv. Rept. Series, Ottawa*, No. 36. 41pp.
- Petersen, B., Iacobelli A. & Kushny, E. E. 1998. *The Caribou Conundrum: Conservation of Woodland Caribou and Designing Protected Areas*. World Wildlife Fund, Toronto, Poster Presentation 8th North American Conf., Whitehorse, Yukon.
- Peterson, R. O. 1977. *Wolf Ecology and Prey Relationships on Isle Royale*. U.S. National Park Service Sci. Mon. Series No. 11.
- Peterson, R. O., Thomas, N. J., Thuber, J. M., Vucetich J. A., & Waite, T. A. 1998. Population limitation and the wolves of Isle Royale. – *J. Mammal.* 79: 828-841.
- Pimm, S. L. 1991. *The Balance of Nature?: Ecological Issues in the Conservation of Species and Communities*. University of Chicago Press, Chicago.
- Racey, G. D. & Armstrong, T. 2000. Woodland caribou range occupancy in northwestern Ontario: past and present. – *Rangifer* Special Issue No. 12: 173-184.
- Rettie, J., Rock, T. & Messier, F. 1998. Status of woodland caribou in Saskatchewan. – *Rangifer* Special Issue No. 10: 105-109.
- Riis, P. B. 1938. Woodland caribou and time. – *Parks and Recreation* (Pt.1 ) 21 (10): 529-535, (Pt. 2) 21 (11): 594-600, (Pt. 3) 21 (12): 639-645, (Pt. 4): 22 (1):23-30.
- Russell, D. E., Kofinas, G. & Griffith, B. 2002. *Barren-Ground Caribou Calving Ground Workshop: Report of Proceedings*. Technical Report Series No. 390. Canadian Wildlife Service, Ottawa, Ontario, 39pp.
- Sargeant, A. B., Greenwood, R. J., Sovada, M. A. & Schaefer, T. L. 1993. *Distribution and abundance of predators that affect duck production: Prairie Pot-hole Region*. U.S. Fish and Wildl. Serv. Resour. Publ. 194.
- Schaefer, J. A. 2003. Long-term range recession and persistence of caribou in the taiga. – *Cons. Biol.* 17: 1435-1439.
- Schaefer, J. A., Bergman, C. M. & Luttich, S. N. 2000. Site fidelity of female caribou at multiple spatial scales. – *Landscape Ecology* 15: 731-739.
- Schmelzer I. *et al.* 2004. *Recovery strategy for three woodland caribou herds (Rangifer tarandus caribou; Boreal population) in Labrador*. Fish & Wildlife Division, Dept of Environment and Conservation, Govt. Nfld. and Labrador. 51pp.
- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. – *Can. J. Zool.* 70: 492-503.

- Shoosmith, M. W. & Storey, D. R. 1977. Movements and associated behavior of woodland caribou in central Manitoba. – *Proc. International Congress of Game Biologists* 13: 51-65.
- Simkin, D. W. 1965. *A preliminary report of the woodland caribou study in Ontario*. Dept. of Lands and Forests, Ontario. Sect. Rept. 59, 76pp.
- Singer, F. J., Harting, A., Symonds, K. K. & Coughenour, M. B. 1997. Density dependence, compensation, and environmental effect on elk calf mortality in Yellowstone National Park. – *J. Wildl. Manage.* 62: 12-25.
- Thomas, D. C. 1995. A review of wolf-caribou relationships and conservation. – *In*: L. N. Carbyn, S. H. Fritts, & D. E. Seip. (eds.). *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute Occasional Publication No 35, Edmonton, Alberta, pp. 261-273.
- Townsend, C. C. (ed.) 1911. *Captain Cartwright and his Labrador Journal*. London: Williams and Norgate.
- Van Ballenberghe, V., Erickson, A. W., & Byman, D. 1975. Ecology of the Timber Wolf in Northeastern Minnesota. – *Wildl. Monogr.* No. 43.
- Vors, L. S., Schaefer, J. A., & Pond, B. A. *In press*. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. – *J. Wildl. Manage.*
- Walters, C. J. & Hilborn, R. 1978. Ecological optimization and adaptive management. – *Rev. Ecol. Syst.* 9: 157-188.
- White, P. J. & Garrott, R. A. 2005. Northern Yellowstone elk after wolf restoration. – *Wildl. Soc. Bull* 33: 942-955.
- Wilmers, C. C., Post, E., Peterson, R. O., & Vucetich, J. A. 2006. Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. – *Ecology Letters* 9: 383-389.
- Wittmer, H. U., McLellan, B. N., Seip, D. R., Young, J. A., Kimley, T. A., Watts, G. S. & Hamilton, D. 2005. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. – *Can. J. Zool.* 83: 407-418.