Predation and caribou populations

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Abstract: Predation, especially wolf *(Canis lupus)* predation, limits many North American caribou *(Rangifer tarandus)* populations below the density that food resources could sustain. The impact of predation depends on the parameters for the functional and numerical response of the wolves, relative to the potential annual increment of the caribou population. Differences in predator-avoidance strategies largely explain the major differences in caribou densities that occur naturally in North America. Caribou migrations that spatially separate caribou from wolves allow relatively high densities of caribou to survive. Non-migratory caribou that live in areas where wolf populations are sustained by alternate prey can be eliminated by wolf predation.

Keywords: Caribou, wolves, predator-prey relationships, population dynamics.

Caribou populations without predators

In the absence of major predators or high levels of human harvest, caribou and reindeer *(Rangifer tarandus)* populations generally increase until their populations become regulated by density-dependent competition for food (Klein 1968, Leader-Williams 1980, Skogland 1985). Competition for food results in reduced nutrient intake due to lower forage intake rates and reduced diet quality as less nutritious food items are incorporated into the diet (White 1983). Energy expenditures for movement and cratering may also increase as it becomes more difficult to obtain food. Decreased nutrient intake and increased energy costs lead to a reduced pregnancy rate, low calf survival and higher adult mortality rates in *Rangifer* populations (Leader-Williams 1980, Skogland 1985, Messier *et al.* 1988, Thomas 1982).

Density-dependent competition results in a dome-shaped annual increment curve (Caughley 1977) (Fig. 1). At low densities, annual increment is small because although there is little competition and the population growth rate is high, there is a small breeding population. The maximum annual increment occurs at an intermediate density where there is a moderate sized breeding population and the growth rate is still relatively high because competition is not yet severe. At high densities, annual increment again becomes small because despite an abundant breeding population, the growth rate is low due to density-dependent competition for resources. In the absence of predators or harvesting, the population will generally increase until competition for resources reduces the growth rate and annual increment to zero. *Rangifer* populations regulated by competition for food resources often attain densities exceeding $2/km^2$ (Table 1).

POTENTIAL ANNUAL INCREMENT
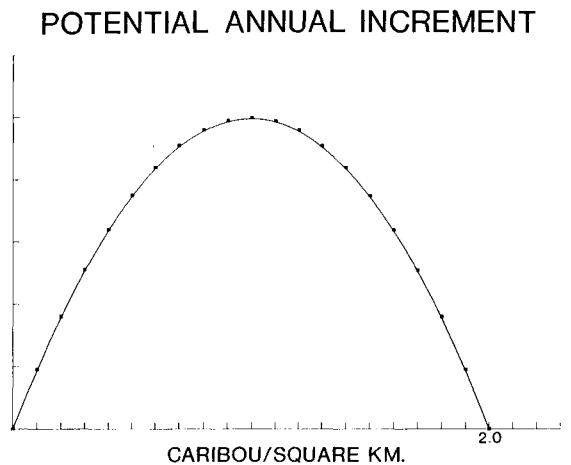

CARIBOU/SQUARE KM.

Fig. 1. Annual increment curve for caribou populations in absence of major predators or human harvest.

Predator-prey dynamics

When predators are present, especially wolves *(Canis lupus)*, caribou populations are often reduced below the density that food resources could sustain. The predation rate depends on the number of predators and the number of prey killed by each predator. In general, the number of predators (numerical response) and the number of prey killed by each predator (functional response) will change as a function of prey density (Holling 1959). The number of prey killed/predator will initially increase with prey density as prey become easier to find but will eventually reach a plateau as each predator becomes satiated (Fig. 2b). Various numerical responses are possible (Fig. 2c). The number of predators may increase with prey density if the predator population is limited by availability of the prey species of interest (Fig. 2c, line a). At high prey densities, the numerical response may reach a plateau if some factor other than availability of the prey species of interest begins to limit predator population growth (Fig. 2c, line b). If the predator population is regulated by availability of some other prey species or limiting factor, there may be no numerical response of predators to changes in density of the prey species of interest (Fig. 2c, line c). The functional and numerical response of predators to changes in caribou density have not been quantified. However, Messier and Crete (1985) demonstrated that wolves had a higher rate of consumption and reached higher densities in an area of high moose *(Alces alces)* density compared to areas of low moose density. Fuller (1989) summarized data from numerous studies of wolves to demonstrate the numerical response of wolves to increasing prey densities.

The number of prey killed by predators is the product of the number of predators and the number of prey killed by each predator (Fig. 2a). In general, few prey will be killed when they are at low densities because predators will also be at low numbers and the sparse prey are very difficult to find. As prey densities increase, the number of prey killed may increase exponentially due to the multiplicative effect of an increasing numerical and functional response of predators. If either the functional or numerical response levels off, the number of prey killed will increase linearly with prey density. If both the numerical and functional response level off, the number of prey killed will remain constant with further increases in prey density. Consequently, the predation rate (proportion of prey killed) will often be density-dependent at low prey densities, density-independent at intermediate prey densities and inversely density-dependent (depensatory) at high prey densities.

The impact of predation depends on the magnitude of predation losses compared to the potential annual increment that the prey population would produce in the absence of predation (Fig. 1). If losses to predation exceed the potential annual increment, the prey population will decline. If losses to predation are less than the potential annual increment,

Table 1. Density of *Rangifer* populations in relation to the level of predation.

Category	Location	Density	Source
Major predators rare or absent	Slate islands	4–8/km²	Bergerud 1983
	Norway	3–4/km²	Skogland 1985
	Newfoundland (winter range)	8.9/km²	Fong *et al.* 1991
	South Georgia	2.0/km²	Williams and Heard 1986[a]
Migratory Arctic herd	George River	1.1/km²	Messier *et al.* 1988
	Porcupine	0.6/km²	Williams and Heard 1986
	Northwest Territories	0.6/km²	Williams and Heard 1986
Mountain dwelling herds	Finlayson	0.15/km²	Farnell and McDonald 1987
	Little Rancheria	0.1/km²	Farnell and McDonald 1990
	Central Alaska	0.2/km²	Williams and Heard 1986
Forest dwelling herds	Quesnel Lake	0.03/km²	Seip 1991
	Ontario	0.03/km²	Williams and Heard 1986
	Saskatchewan	0.03/km²	T. Rock, pers comm

[a] Densities calculated from data presented in Williams and Heard 1986
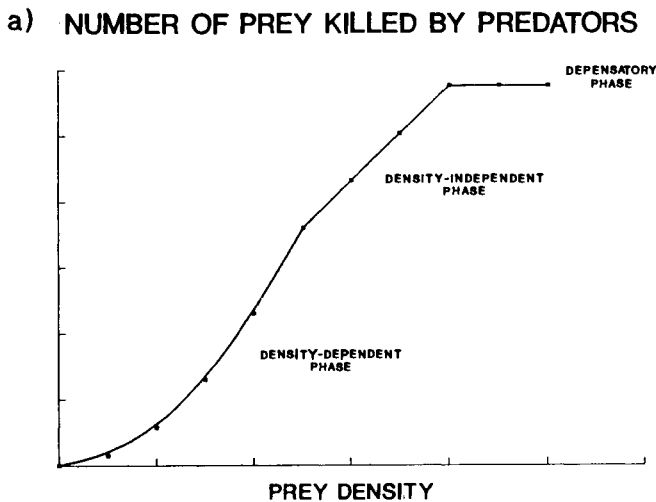
the prey population will increase, although more slowly than if predators were absent. The prey population will stabilize at a density where losses to predation equal the potential annual increment. Time lags and variations in density-independent limiting factors will cause fluctuations around the equilibrium density.
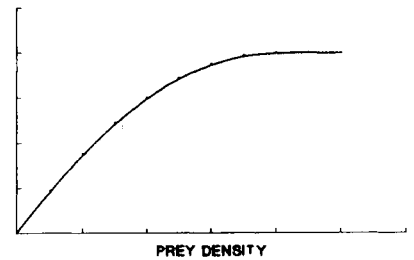
Migratory Arctic caribou

A high prey-predator equilibrium will occur when the number of prey killed by predators increases slowly as a function of prey density relative to the annual increment curve (Figure 2). That situation will occur when the prey have an effective anti-predator strategy or when the capacity of the predator population to respond to increasing prey is limited by other factors. The prey population will be regulated by the combined density-dependent effects of predation and competition for resources. It appears that many migratory Arctic caribou populations exist at a high prey-predator equilibrium. Wolf predation is usually a major limiting factor, especially of calves (Miller and Broughton 1974, Whitten *et al.* 1988), but caribou remain abundant and can sustain

a substantial human harvest. It appears that migratory Arctic caribou populations are able to reach a high prey-predator equilibrium because their annual migrations are an effective anti-predator strategy. Arctic wolves are sustained almost exclusively by caribou (Kuyt 1972). However, the capacity for wolf numbers to increase in response to increasing caribou numbers is severely limited by the long distance migrations of the caribou. Reproductive wolves are restricted to the area near the den during summer months. Most wolves den near treeline and few den near the calving grounds (Heard and Williams 1991). Consequently, most wolves are unable to prey on caribou on the calving grounds. Also, most of the wolves are unable to take advantage of increasing numbers of caribou to feed their pups during the denning period so the numerical response of wolves to increasing caribou numbers is greatly limited.

In some cases, the numerical response of predators is so limited that Arctic caribou populations essentially escape any significant limitation due to predators and caribou increase until they are regulated primarily by competition for food (Fig. 3). This situation has been reported for the George River ca-

b)
FUNCTIONAL RESPONSE
NUMBER OF PREY KILLED/PREDATOR

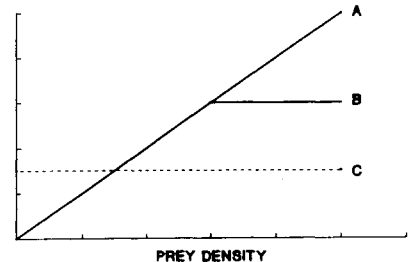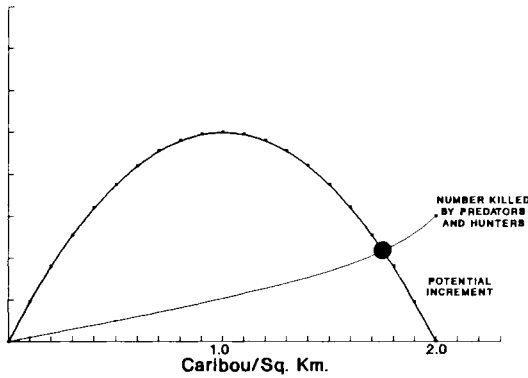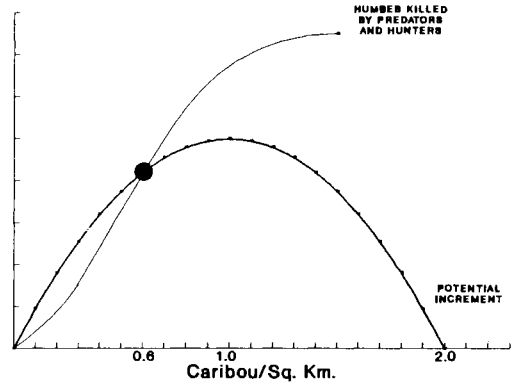a) **NUMBER OF PREY KILLED BY PREDATORS**

c)
NUMERICAL RESPONSE
NUMBER OF PREDATORS

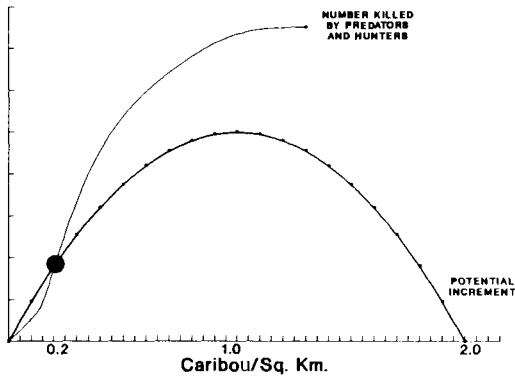Fig. 2 General relationships between prey density and predation.

FEW PREDATORS AND LOW HARVEST

NUMBER KILLED
BY PREDATORS
AND HUNTERS

POTENTIAL
INCREMENT

1.0   2.0
Caribou/Sq. Km.

MIGRATORY ARCTIC CARIBOU

NUMBER KILLED
BY PREDATORS
AND HUNTERS

POTENTIAL
INCREMENT

0.6   1.0   2.0
Caribou/Sq. Km.

MOUNTAIN DWELLING CARIBOU

NUMBER KILLED
BY PREDATORS
AND HUNTERS

POTENTIAL
INCREMENT

0.2   1.0   2.0
Caribou/Sq. Km.

SOUTHERN BOREAL FOREST CARIBOU

NUMBER KILLED
BY PREDATORS
AND HUNTERS

POTENTIAL
INCREMENT
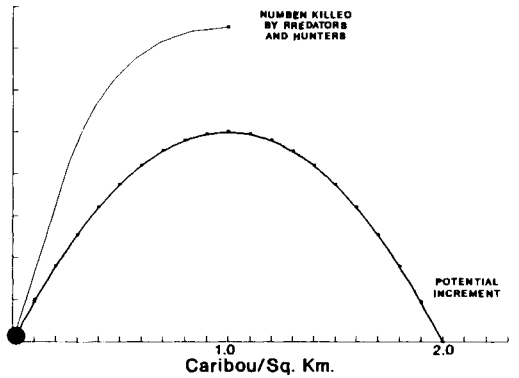
1.0   2.0
Caribou/Sq. Km.

Fig. 3. General predator-prey relationships for caribou populations in different areas of North America. The ● indicates the point of predator-prey equilibrium.

ribou herd in northern Quebec which attained a density of about 1/km² (Messier *et al.* 1988). A high mortality rate of wolves and a low human harvest of caribou will increase the likelihood that migratory Arctic caribou will escape from being regulated by predation.

In other cases, predation rate and human harvest rate appear to be adequate to restrict the growth of Arctic caribou herds before competition for food becomes extreme (Fig. 3). Many barren-ground caribou herds in northern Canada and Alaska appear to have a medium prey-predator equilibrium at densities of about 0.6/km² (Table 1). Wolf predation is more likely to regulate Arctic caribou populations at a medium density if wolves are reasonably abundant and there is also a significant human harvest on caribou. Caribou herds at a medium prey-predator equilibrium density would exhibit some nutritional stress due to competition for food but predation and human harvest would be the primary limiting

factors. This situation is probably the ideal case for management because caribou are abundant and in good physical condition, natural predator populations are present and the herd is providing a sustainable harvest for human use. The population is also easily subject to management by modified harvest levels or wolf control. In contrast, high density, food regulated caribou populations are vulnerable to major population crashes (Klein 1968). Adequate predator populations should be maintained and appropriate human harvest levels should be encouraged to prevent excessive growth of caribou populations. Otherwise, caribou populations may increase so rapidly that they cannot be effectively managed and become susceptible to catastrophic population crashes.

Forest-dwelling caribou

A low prey-predator equilibrium will occur when the number of prey killed by predators increases ra-

pidly as a function of prey density relative to the annual increment curve (Fig. 3). That situation will occur when the prey lack an effective anti-predator strategy or when predators are sustained by alternate prey species even when the prey species of interest is at low densities. Caribou populations below treeline in North America are more vulnerable to wolf predation than Arctic caribou because wolf populations are maintained by a variety of prey species and the caribou do not have long-distance migrations to space themselves away from wolves. Also, other predators such as bears (*Ursus* spp.) are more abundant than in Arctic areas and remove an additional component of the annual increment. Wolf populations are sustained by a variety of prey species including caribou, moose, mountain sheep (*Ovis* spp.), elk (*Cervus elaphus*) and deer (*Odocoileus* spp.). Therefore, wolf numbers can remain high even if predation has drastically reduced one of the prey species. Increases in the abundance of one of the prey species may support increased wolf numbers and thereby have deleterious effects on one or more of the other prey species. Caribou are extremely vulnerable to wolf predation compared to most other ungulate species. They are unable to fight off predators the way moose can, they do not use escape terrain like mountain sheep and mountain goats (*Oreamnos americana)*, and they have a low reproductive rate compared to most other ungulates such as deer so they cannot sustain high levels of predation. Therefore, caribou populations are usually the most vulnerable species in multiple prey-predator systems. Wolf predation can eliminate caribou from areas where the wolf population is sustained by other prey species because there is no negative feedback on the number of wolves as caribou decline (Seip 1991).

Woodland caribou in the mountainous regions of Yukon, Alaska and northern British Columbia are usually able to co-exist with wolves, bears and alternate prey species such as moose. Although major declines have occurred in some areas, possibly due to increases in moose numbers and/or excessive human harvest (Bergerud 1974), viable populations of caribou continue to survive at densities of about 0.2/km² (Table 1, Fig. 3). Seasonal migrations of caribou to alpine areas and habitat segregation between different ungulates species generally results in sufficient spatial separation from wolves and alternate prey to allow caribou populations to persist (Bergerud *et al.* 1983, Seip 1990). However, predation and human harvest are usually the primary limiting factors so caribou populations in those mountainous regions respond quickly to changes in the harvest rate and use of wolf control (Gasaway *et al.* 1983, Farnell and McDonald 1988, Bergerud and Elliot 1986).

It appears that caribou populations in the boreal forests of North America historically co-existed with wolves at a low prey-predator strategy (Bergerud and Page 1987). By spacing out and living at low densities, caribou reduce the predation rate by becoming difficult for predators to find. Living at low densities can reduce both the functional and numerical response of predators. However, that anti-predator strategy is only effective if caribou are the primary prey species in the area.

Forest-dwelling caribou populations throughout North America have undergone major declines during the 1900's (Bergerud 1974). Wolf predation and human harvest have been implicated as the major cause of many of those declines. Increased wolf predation on forest-dwelling caribou populations appears to be related to the range expansion of moose in North America (Bergerud 1974, Seip 1990). Moose expanded their range during the 1900's, especially in northern Ontario, British Columbia, Yukon and Alaska (Peterson 1955). The colonization of moose was followed by reports of declining caribou populations in many of those areas (Edwards 1956, Darby *et al.* 1989). The presence of moose provided an alternate prey which sustains increased wolf numbers (Seip 1991). The increased wolf population results in an increased predation rate on caribou and declining caribou numbers (Seip 1991). Because the predator population is sustained primarily by moose, it is possible for the wolves to totally eliminate the caribou population without any decline in wolf numbers (Fig. 3).

Forest-dwelling caribou have declined or been eliminated from large parts of their historic range in northern Ontario, Saskatchewan, Alberta and non-mountainous regions of British columbia. Caribou densities of 0.03/km² are common for remnant herds (Table 1) but many of those herds are continuing to decline to extinction. Only caribou which have a predator-avoidance strategy such as calving on islands (Cumming and Beange 1987) or caribou in the extreme north of the boreal forest where moose and human harvest are less common appear to be able to maintain their populations.

Unless wolf control and/or reduction of moose populations is undertaken, caribou will probably continue to disappear from much of their historic range in the southern part of the boreal forest. Any habitat modifications, such as fires, which enhance populations of moose or other prey species are like-

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ly to accelerate the decline of caribou. Also, any reduction in caribou habitat resulting from logging or fire will concentrate the remaining caribou into the remaining area and effectively increase their density. That reduction in their ability to space out makes it easier for predators to locate them and will also contribute to a more rapid decline. Roads may also improve access to caribou for predators and hunters.

Summary

Numerous limiting factors including winter severity, insect harassment, diet quality and accidents undoubtedly have an impact on caribou populations and result in year to year (primarily density independent) fluctuations in caribou populations. However, when wolves are present, it appears that wolf predation is the dominant, natural regulating factor. Differences in the effectiveness of predator-avoidance strategies appear to explain the major differences in caribou density that occur naturally in different regions of North America. Caribou generally appear unable to survive in areas where there is extensive overlap with wolves and alternate prey species. Caribou populations rely on migrations to become spatially separated from wolves or spacing out and living at low densities to minimize the predation rate. The number of caribou in an area depends on the effectiveness of those strategies at avoiding predators.

For migratory caribou in Arctic areas, manipulation of predator numbers and human harvest rates can be used to maintain abundant caribou populations while preventing excessive population growth that increases the risk of catastrophic population crashes. In forested habitats, in addition to managing predator numbers and harvest rates, habitat management is also important. Habitat changes which enhance alternate prey species or a reduction in habitat which concentrates the caribou and increases their density may undermine their predator avoidance strategies and lead to increased predation rates.

References

Bergerud, A. T. Decline of caribou in North America following settlement. – *Journal of Wildlife Management* 38: 757 – 770.

Bergerud, A.T.1983. The natural population control of caribou. – In: Bunnell, F. L., Eastman, D. S. and Peek, J. M. (eds.), *Symposium on natural regulation of wildlife population.* For. Wild. Range Exp. Stn., Univ. Idaho, Moscow.

Bergerud, A. T., Butler, H. E. and Miller, D. R.1983. Antipredator tactics of caribou: dispersion in mountains. – *Canadian Journal of Zoology* 62: 1566 – 1575.

Bergerud, A. T. and Elliot, J. P. 1986. Dynamics of caribou and wolves in northern British Columbia. – *Canadian Journal of Zoology* 64: 1515 – 1529.

Bergerud, A. T. and Page, R. E. 1987. Displacement and dispersion of parturient caribou at calving as an antipredator tactic. – *Canadian Journal of Zoology* 65: 1597 – 1606.

Caughley, G. 1977. *Analysis of vertebrate populations.* John Wiley and Sons, New York.

Cumming, H. G. and Beange, D. B. 1987. Dispersion and movements of woodland caribou near Lake Nipigon, Ontario. – *Journal of Wildlife Management* 51: 69 – 79.

Darby, W. R., Timmermann, H. R., Snider, J. B., Abraham, K. F, Stephanski, R. A. and Johnson, C. A. 1989., Woodland caribou in Ontario. Background to policy. – *Ontario Ministry of Natural Resources 38.*

Edwards, R. Y. 1956. Snow depths and ungulate abundance in the mountains of western Canada. – *Journal of Wildlife Management* 20: 159 – 168.

Farnell, R. and McDonald, J. 1987. *The demography of Yukon's Finlayson caribou herd 1982 – 1987.* Yukon Dept. Renewable Resources, Whitehorse.

Farnell, R. and McDonald, J. 1988. The influence of wolf predation on caribou mortality in Yukon's Finlayson caribou herd. – In: *Proceedings of the Third North American Caribou Workshop, Alaska. Dep. Fish and Game, Juneau. Wildlife Technical Bulletin No.* 8: 52 – 70.

Farnell, R. and McDonald, J. 1990. *The distribution, movement, demography, and habitat use of the little Rancheria caribou herd.* Yukon Dept. Renewable Resources, Whitehorse.

Fong, D., McGrath, M., Mercer, E. and Yake, K. 1991. Mark-recapture of Newfoundland caribou. – In: Butler, C. E. and Mahoney, S. P. (eds.) *Proceedings Forth North American Caribou Workshop.* St. John's, Newfoundland. pp. 231 – 236.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. – *Wildlife Monographs* 105.

Gasaway, W. C., Stephenson, R. O., Davis, J. L., Shepherd, P. E. K. and Burris, O. E. 1983. Interrelationships b etween wolves, prey and man in interior Alaska. – *Wildlife Monographs* 84.

Heard, D. and Williams, M. 1991. Wolf den distribution on migratory barren ground caribou ranges in the N.W.T. – In: Butler, C. E. and Mahoney, S. P. (eds.) *Proceedings Forth North American Caribou Workshop.* St. John's Newfoundland. pp. 249 – 250.

Holling, C. S. 1959. Some characterstics of simple types of predation and parasitism. – *Canadian Entomologist* 91: 385 – 398.

Klein, D. R. 1968. The introduction, increase and crash of reindeer on St. Matthew Island. – *Journal of Wildlife Management* 32: 350 – 367.

Kuyt, E. 1972. Food habits and ecology of wolves on barren-ground caribou range in Northwest Territories. – *Canadian Wildlife Service Report No. 21.*

Leader-Williams, N. 1980. Population dynamics and mortality of reindeer introduced to South Georgia. – *Journal of Wildlife Management* 44: 640 – 657.

Messier, F. and Crête, M. 1985. Moose-wolf dynamics and the natural regulation of moose populations. – *Oecologia* 65: 503 – 512.

Messier, F., Huot, J., Le Henaff, D. and Luttich, S. 1988. Demography of the George River caribou herd: Evidence of population regulation by forage exploitation and range expansion. – *Arctic* 41: 279 – 287.

Miller, F. and Broughton, E. 1974. Calf mortality on the calving ground of Kaminuriak caribou. – *Canadian Wildlife Service Report Series No. 26.*

Peterson, R. L. 1955. *North American moose.* Univ. Toronto Press, Toronto.

Seip, D. R. 1990. Ecology of woodland caribou in Wells Gray Provincial Park. – *British Columbia Ministry of the Environment. Wildlife Bulletin No. B-68.*

Seip, D. R. 1991. Habitat use and population status of woodland caribou in the Quesnel Highlands. – *British Columbia Ministry of the Environment. Wildlife Bulletin No. B-69.*

Skogland, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. – *Journal of Animal Ecology* 54: 359 – 374.

Thomas, D. C. 1982. The relationship between fertility and fat reserves of Peary caribou. – *Canadian Journal of Zoology* 60: 597 – 602.

White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. – *Oikos* 40: 377 – 384.

Whitten, K. R., Mauer, F. J. and Garner, G. W. 1988. Calf mortality in the Porcupine caribou herd. – In: *Proceedings of the Third North American Caribou Workshop, Alaska. Dep. Fish and Game, Juneau. Wildl. Tech. Bull. No. 8:* 88.

Williams, T. M. and Heard, D. C. 1986. World status of wild *Rangifer tarandus* populations. – *Rangifer Special Issue No. 1:* 19 – 28.

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