Tı̨ch’ádíı hé Gots’edı – Living with Wildlife: Caribou Predators and Competitors

Science Review of Predation and Competition in Caribou in the Sahtú

Prepared for the ʔehdzo Got’ı̨nę Gots’ę́ Nákedı
(Sahtú Renewable Resources Board)

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January 2021

EXECUTIVE SUMMARY

This report has been prepared to provide a western science perspective on predation and competition as they relate to barren-ground caribou herds in the Sahtú. The report will act as background information for participants in the Délı̨nę 2021 Public Listening Session as part of the exchange of knowledge.

One of the issues driving the need for information on predators in the Sahtú is the strategy adopted by Environmental and Natural Resources (ENR) and its co-management partners to control the number of wolves on the wintering grounds of the Bluenose-East and Bathurst barren-ground caribou herds. The herds have continued to decline despite reduced harvesting, and the culling of wolves is intended to reduce the loss of adult females and calves, and to restore the herds to levels that will again support harvest. Anecdotes of grizzly bears preying on calves on the calving grounds suggest a significant loss of calves soon after calving which adds some urgency to reducing predation as much as possible.

A review of the literature shows that the opinions of scientists on the effectiveness of wolf culls vary significantly; from outright support for the continuing removal of wolves using any number of methods to detailed analysis of studies of the effectiveness of wolf culls showing little improvement in caribou growth rates or increases in herd abundance. Clear successes of improving caribou numbers are usually accompanied by reduced harvesting, long-term, continued wolf removal over several years and mild winters that reduce natural mortality. Some boreal caribou herds have shown improvement with wolf culls, but they are usually in areas with disturbed habitat (e.g., industrial activity, reduced mature forest, seismic lines that aid wolf movement, etc.) where natural predator avoidance is not possible. Wolf control for migratory barren-ground herds with large ranges and large migratory cycles, is not well studied.

Wolves and bears are "apex predators" whose role can extend through all components of ecosystems by a process known as a "trophic cascade". The re-introduction of wolves into natural ecosystems seventy years after removal has shown changes throughout the ecosystem largely due to the reduction in the numbers of overabundant ungulates. In Yellowstone Park in the U.S, the immediate impact was the lowering of the elk population and smaller predators, such as coyotes, and the recovery of aspen, willow, and berry-producing shrubs. The latter change allowed the return of several songbird species. The impacts of removing a large proportion of wolves in areas of the NWT could change the numbers of some species and alter the relationships between species. It may also reduce predation on other ungulates, such as muskox, that are becoming more common throughout the Sahtú.

Public concern over the killing of wolves has led to a re-evaluation of programs by some governments, such as in the Yukon (Farnell 2009) and in Alaska, where a national boycott on tourism led to a major review and justification of the predator control programs (NRC 1997). The costs of non-lethal methods, such as the relocation of bears and wolves, sterilising breeding wolf pairs or diverting predators from calving areas with road kills, are very high and are usually only attempted on a trial basis. Farnell (2009) reports that sterilizing breeding pairs of wolves was effective in reducing predation in Yukon herds and was more acceptable to the public than lethal methods.

Competition is another central theme in ecological science. Individuals compete with other members of their species and with other species for the use of resources such as food and water. Sahtú community members have suggested that the increasing number of muskox in the region is displacing the barren-ground caribou herds. Research projects have attempted to show avoidance of muskox by caribou, but western science has not shown any clear examples. Research on Peary caribou has included avoidance of muskox as a predictor of caribou behavior due to the odour of muskox and trampling of lichen. Other studies have shown that caribou and muskox, and other species, can feed in the craters created by the muskox, although each species feeds on different species of plants. Where muskox is the primary prey of wolves, preying on caribou also has been termed "apparent competition" and may lead to higher numbers of caribou being taken by predators.

Conclusions

- Caribou and the apex predator wolves and bears have co-existed in northern Canada for thousands of years, and all play key roles in northern ecosystems. The large-scale control of predators, usually to protect livestock and to maintain large ungulate herds for harvesters, has developed over the last centuries. It usually involves removing wolves by poisoning, aerial and ground shooting, trapping or snaring. Public concern over wolf culls has led to the use of non-lethal methods, but costs are prohibitive.

- In the Sahtú, the priority is to protect and support the declining Bluenose-East and Bluenose West herds that are a source of cultural, social and nutritional strength to the Sahtú Got'ı̨nę. ENR is harvesting a large proportion of the wolves in the winter range of the herds in the Tłı̨chǫ region in the hope of reducing mortality and allowing the herds to recover.

- Caribou herds decline when the mortality rate exceeds the recruitment rate of young caribou to become reproducing adults. Vital rates are usually measured by the calf:cow ratio and the survival of the calves through the first year. Mortality occurs from natural causes, harvesting or predation on adult females and calves. To be effective, predator control programs must determine that the predators in question are reducing the herd and that the program is effective enough (>65% of the wolves) and long enough in duration (usually several years) to be able to show positive changes in the herd. As stated by Russell (2010, Pg 20) "In summary, predators must be limiting ungulate populations, the habitat must be able to support more ungulates, control must be effective in targeting the right predators, and control must occur for long enough and remove enough of the target predator."

- Published supporting evidence for impacts of wolf predation on barren-ground caribou herds in the NWT is scarce but the need to do anything necessary to support the declining herds, particularly the Bathurst herd, adds urgency to removing all known threats to the herds. The results of programs to monitor the herds, the wolf population and metrics used to determine the effectiveness of the wolf control program should be published for review by independent experts.

- A comprehensive review of predator control programs as a general support strategy for ungulate herds has shown a slight improvement in recruitment, calf:cow ratios, and total herd numbers with wolf control, but several studies show no improvements to caribou demographics at all. One exception is woodland caribou herds in Alberta, where predation by wolves is one factor in their decline but habitat loss and alteration (e.g., the presence of seismic lines used by wolves) is the major reason for herd declines.

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Introduction

This review is being prepared as information for the Tı̨ch'ádíı hé Gots'edı – Living with Wildlife: Caribou Predators and Competitors. It is intended to provide background on the western science behind understanding the impacts of predation on caribou, and competition in wildlife in the Sahtú. Western scientists have been studying predators and caribou in northern Canada since the 1950's to understand the relationship between caribou and other ungulates (e.g., moose, muskox, deer) and predators such as wolves, bears, coyotes, lynx, eagles, etc. The stated goal of the research was to ensure maintenance of large caribou herds which will allow high harvest levels, usually by indigenous, resident and non-resident hunters.

This review of the impacts of predators focuses mostly on wolves because there are many more programs for wolf control than for other predators. Wolf control effectively removed wolves from the lower 48 U.S. states by the 20th century. The most effective wolf control programs are those where specific wolf packs have been observed preying on a caribou herd and the control program monitors specific rates in the respective caribou herds. Vital rates (calf:cow ratio, recruitment, etc.) of the herd are then monitored and interpreted in terms of other issues such as habitat quality, carrying capacity and climactic conditions. In Alaska, wildlife managers have tried relocating bears and using diversionary feeding to distract wolves and bears during calving time, but the costs are prohibitive. Bears are also known to be significant predators on some caribou herds, with up to 6.3 calves of the Porcupine herd killed per bear per day by female bears with cubs (Young and McCabe 1997).

Several reviews of the western science behind predator control have been published, mostly as a means of rationalising wolf control to the public. Notable reviews of the science behind wolf control have been published by the U.S. National Research Council (1997), Russell (2010) for the Yukon and by McLaren (2010) for ENR. The results of each will be summarised in this report (see below). Farnell (2009) reviewed the results of wolf control in the Yukon up to 2009. This review extends this earlier work and updates these reports where possible.

The consensus from western scientists is that wolf control is sometimes necessary to help endangered caribou herds. However, the impacts of other factors such as the loss of habitat from climate change and fire, weather and the presence of other ungulate species and smaller predators (e.g., coyote, fox, lynx) are largely ignored and not monitored. In northern ecosystems, the impacts of predators on migrating barren-ground herds and the role of wolves as apex predators are poorly understood. Scientists have long understood that predation may be a major contributor to declining caribou herds but, depending on the location and surrounding environment, factors such as human development, climatic extremes, hunting, food limitation, insects, parasites, disease and natural loss of habitat (e.g., fires) and combinations of many of these factors may cause significant declines in any caribou population (Klein 1991).

Scientific opinions on the issue of wolf control and its impact on caribou numbers vary widely. Opinions range from wolf management being essential to maintain caribou populations at peak numbers (Bergerud 1988, 2006) to a meta-analyses of 62 studies that show wolf control to be only mildly effective at increasing growth rates, but not the total abundance, of caribou (Clark and Hebblewhite 2020). The one exception is woodland caribou herds in Alberta that have been affected by habitat loss and are restricted to small numbers. A survey of wildlife managers shows that over half of wildlife managers feel that wolf control is an important tool to maintain and support caribou populations (Lute 2018).

The reasons behind the declines of the Bluenose-East and Bathurst herds are still poorly understood but ENR, in conjunction with co-management partners, has undertaken the culling of >65% of wolves to slow mortality of caribou adults and calves, and to promote a return of the herds to previous levels. An important consideration in southern herds is the presence of other ungulates, such as moose, deer or elk that are alternate prey and support wolves when caribou are not available. Muskox and moose might take the role of alternate prey in the Sahtú but its not clear if that is occurring. Community members suggest that muskox might be competing with barren-ground herds and cause caribou to move out of prime habitat.

Questions to be addressed in the review:

- *Does western science support the view of removing wolves to support migratory barren-ground caribou?*

- *What is the role that wolves play in the northern ecosystem and what is the possible impact to other species when removing the majority of wolves from the ecosystem?*

- *How is the effectiveness of the predator control being monitored? Is ENR measuring the number of kills in the herds relative to historic levels?*

- *What other studies are being conducted that are associated with the wolf removal? Are there studies of smaller predators and other species that may benefit, or decline, from the removal of wolves? Are there studies on the impacts of bear predation on the herds relative to wolf predation?*

Ecology

Ecology is the science of understanding the relationships between organisms, and between organisms and their environment. Research areas like predation, competition, habitat, food chains, and the effects of changes in food sources help scientists to understand the relationships between wildlife species and how animals live within their habitat. For example, types and amounts of foods eaten, interactions with other species (e.g., avoidance, predation, competition for resources), denning or nesting areas, migratory behaviors, and diseases. The usual levels of study in ecology are the organisms, populations, communities, and ecosystems.

One important ecological concept for populations is the *carrying capacity* of the ecosystem in which the population exists. The *carrying capacity* is the maximum number of individuals of a population that the environment can support. It is based on the amount of suitable habitat (for example, food and water resources, calving or denning areas, migration routes, areas where individual animals can go to avoid predators or human disturbance, etc.) available to a population. It is an important concept for caribou because large populations may exceed the carrying capacity of their habitat, which results in a decline in numbers as food becomes scarce. Removing predators may allow herds to expand to the carrying capacity, which will increase the competition between individuals to gain enough resources to survive and breed.

The *carrying capacity* may change through the year from major events such as fire, drought, ice storms and flooding, or change over the long-term as plant species used for food change in abundance due to climate change. Lichen species may be replaced by shrubs, reducing the carrying capacity for barren-ground herds. Predation is one factor that may reduce the population to a level below the *carrying capacity*. The goal of many predator control programs is to allow the prey species to reach its carrying capacity, which will allow a maximum harvest for hunters.

A second concept to consider for the role of wolves in ecosystems is the *trophic cascade*. Wolves are called “apex predators” and, through their actions, are known to have larger impacts on the system than preying on dominant ungulate species (Wallach *et al.* 2015). They consume large and small prey species, which in turn consume vegetation, and by doing so play an important role in how the ecosystem function. This is termed a *trophic cascade* due to the larger impacts on the ecosystem than just through the predation of dominant species. Wolf presence in the ecosystem results in changes to ungulate behavior and avoidance of predators, such as movement to higher altitudes for mountain caribou or avoidance of seismic lines and roads by female boreal caribou with young. On the tundra, movement to calving grounds is partly to avoid predators during calving.

There is a significant shortage of good scientific studies to examine how effective the control of wolves is on barren ground herds. To provide accurate, high quality information to the public and managers of resource programs, science requires well designed studies with controlled or well documented changes in habitat, prey demographics and condition, numbers, and conditions of competing species (for example, moose populations near caribou herds), predator numbers and demographics and habitat use, as well as environmental conditions.

Wolf Ecology in Northern Ecosystem

The grey wolf has one of the largest distributions of any terrestrial mammal (Musiani *et al.* 2007) and is known as a keystone species due to its apex predator status. Wolves have been historically distributed throughout North America, including Alaska and Greenland. There is a general understanding that wolf densities will continue to increase with prey density in a linear fashion (Mech 2017), however there is some evidence that there is a limit on pack size due to density-dependent factors such as competition with other wolves, dispersal to new territory and changes in territory size (Cariappa *et al.* 2011). It is apparent that the dynamics of wolf populations are as complex as in any prey population and the impacts of human control (Mech 2017) on pack size and composition need to be considered as well.

There are also different ecotypes of wolves depending on their prey and location. Genetic analysis shows that central Arctic and northern Saskatchewan wolves are close genetically to Alaska wolves and are similar to, but distinct from, far northern wolves on Banks Island and Baffin Island (Sinding *et al.* 2018). Research into the genetics and behavior of wolves in the NWT showed physical and behavioral differences between wolves on the tundra and those in the forested areas of the NWT. Lighter coloured tundra wolves moved with the migrating caribou herds while darker coloured forest wolves remained in home ranges (Musiani *et al.* 2007). Tundra wolves were also notably lighter in colour than forest wolves. This corresponds to studies in Ontario showing wolves associated with moose (called "moose-wolves) could be distinguished from wolves preying on boreal caribou (called "caribou-wolves"). The main difference between the two types was in their size, with moose wolves considerably larger in several respects (Wiwchar and Mallory 2010).

The NWT Species Monitoring Infobase[1] reports that there are grey wolves in 100% of the NWT, with a rough estimate of 4,000 to 5,000 individuals. Regional populations of wolves vary, with some regions in decline and other at relatively high densities. Threats to the populations come from declining ungulate populations, localised overharvest, and diseases, such as rabies. A review of the diet of harvested wolves in the Dehcho showed evidence of a wide range of food items, including boreal caribou, moose, wood bison, deer, marten, snowshoe hare, beaver, voles, birds, and fish (Larter 2016). Similar results were reported in the 1960s, where wolves in the central Arctic fed almost exclusively on caribou in the winter but fed on small rodents, passerine birds, eggs and fish in summer (Kuyt 1969). A similar survey of diets of 129 harvested wolves on Banks Islands found muskox in 90% of the stomachs (88% of stomachs from northwest Victoria Island), Peary caribou, arctic hare, arctic fox, snow goose and ptarmigan (Larter 2013). The amount of muskox in the diet of the wolves is significant as it may indicate that an intact population of wolves may help reduce the population of muskox in the Sahtú.

[1] https://www.nwtspeciesatrisk.ca/content/search-infobase

A key series of studies on wolf ecology was conducted on central Arctic wolves. Wolves in the central Arctic den in eskers and prey on migratory barren-ground caribou, although prey are scarce for the summer when caribou migrate to the calving and post-calving grounds (Klaczek *et al.* 2015). The grey wolf is highly territorial, and a breeding pair remains within its home range. As the herds declined and moved further north, the wolves remained in the territory near their dens, allowing separation from their prey. Presumably, this reduces the fitness of the wolves and the condition of the young (Klaczek *et al.* 2015). This was confirmed in a subsequent study where wolf densities in the central Arctic declined significantly and wolf reproductive success was limited by the decreasing availability of caribou as the barren-ground herds declined by roughly 90% (Klaczek *et al.* 2016).

The Role of Wolves as Apex Predators

A prime example of the complexity of the role of the wolf as apex predators in ecosystems was demonstrated in studies in Yellowstone Park. The last wolf was removed in 1925 and a group of more than 30 re-introduced to the park in 1995/96. Between 1930s and 1950s the elk population varied between 8,000 -11,000 elk (Ripple and Beschta 2004). The government culled the elk by live trapping and shooting to about half the maximum size (4000 to 8000). Culling was stopped in 1969, resulting in an increase in the population to 12,000 to 18,000 animals by the mid-1990s. Several studies showed that the elk population was exceeding the carrying capacity of the range and was severely overgrazing aspen, willow and berry-producing shrubs.

The re-introduction of 31 wolves to the park in 1995/96 and the impact of the introduction of the wolves on the ecosystem was dramatic. The presence of wolves resulted in lowering the number of elk, controlled the numbers of smaller predators, such as coyotes, and allowed the recovery of plant species like aspen, cottonwood and willow (Beyer *et al.* 2007). Elk numbers fell from about 16,000 in 1994 to about 5,000 by 2017 (Beschta and Ripple 2019) partly due to predation by wolves and cougars and partly due to movement of elk out of the park due to the presence of the wolves. A review of 24 studies of vegetation of deciduous woody plants over 20 years after the wolf introduction showed significant recovery of willow, aspen, cottonwood and berry-producing shrubs. The changes were due to the reduction of elk numbers and not due to favourable weather (Beschta and Ripple 2016). Beaver colonies increased from 0 in 1998 to 19 by 2017. Species of serviceberries (*Amelanchier alnifolia*) also became a significant portion of grizzly bear diet as berry species began to recover (Ripple *et al.* 2015).

The studies demonstrated an ecological concept termed a *trophic cascade* where the presence of an apex predator, such as the grey wolf, is shown to have an impact on plants and animals at the lowest trophic level (Fig. 1). Studies with large carnivores have shown these "*trophic cascades*" in several ecosystems (Ripple *et al.* 2014) and are one of the services that large predators provide to ecosystems. In Alberta, Hebblewhite *et al.* (2005) reported on the impacts of low-wolf density and high-wolf density areas in Banff National Park on elk, aspen, songbirds and beaver density. The presence of higher wolf numbers resulted in lower survival of elk females and lower recruitment of elk calves. The number of beaver lodges was associated with lower elk density and elk grazing reduced songbird diversity and abundance (Hebblewhite *et al.* 2005). A similar study in Jasper national park showed a recovery of aspen with the recovery of the wolf population in the 1960s and a reduction in elk (Beschta and Ripple 2007). These studies support the view of the important role that wolves play in some ecosystems by controlling large herbivore populations and smaller predators. Examples of large populations of deer, elk and moose in the absence of wolves has led to habitat degradation resulting in a need to better understand the relationship between species to maintain a balance (Soulé *et al.* 2003).

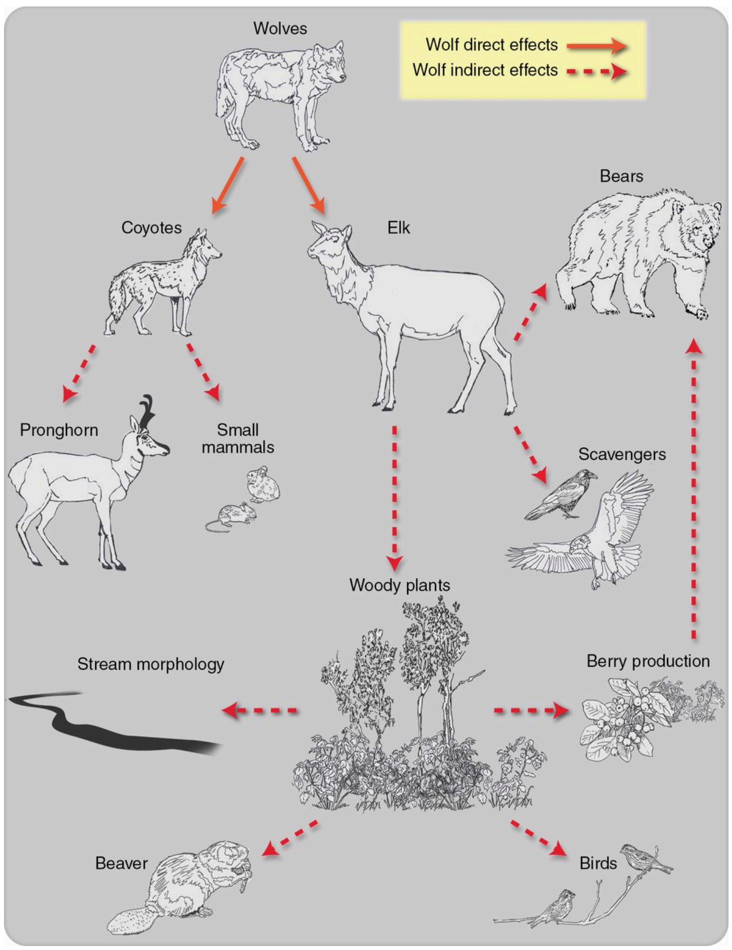

Figure 1 A simplified diagram of some of the impacts in the Yellowstone ecosystem with the re-introduction of roughly 35 wolves in 1995 and 1996. The direct impacts were through the reduction of coyote and elk populations. The decline in elk led to the recovery of aspen, willow, cottonwood and berry-producing shrubs (Source: Ripple *et al.* 2014).

Control of Wolves

Even though caribou and predators have co-existed for thousands of years in northern environments, there is a long history of culling wolves in Canada. Wolves and other predators have been present when caribou have been increasing, at peak numbers, and during a decline phase. Settlers controlled wolves to protect livestock and to protect humans before the establishment of communities. Due to bounties on wolves in the lower US states, the wolf almost disappeared from the U.S. until it was declared endangered in the early 1970s and has now recovered to about 6,000 individuals in the US. Wolves have now been removed from the endangered list as of January 4, 2021. Stelfox (1969) reported on high wolf numbers in Alberta in the 1800s and attempts to control them with poison as far back as the 1850s. Around 1900, wolves were scarce and, apparently, so were elk and bighorn sheep, but wolf numbers increased sharply until the 1960's when roughly 2500 were in the province (Stelfox 1969).

Wolf control used by agencies as a wildlife management tool by wildlife biologists goes back several decades with recommendations by Bergerud (1988), who recommended control when wolf densities exceed 6.5 wolves per 1000 km^2. This recommendation came at a time of high numbers of barren-ground and boreal caribou herds. With little data support, he dismissed the effects of human development and disturbance and proposed "*through management of wolf numbers, to increase further the abundance of caribou and wolves and provide surpluses of both species for northern peoples yet maintain a viable large mammal ecosystem in the Arctic*." It's not clear how the caribou herds could expand further, given their numbers in the 1980's, or how wolf numbers could increase by reducing their numbers. He repeated similar opinions in relation to boreal caribou herds in Ontario where, despite the loss of habitat due to forest fires, timber operations and spruce budworm infestation, he recommended only the culling of wolves.

Control of Wolves in the NWT

Environment and Natural Resources (ENR), in conjunction with co-management partners, has adopted a wolf management plan to support the Bathurst and Bluenose-East barren-ground caribou herds (Fig 2). The herds have undergone significant declines over the last two decades (ENR website, accessed December 2020). The plan is part of a larger initiative working with communities and resource management boards which includes harvest restrictions, to protect the herds and allow them to recover to former levels. The goal of the program is to remove 60 to 80% of the wolf population on the winter range by aerial shooting and using hunter incentives. In 2019, 54 wolves were removed from the Bluenose-East range and 31 from the Bathurst range. No data were presented on the ages or sexes of the wolves taken or what metrics will be used to judge the effectiveness of the program. The goal is for the program to last for five years. (ENR website, accessed December 2020).

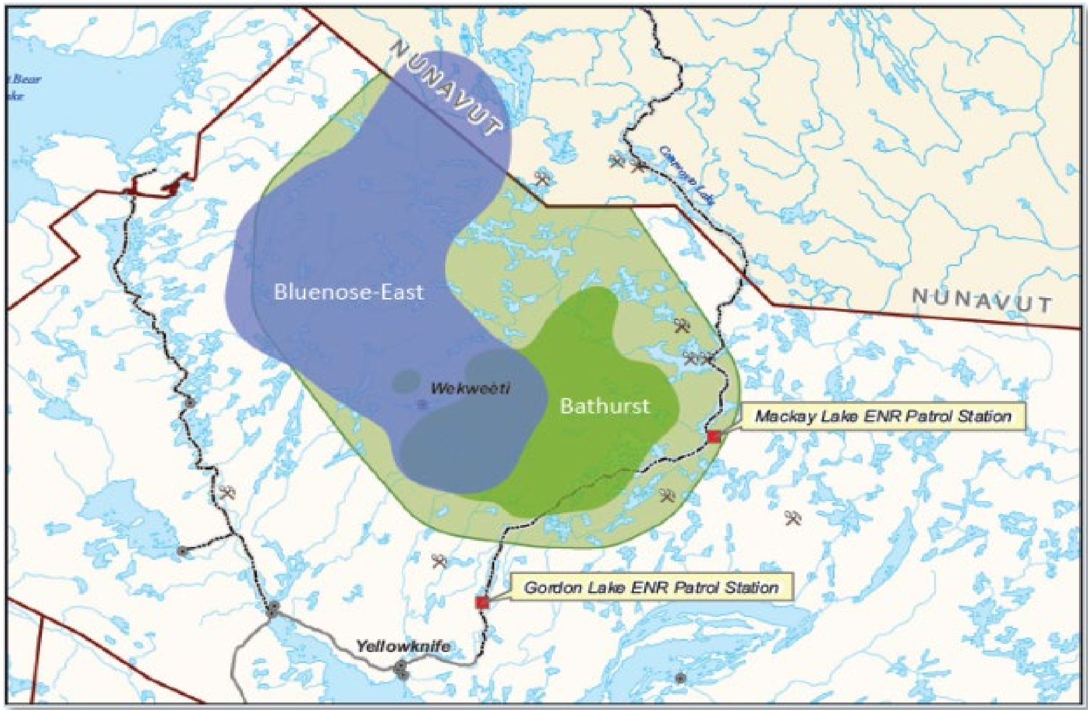

Figure 2 – North Slave wolf harvest incentive area. (ENR Website, accessed December 2020).

2019-2020	
Bathurst	**Bluenose-East**
31 wolves removed	54 wolves removed
Target 29-39	Target: 73-97 wolves

Table 1 The number of wolves harvested by hunting and aerial removal from the Bathurst and Bluenose-east caribou winter ranges in 2019-2020.

The control of wolves also raises the question of how to humanely reduce wolf populations. Methods used through the years include shooting (from aircraft and helicopters and on the ground), trapping, snaring, poisoning (by strychnine, cyanide, and other chemicals) and gassing of litters in dens with carbon monoxide. Non-lethal methods include sterilization of the dominant male and female (possibly followed by killing of the rest of the pack) and diversionary feeding which attracts the predators away from an endangered herd, usually during calving. McLaren (2016) discussed the humaneness of methods and their relative costs in her report to ENR on wolf control methods.

Reviews of Wolf Control Studies

This review focuses primarily on issues relating to wolves in the Sahtú, both for their role as apex predators in northern ecosystems and their impact on declining caribou herds. It also examined whether there is evidence that harvesting wolves will help the barren-ground herds return to higher numbers. Apex predators like wolves, black bears and grizzly bears are known to hunt large mammals like caribou, moose, muskox and deer but also smaller prey such as coyotes, beaver and smaller predators. By controlling prey numbers and their impact on declining populations of the large mammals, predators also keep those populations below the carrying capacity of their environment.

Science measures the health of caribou populations using several measurements of the numbers and health of individuals animals within the herd. The success of wolf control is measured in increasing numbers of adult caribou (i.e., its abundance), the increased survival rates of adult females and calves (e.g., % survival and calf:cow ratio) and the number of calves that survive their first winter to become reproducing adults in the population (called recruitment) (Clark and Hebblewhite 2020). Many of the wolf control studies have focused on the methods of killing wolves and little on the effectiveness of the program.

Few studies examine the large number of factors associated with population fluctuations of caribou herds, and scientists are still studying and debating the impact of predation by wolves on different caribou ecotypes (barren-ground, boreal, mountain caribou). Hervieux *et al.* (2014) found a 4.6% increase in the growth rate of a boreal caribou herd in Alberta due to increased survival of young, which appeared to stabilize the herd size, but habitat conservation remained the main factor required to increase herd size. This is consistent with others that have determined that the declines in boreal caribou herds that have occurred over the last 30 years are consistent with industrial disturbance from oil and gas development (Stewart *et al.* 2020).

A study of the effect of three wolf packs on the Nushagak caribou herd in Alaska found that only one of the packs regularly hunted a specific caribou herd, usually during the calving season. The wolves also spent a disproportionately large amount of time near the herd during the late summer and fall, and preyed almost exclusively on bulls that were weak, malnourished and possibly injured after the rut (Walsh and Woolington 2019). The herd continued to increase in the presence of wolves and no control of local wolves took place. Similar results were found for boreal caribou in British Columbia (Wittmer *et al.* 2007) where the survival of adult females was greater in old growth forests and lower in younger forests, where moose were more common.

A model of the impacts of predation on the Porcupine barren-ground herd indicated that, although significant by removing an estimated 7600 adult caribou a year during a cyclic maximum of 175,000 adults, or roughly 5.8 to 7.4%, when the herd declined in the 1990s, predation was less significant than climatic features. Hawes and Russell (2000) suggested that large migratory herd numbers tend to be cyclic and that cycles occur due to changes in forage and weather events, such as the North Pacific and North Atlantic Oscillations (Hebblewhite 2005). A study of predation of moose, caribou and wolves in BC showed that moose was the primary prey of wolves throughout the year, but predation also caused high mortality rate in caribou adults and calves (Seip 1992). A second herd avoided wolf predation by migrating, and thereby separating from moose and wolves.

Although the predation on caribou herds by wolves appears to be relatively clear cut, large scale experiments in Alberta and British Columbia have tried to show the impacts of predation on moose and boreal caribou in ecosystems affected by forestry and human development (Serrouya *et al.* 2019). The studies included wolf removal, moose reduction, and different combinations of protection for caribou. The study measured the growth rate of 12 caribou herds in treatments and 6 control populations, many of them small with few reproducing females. Wolf reduction for 8 years showed little improvement in growth rate for the adjoining herd. The overall results of the study showed that the most consistent increase in growth rate of the boreal caribou was by wolf removal and penning of the females (Serrouya *et al.* 2019). Harding *et al.* (2020) reanalysed the data from the Serrouya study and found that the differences between treatments were not significant, but the results were influenced by the different ecotypes of caribou, their behavioural characteristics, and responses to industrial disturbance.

National Research Council (1997)

One of the most studied predator-prey systems in northern climates is situated in Alaska. Sport hunting of moose appears to be the priority of wildlife management programs, so the goal of ungulate management is to increase the numbers of moose, usually by killing wolves and re-locating bears, or killing bears using bait stations. In 1995, the state governor requested the National Academy of Science (NAS) to review predator control programs due to public sentiment against the killing of predators and socioeconomic factors, such as maintaining harvest of moose and caribou for residents (both indigenous and non-indigenous) and non-residents. Wolf control had been a long-standing practice in the state (through aerial and ground shooting, poisoning, snaring, translocations, sterilization, diversionary feeding, gassing of litters, etc.) but the governor asked the NAS to review wolf control due to public sentiment, which included a call for a national boycott of tourism to the state. The request followed an incident where a biologist with an animal rights group attended a snared wolf with reporters and found four wolves snared, but only one dead. A Fish and Wildlife employee attended to shoot the wolves but had the wrong ammunition and it took five shots to kill one of the wolves. The incident was filmed and aired widely on television in the U.S. (NRC 1997, Pg 19).

The NRC committee consisted of scientists with a background in biology or economics and members of the public. It was asked to review predator management (setting bag limits, seasons for control and the methods used to control predators) and control (primarily reducing the wolf population) from a scientific, sociological and economic standpoint. The predator control programs would be reinstated if 1) they must be based on solid science, 2) they must make economic sense to Alaskans and, 3) they must have broad public support. In terms of the current review of predators, the NRC report provides one of the strongest technical reviews of the science behind the predator-prey relationship in a jurisdiction with the resources available to examine how, and whether, predator control can be justified.

The review provides a balanced evaluation of the science knowledge and gaps in understanding the factors affecting the respective prey and predator populations. Several examples in Alaska are presented outlining when predator control (shooting wolves) resulted in increased caribou calf survival and increases in total numbers of caribou. They also report studies where control of wolves had no impacts on caribou calf survival or moose survival. An extensive wolf control program (shooting up to 85% of wolves from aircraft) for 7 years around the Finlayson herd in the Yukon appeared to allow the numbers of caribou to increase from 3073 to 5950, an increase of 18% per year. Harvesting was also reduced during this time. Calf:cow ratio increased from 25.5 calves/100 cows before wolf control to 50.2 during the control period. The pack size recovered in 4 years after wolf control ended. A similar program of wolf and bear reductions showed little impact on the numbers of moose in three populations of moose in the south Yukon. Eighty percent of 132 collared moose calves died in the first year, with 58% killed by bears and 27% by wolves. Wolves were also responsible for half of the adult female moose and 27% of calves killed, but the survival of adult moose was the same between areas with or without wolf reduction. The program cost $1.38 million, which far outweighed the benefits to the moose population.

The conclusion from these studies is that wolf control may sometimes result in greater numbers in caribou herds, but other factors such as snow depth, storms during calving, mine development in the area and other factors might also be affecting the results. Overall, the review concluded that caribou, and sometimes moose, populations increased with drastic wolf control (>80% of the wolf population), but most studies to document the effects were poorly designed and monitoring of ultimate hunter success (the main reason for predator control) was not conducted. Some of the conclusions from the NRC study are given in Table 2.

Table 2 - Conclusions and recommendations from the NRC report on predator control activities in Alaska. (NRC 1997).

Conclusion	Recommendation
Wolves and bears in combination can limit prey populations.	There is clear evidence that wolves and bears can, under certain conditions, keep moose and caribou populations suppressed for many years, but evidence is insufficient to establish the existence of dual stable states, one of which has high densities of both predators and prey.
Wolf control has resulted in prey increases only when wolves were seriously reduced over a large area for at least four years.	Wolves and bears should be managed using an "adaptive management" approach in which management actions are planned so that it is possible to assess their outcome. That way managers can learn from the experience and avoid actions with uninterpretable outcomes or low probability of achieving their stated goals. Management agencies should be given the resources to conduct their management projects as basic research.
Expectations that managed populations in Alaska will remain stable are not justified.	Management objectives aimed at achieving stable populations of wolves, bears, and their prey should recognize that fluctuations in populations can be expected and provisions made for them in management plans. Before any predator management efforts are undertaken, the status of the predator and prey populations should be evaluated (including whether they are increasing or decreasing), and the carrying capacity of the prey's environment should be evaluated.
The design of most past experiments and the data collected do not allow firm conclusions about whether wolf and bear reductions caused an increase in prey populations that lasted long after predator control ceased.	Future experiments should be based on more thorough assessment of baseline conditions and should be designed so the causes of subsequent population changes can be determined.
Many past predator control and management activities have been insufficiently monitored.	All control activities should be viewed as experiments with clear predictions. Control activities should be designed to include clearly specified monitoring protocols of sufficient duration to enable determination of whether the predictions are borne out and why.

Russell (2010)

The Yukon Wolf Conservation and Management Plan Review Committee contracted Russell to review the 1992 Yukon Wolf Conservation and Management Plan and to provide background on predator-prey systems. The report is an excellent review of studies on predation in the major western and northern jurisdictions (NWT, BC, the Yukon, Alberta, and Alaska). Russell summarised four hypotheses from Boutin (1992) which describe the general understanding of the relationship between predators and their prey. Boutin's research refers primarily to moose-wolf research but also applies to wolf predation in general. The four hypotheses are (summarised from Russell):

Predation Limitation – predation is the main factor that limits prey populations even though other factors (food availability, disease, etc.) are also present. It is expected that this system may be present with a simple wolf-moose or wolf-caribou system with little impact from other prey or predator species.

Predation Regulation - Predation regulates prey density at a low-density equilibrium. Predation rates follow prey densities, as prey declines the number of prey taken by predators declines.

Predator Pit – this hypothesis states that predators keep prey populations at low densities until conditions favour the prey population increase significantly, at which time the prey population reaches a new equilibrium at a higher density. The conditions might include a warm winter or lower predation rates for a limited time. The higher density population is determined by the carrying capacity of the environment. Several studies have attempted to demonstrate the predator pit hypothesis but have not been successful.

Stable Limit cycle hypothesis – this hypothesis proposes that some cohorts of young are born during poor environmental conditions and are more vulnerable to predation as adults. This results in population cycles or high annual variability.

Russell repeats Boutin's assertion that predators probably have some limiting effect on moose (and hence caribou), but the effect of predation is no larger than other factors such as hunting. Analysis of moose population studies shows that grizzly and black bears can take up to 50% of calves and that these losses were the major mortality factor. Reduction of wolves resulted in an increase in calf survival in 2 out of 5 studied cases (Boutin 1992).

Russell (2010) concludes that wolf control is effective if:

- It is established that wolf predation is known to be a limiting factor for a particular ungulate (moose or caribou) population,

- Wolf numbers need to be reduced by 65 to 80% of pre-control levels,
- Control occurs over a sufficient time period. This is usually at least four years, some programs for the Forty Mile herd in Alaska have been conducted up to seven years,
- Control occurs over a sufficient area,
- Habitat can support higher moose or caribou numbers,
- Hunting is curtailed at the same time that wolf control is occurring.

McClaren (2016)

McLaren was commissioned by ENR to conduct a scientific review of wolf management options, including the effectiveness, costs and its long-term success and the limitations to determine options for supporting the Bathurst barren-ground herd. The report follows the work of Russell but is intended to be focussed on options available to ENR and how to choose the best option for slowing the losses to the Bathurst and other barren-ground herds from wolves.

The report summarises lethal (aerial shooting, trapping and ground shooting, poisoning) and non-lethal methods (diversionary feeding, relocation, and sterilization) for controlling wolf numbers. In some programs, sterilization involves spaying the dominant female, vasectomy for the dominat male and lethal removal of all subordinate individuals. Other support methods for threatened herds are maternity pens (used for boreal herds), alternate prey reduction (e.g., removal of moose that act as primary or alternate prey for wolves) and prescribed burning, usually implemented to support moose populations since burns provide prime moose browse for about 25 years. There is a discussion of the humaneness of the lethal methods, but no consideration is given for the impact to the ecosystem by the removal of the wolves in northern ecosystems, either above or below the treeline.

Clark and Hebblewhite (2020)

In an extensive analysis of predator control studies, Clark and Hebblewhite analysed vital demographic rates of 52 studies to determine the size of the effect (e.g., the amount of improvement) after predator removal and the factors that increased the vital rates (calf:cow ratio, adult survival, recruitment). They found that predator removal increased the vital rate response by an average of 13%, but prediction intervals overlapped zero (95% prediction interval = -34% to 93%) suggesting no improvement for many studies. The greatest success was in improving recruitment but was neutral in improving adult survival and overall ungulate abundance.

Average calf:cow ratios increased by 19.5%, calf survival by 26.1% and recruitment by 44%, although confidence intervals for two of the metrics overlapped with zero. The higher calf survival did not translate into higher herd abundance, possibly due to factors other than predation. Predator removal increased adult survival by 5.35%. Pooled metrics showed an increase of 13.4% for all studies (Fig. 3), although the response dropped to 8% when only management removal projects were considered. The authors found poor design of many of the studies, poor monitoring and lack of replication which led to high uncertainty in the results. The high uncertainty led to a lack of confidence in the effectiveness of wolf control programs.

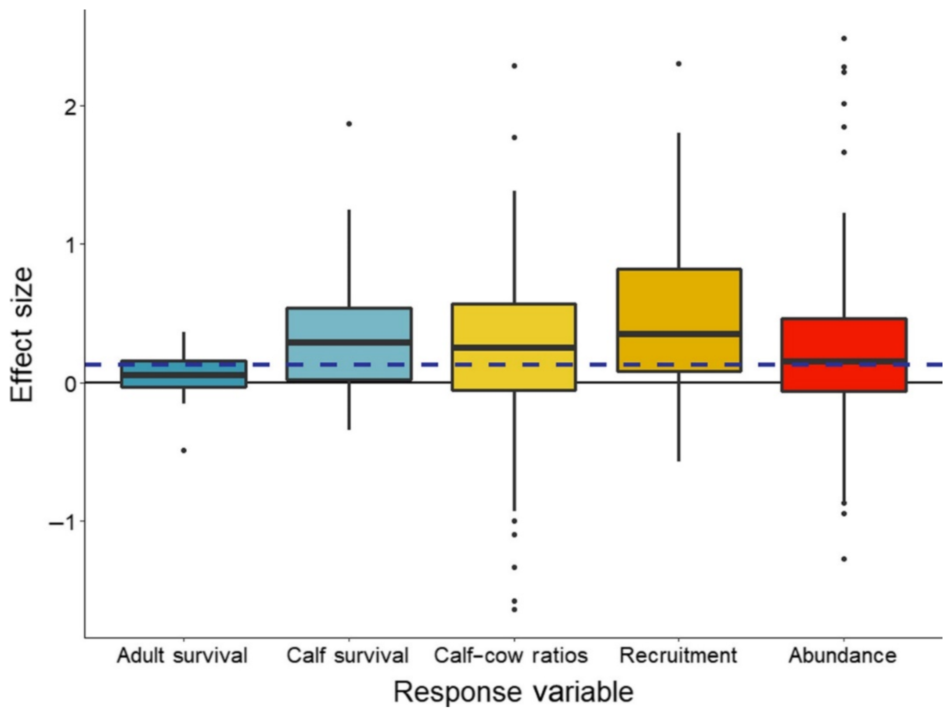

Fig 3 Average effect size responses by ungulates following predator removal. The dashed blue line represents the overall mean of the effect size (i.e., average of all five measurements) of all predator removal experiments (Source: Clark and Hebblewhite 2020).

Overall, the study concluded that it is not possible to predict if predator removal experiments will have the desired effects, as judged by increased abundance, on ungulates. The authors noted one possible exception; woodland caribou in Alberta, where predation is one factor reducing herd abundance but habitat loss and alteration are the ultimate reasons for herd decline. The average effect of predator removal is 14% and there is likely a positive effect from predator removal (Clark and Hebblewhite 2020).

Farnell (2009)

Upon his retirement, Rick Farnell reviewed wolf control programs conducted to support woodland caribou herds in the Yukon over his career. The Finlayson herd recovery program (as described above) began in 1982. The wolf population was reduced to 58% of the original population size in the first year and thereafter to 14-17% until 1989. During that time caribou increased substantially. As the wolf population recovered back to its original density of 10.3 wolves per 1000 km^2 the herd again declined. No other factors at the time could explain the caribou demographic trends, other than wolf predation and control. Although the program appeared to be a success over the short term, it failed as a long-term solution. Harvest by humans was reduced through outfitter quotas, permits for resident hunters and voluntary compliance by First Nations. A second control program on the Aishihik herd used sterilisation of breeding pairs in addition to aerial shooting of wolves. Through the years, the management of the herds changed from unilateral decisions of controlling wolves, which raised public concerns, to increasing public awareness, using local knowledge, eliminating harvest and to monitor predator and caribou populations and harvest rates. The later programs were better accepted by the public and by indigenous stakeholders due to their involvement.

Summary

Several examples of successful wolf control programs to build herd numbers are present in the literature (e.g., BC, Yukon, Alaska) but there are other examples where predation is one factor among many that affect the caribou herds. For example, Hayes and Russell (1998) estimate that 7600 caribou per year in the Porcupine herd are predated per year (assuming a daily rate of 0.08 caribou/wolf/day, and a density of 6 wolves/1000 km^2), yet the Porcupine herd continues to increase when others are declining. They propose that large migratory herds, such as those in the Sahtú, are cyclic in number and trends are linked to changes in forage or weather events. Control of wolves for the depleted herds in the Sahtú might be able to buy time for replenishment of forage or changes to more favourable climactic conditions.

Competition

Competition is one of the most widely studied aspects of ecological science. Generally, competition is divided into "*intraspecific competition*", where individuals compete with members of their own species for food, water, or reproductive mates, and "*interspecific competition*" where species compete with other species for resources within their environment. All species, and individuals of those species, must compete for resources with other members of their species and possibly other species. In environments near the carrying capacity, individuals within a population must compete for limited food and water and for mates leading to aggression or dispersal. The most obvious examples of competition are males competing for females during the rut but individuals competing for food, water, nesting/denning/calving sites and other resources are also dominant themes in population ecology.

There are few studies available that have investigated the interaction between muskox and caribou. Muskox were almost wiped out at the beginning of the last century but have since reached high numbers on Banks and Victoria islands, but have since declined. Since moving onto the mainland, muskox have moved south and are now increasing in numbers in the Sahtú (ENR Infobase, accessed January 2021). ENR estimates about 36,000 to 40,000 total muskox in the NWT, although most population estimates are old and probably out of date. Populations surveys reported 1,457 muskox in 1997 in the Sahtú and 8,098 in the north Great Slave in 2018 (Cuyler *et al.* 2019). The muskox population in both these regions has been increasing.

One example of interspecific competition is a concept called "*apparent competition*" where one species might support a predator population, which then preys on a second species. For example, moose or muskox might be the primary prey of wolves, which then prey on adjacent caribou herds (Kaluskar *et al.* 2020). The possibility of apparent competition between muskox and Peary caribou was invoked on Banks Island to explain wolf-caribou encounters and selective preference for caribou by wolves. Kaluskar *et al.* (2020) also considered avoidance of muskox by caribou in their model of habitat conditions for Peary caribou based on the traditional knowledge of local harvesters.

A study in western Alaska was designed to detect avoidance of muskox by reindeer after herders voiced concern about competition between the species (Ihl and Klein 2001). They examined feeding sites, cratering microsites and diets of the two species on the Seward Peninsula. Both species selected similar feeding sites on upland areas, choosing sites with less snow and lower snow hardness. The authors concluded that the habitats of the two species overlap in their use of feeding areas, but they select different forage plants (Ihl and Klein 2001).

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