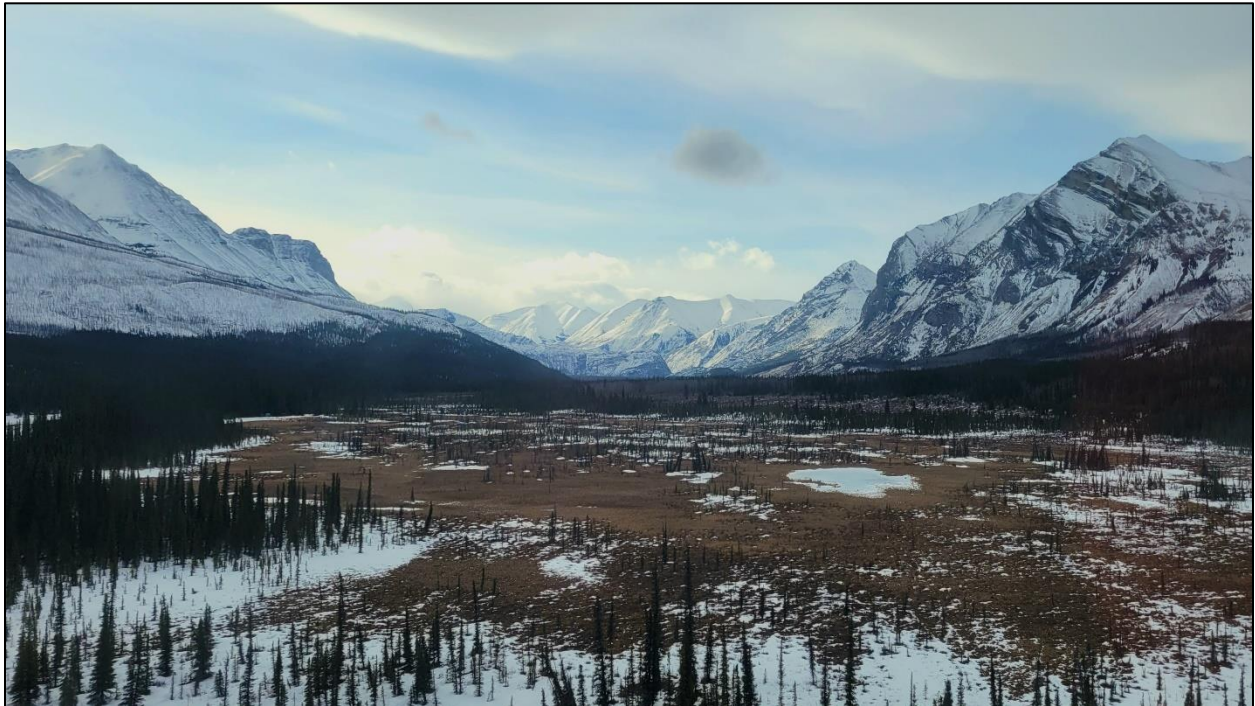




Predator Reduction to Support Caribou Recovery: 2021-2022 Summary



BC Ministry of Land, Water and Resource Stewardship

Caribou Recovery Program

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VISION: Conservation and recovery of British Columbia's caribou through excellence in resource stewardship.

Executive Summary

The reduction of predator densities has been shown to be an effective short-term action for recovering threatened caribou herds when applied in an adaptive management framework. Predator reduction programs require scientific rigour, high standards for humaneness, and ongoing monitoring and assessment. Aerial-based wolf reduction was applied to 13 of the 54 identified caribou populations in British Columbia. Of those 13 caribou populations, ground-based cougar reduction was applied in two of those herds as well. A total of 279 wolves were removed through aerial shooting and seven cougars were removed through ground-based hunting, at a cost of approximately \$1.75 million. Wolf reduction targets were achieved across nearly all treatment herds and the efforts are expected to contribute to caribou population stabilization or growth. Targeted removal of cougars from caribou habitat is also anticipated to contribute to caribou recovery in those herds. Monitoring of the caribou population response to predator reductions will continue to occur throughout the year.

Background

Woodland caribou (*Rangifer tarandus caribou*) populations have experienced significant declines in British Columbia (BC). The Boreal ecotype is designated federally as ‘Threatened’ and is ‘Red-Listed’ provincially, the Northern Mountain ecotype is designated federally as ‘Special Concern’ and is ‘Blue-Listed’ provincially, and the Southern Mountain ecotype was recently designated by COSEWIC as ‘Endangered’ (with eight local population units under imminent threat) and is ‘Red-Listed’ provincially. Unsustainable rates of predation on caribou by wolves (*Canis lupus*) due to apparent competition – defined as an indirect interaction between two or more prey species through a shared predator – is identified as the primary proximate cause of caribou population declines (Seip 1991). The ultimate cause of this interaction is landscape disturbance resulting in high proportions of early seral habitat that support primary prey populations above historic levels, due primarily to forestry (Ehlers et al. 2016). Wolf predation can be further amplified by linear features in caribou habitat that enable wolves to travel efficiently and encounter caribou at higher rates than would occur in an undisturbed landscape (Dickie et al. 2017).

The interaction between caribou, predators, and primary prey populations can be managed to benefit caribou in several ways: 1) managing the habitat composition in core and matrix caribou habitat to support less primary prey and predator abundance, 2) actively reducing primary prey populations so the landscape supports less predators, and 3) directly reducing predator populations (Serrouya et al. 2019).

Throughout most of BC, wolves are the primary predator responsible for high predation rates on caribou, however, at the southern extent of caribou range, cougar (*Puma concolor*) predation is often a larger contributor to caribou mortality (Kinley and Apps 2001, Wittmer et al. 2005). Although landscape-level habitat management is the key to achieving and supporting self-sustaining caribou populations, it may be decades before the benefits of habitat management are attained. Direct management of primary prey populations has less lag time between application and realized benefits, and the direct management (i.e., reduction) of predators has the most rapid effect. The direct management of primary prey or predator populations are considered short-term management actions and will not address the ultimate cause of caribou population declines if habitat protection and restoration does not occur concurrently. If the management of predators and their primary prey is halted, and the habitat issues have not been addressed, threatened caribou populations are likely to continue to decline towards extirpation.

In order to manage towards the successful recovery of certain at-risk caribou populations, intensive reduction of wolf populations may be required (Seip 1992, Serrouya et al. 2019). A five-year pilot project in the South Peace region of BC has demonstrated the effectiveness of intensive wolf reduction to reverse declines in threatened caribou populations (Bridger 2019). The effects of predator reduction may be further enhanced when combined with additional short-term recovery actions, as demonstrated in the Klinse-Za caribou herd, where wolf reduction and maternal penning has rescued the herd from the brink of extirpation (McNay et al. 2022).

In accordance with the provincial Caribou Recovery Program Interim Aerial Wolf Reduction Procedure (BC FLNRORD 2021), proactive wolf reduction was continued during this most recent winter of 2021-2022 on a subset of provincial caribou herds (Figure 1). This year’s predator reduction activities commenced in December of 2021. Wolves were dispatched by aerial shooting from a helicopter, as it is deemed the most humane and effective method of reducing wolf populations across large geographical areas while reducing any risk of bycatch. The extent and topography of the areas that must be covered to effectively reduce wolf populations in core and matrix caribou habitat necessitates the use of aircraft. The combination of GPS/VHF radio-tracking collars and aerial shooting to kill wolves has been demonstrated

to be an effective method of removing entire wolf packs and reducing the risk of predation to caribou populations (Bridger 2019). The federal and provincial target for wolf densities in caribou recovery areas is less than three wolves per 1000 km². To achieve that target, wolf reduction generally aims to remove greater than 80% of wolves within a treatment area. Intensive wolf reduction must occur on an annual basis to account for wolves' high reproductive capability and ability to recolonize rapidly from adjacent areas. Wolves are tracked and lethally removed during the winter months when snow depth concentrates wolves and their primary prey in valley bottoms, and their mobility is limited by snow. Reducing wolves during winter has an additional benefit of providing the caribou a reprieve from high wolf predation rates during calving season in the spring (a vulnerable period for caribou cows and their calves).

Due to their solitary and reclusive behaviour, cougars cannot be effectively reduced using aerial-based methods. Cougars are lethally removed in caribou core and matrix habitat by surveying caribou habitat for cougar sign and tracking those specific individuals using the services of professional dog handlers.

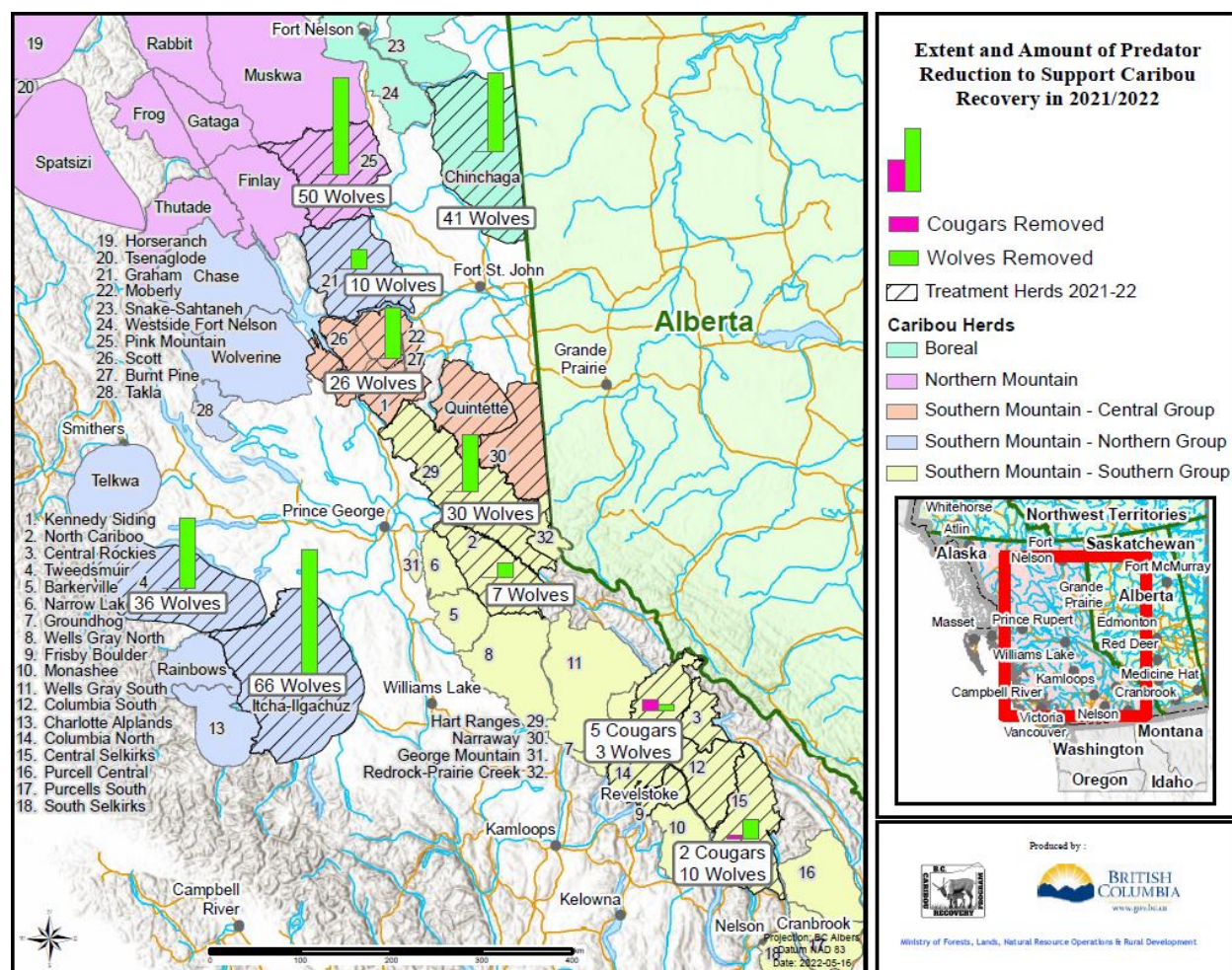


Figure 1. Distribution of predator reduction to support caribou recovery in 2021/2022.

Summary

Provincial

In total, 279 wolves were lethally removed via helicopter-based shooting, and seven cougars were removed via ground-based hunting (Table 1). To achieve sufficient wolf reduction levels, aerial crews made multiple reduction attempts over the course of the winter across the treatment areas to reduce wolf densities below three wolves per 1000 km². Preliminary estimates suggest that target wolf densities were achieved across all but one treatment area. The total cost of this year's predator management activities was \$1,749,150. The primary expense was the contracting of helicopter services to support the aerial removal of wolves, while secondary expenses included costs associated with radio collar purchases, fuel, fixed-wing aircraft support, field equipment, accommodations for crews, and the hiring of professional dog handlers (only in the cougar reduction treatment areas). The activities undertaken were authorized by provincial Wildlife Act permits, Animal Care Applications, BC Parks Letters of Authorization, and federal Aviation Security Exemptions.

The caribou population response to the 2021-2022 predator reductions will be assessed over the following year into the winter of 2023. Early observations among several of the new caribou herds receiving predator reduction treatment show indications of population growth through increased calf recruitment and adult female survival; however, further treatment and monitoring will be required to fully assess the population-level effects. The South Peace caribou herds, which have received longer-term treatment, have combined for an estimated 106% population increase since the onset of wolf reduction in 2015.

Table 1. Predator reduction summary and associated costs per caribou herd.

Ecotype and Herd	Wolves Removed	Cougars Removed	Cost ¹
Boreal			
Chinchaga	41		\$120,000
Northern Mountain			
Pink Mountain	50		\$225,300
Southern Mountain - Central Group			
South Peace ²	26		\$320,000
Southern Mountain - Northern Group			
Graham	10		\$179,600
Itcha-Ilgachuz	66		\$180,000
Tweedsmuir	36		\$267,600
Southern Mountain - Southern Group			
Central Selkirks	10	2	\$96,750
Columbia North ³	3	5	\$130,000
Hart Ranges	30		\$179,900
North Cariboo	7		\$50,000
Total	279	7	\$1,749,150

¹ Costs may include helicopter services and fuel, fixed-wing aircraft services, radio-collar purchase, equipment, and accommodations.

² South Peace includes Klinse-Za, Kennedy Siding, Quintette, and Narraway caribou herds

³ Includes portions of Columbia South and Frisby Boulder herds

Although the rate at which wolves recolonize the treatment areas fluctuates annually, the wolf populations have shown to be resilient, recovering in the treatment areas at rates of 30–100% by the following winter. The ability for wolf populations to expand through reproduction and dispersal reduces the risk associated with broad population-level impacts to wolves in BC. Wolf recovery and recolonization within and adjacent to the treatment areas will continue to be monitored annually.

Chinchaga

The Chinchaga caribou herd is the only Boreal ecotype that currently receives wolf reduction treatments to support population recovery. The Chinchaga herd was selected as a recipient of wolf reduction treatments in response to sharp population declines over the past ten years, and the program was developed in collaboration with the Blueberry River First Nation. The program was initially approved for three years, and subsequently approved for an additional five years in fall of 2021. The winter of 2021-2022 was the fourth year of wolf reduction. During the winter's reduction efforts, 41 wolves were removed through helicopter-based, aerial shooting from a 13,900 km² treatment area. Weather conditions were optimal through much of the winter, with deep snow in the treatment area that facilitated effective tracking and removal efforts. The program incurred a total cost of \$120,000, primarily associated with helicopter services.

Eleven wolf packs were encountered, ranging in size from 2–11 wolves, and an average pack size of 4.5 individuals. Wolves were concurrently removed in Alberta where the Chinchaga herd boundary spans the BC-Alberta border. Seventy-four wolves were removed across the Alberta portion of the Chinchaga range (17,600 km²). It was estimated that nine wolves remained within or immediately adjacent to the BC Chinchaga treatment area, for a remaining wolf density of 0.6 wolves/1000 km² and a wolf reduction rate of 82%. The rate of reduction, and the resulting wolf density, is expected to contribute positively to caribou population stability or growth. Following last year's wolf reduction efforts, the Chinchaga herd had the highest calf recruitment rates of all Boreal caribou herds following aerial surveys in March 2022 and has the best population growth rates of all Boreal herds since the onset of wolf reduction in 2019.

Pink Mountain

The Pink Mountain caribou population is the only Northern ecotype that currently receives wolf reduction treatments to support caribou recovery. The Pink Mountain herd was selected as a recipient of wolf reduction treatments in response to population declines over the past decades, and the program was developed in collaboration with the Blueberry River First Nation. The program was initially approved for three years, and subsequently approved for an additional five years in fall of 2021. The winter of 2021-2022 was the fourth year of wolf reduction. During the winter's reduction efforts, 50 wolves were removed through helicopter-based, aerial shooting from a 9,600 km² treatment area. Winter weather conditions were challenging for tracking and removing wolves, with unseasonably warm and windy conditions and little to no snowpack in the valleys through much of February and March. The program incurred a total cost of \$225,300, primarily associated with helicopter services, helicopter fuel, radio collars, and accommodations.

Thirteen wolf packs were encountered, ranging in size from 2–10 wolves, and an average pack size of 4.8 individuals. Despite the challenging weather conditions, it was estimated that only 12 wolves remained within or immediately adjacent to the Pink Mountain treatment area, for a remaining wolf density of 1.3 wolves/1000 km² and a wolf reduction rate of 81%. The rate of reduction, and the resulting wolf density, is expected to contribute positively to caribou population stability or growth. Following last year's wolf reduction efforts, calf recruitment rates reported during aerial surveys in March 2022 were lower than expected, but adult female survival rates remained high throughout the year.

South Peace

The South Peace wolf reduction program includes the Klinse-Za (Moberly and Scott East herds), Kennedy Siding, Quintette, and South Narraway caribou herds. The South Peace herds were selected as recipients of wolf reduction treatments in response to rapid population declines over the past decades. The winter of 2021-2022 was the eighth year of aerial wolf reduction across the South Peace treatment areas and was subsequently approved for an additional five years in the fall of 2021. During the winter's reduction efforts, 26 wolves were removed through helicopter-based, aerial shooting from a 21,500 km² treatment area. Winter weather conditions were sub-optimal for tracking and removing wolves during much of the winter, however there were periods of favourable conditions through February and March. The program incurred a total cost of \$320,000, primarily associated with helicopter services and radio collar purchase.

Ten wolf packs were encountered, ranging in size from 2–11 wolves, and an average pack size of 3.7 individuals. It was estimated that 13 wolves remained within or immediately adjacent to the South Peace treatment area, for a remaining wolf density of 0.8 wolves/1000 km² and a wolf reduction rate of 67%. The rate of reduction, and the resulting wolf density, is expected to contribute positively to caribou population stability or growth. Following last year's wolf reduction efforts, calf recruitment across the South Peace herds was exceptional and survival of radio-collared adult females was nearly 100%. Since the onset of wolf reduction in 2015, the combined South Peace caribou herds have doubled in size, and the Klinse-Za herd specifically (in conjunction with maternal penning [McNay et al. 2022]) has tripled.

Graham

The Graham caribou herd previously served as the experimental control population to compare wolf reduction efforts in the South Peace to a non-treatment herd. However, it became apparent that the Graham caribou population was declining at a rapid rate in comparison to the treatment populations. Thus, wolf reduction was initiated in 2020, and the winter of 2021-2022 was the third year of the program. The program was approved for an additional five years in fall of 2021. During the winter's reduction efforts, 10 wolves were removed through helicopter-based, aerial shooting from a 9,300 km² treatment area. Winter weather conditions were challenging for tracking and removing wolves, with unseasonably warm and windy conditions and little to no snowpack in the valleys through much of February and March. The program incurred a total cost of \$179,600, primarily associated with helicopter services, helicopter fuel, radio collars, and accommodations.

Six wolf packs were encountered, ranging in size from 2–6 wolves, and an average pack size of 4.0 individuals. It was estimated that ten wolves remained within or immediately adjacent to the Graham treatment area, for a remaining wolf density of 1.2 wolves/1000 km² and a wolf reduction rate of 50%. Although the reduction rate was relatively low, the resulting wolf density is expected to contribute positively to caribou population stability or growth. Following last year's wolf reduction efforts, aerial surveys in March 2022 reported calf recruitment rates indicative of positive population growth while the survival rate of radio-collared adult females was 100% throughout the year.

Itcha-Ilgachuz

The Itcha-Ilgachuz caribou population was selected as a recipient of wolf reduction treatments due to an extended period of rapid population declines, primarily attributed to unsustainable rates of wolf predation. Initially this herd was recipient of a two-year emergency wolf reduction program, undertaken during the 2019-2020 and 2020-2021 winters. During the two-year emergency program, 113 wolves were removed within the wolf treatment area. Following consultation and engagement, a further five years of wolf reduction was recommended to support this herd's recovery. The winter of 2021-2022 was the third year

of wolf reduction efforts and 66 wolves were removed through helicopter-based, aerial shooting from a 25,540 km² treatment area. Twelve wolf packs and three lone wolves were detected, with an average pack size was 8.3 wolves and ranging in size between 2–17 wolves. Winter weather conditions presented ideal tracking conditions for wolves and wolf abundance was high in the area, potentially due to low reduction efforts during Year 2 of the program. The program incurred a total cost of \$180,000, primarily associated with helicopter and fixed-wing services, as well as accommodations. Approximately 29 wolves remained within the Itcha-Ilgachuz treatment area, for a remaining wolf density of 1.1 wolves/1000 km². Within core range for the Itcha-Ilgachuz caribou, a wolf reduction rate of 85% was achieved. Aerial recruitment surveys in March yielded relatively low proportions of calves in the population at just 10.5%. Poor recruitment was likely due to low overall wolf reduction rates during the previous winter, when only 10 wolves were removed. It is expected that winter 2021-2022 wolf reduction will contribute positively to caribou population stability or growth.

Tweedsmuir

The Tweedsmuir-Entiako caribou herd had significant annual population declines (>10% per year) between 2014 and 2019 due to high predation rates by wolves. In response to the herd's decline, the Province implemented a 2-year emergency wolf reduction program in the winter of 2020. In the fall of 2021, the program was approved for an additional five years. During the 2022 winter's reduction effort, 10 wolf packs were encountered ranging in size from 1-11 individuals, with an average pack size of 4.5 wolves. Thirty-six wolves were removed from a 15,785 km² treatment area through helicopter-based removal. An estimated 17 wolves remained within or immediately adjacent to the treatment area, for a remaining density estimate of 1.1 wolves/1000 km² and a wolf reduction rate of 72%.

Weather conditions were challenging throughout the winter due to infrequent snowfall, lower than average snowpack, and freeze thaw-events. The program incurred a total cost of \$267,604, primarily associated with helicopter services, fix-wing services, radio collar purchase, and accommodations. Following two years of wolf reduction efforts in Tweedsmuir-Entiako, the population growth rate (λ) changed from $\lambda = 0.89$ (2014-2019; Demars and Serrouya 2019) pre-wolf reduction to $\lambda = 1.03$ (2020-2021) post-wolf reductions. Additionally, estimates of calf recruitment from the 2022 aerial survey were the highest recorded since monitoring began in 2014.

Central Selkirks

The Central Selkirks caribou herd is the southernmost extant caribou population in BC. This herd is at imminent risk of becoming functionally extirpated, thus an emergency effort to reduce both wolves and cougars was initially implemented through 2019-2020 to 2020-2021. The program was approved for an additional five-year period in fall 2021. During this winter's reduction efforts, 10 wolves were removed through helicopter-based, aerial shooting from a 2,872 km² treatment area. Additionally, two cougars were removed through ground-based, targeted removal within caribou habitat. Tracking conditions were favorable across the herd area for much of the winter. The program incurred a total cost of \$96,750 primarily associated with helicopter services and dog handlers. Based on track surveys and observations during helicopter removal, three small packs, averaging 3.3 wolves per pack, and several lone wolves were documented within the treatment area. As of March 2022, approximately three wolves remained within the Central Selkirks treatment area, for a remaining wolf density of 0.9 wolves/1000 km² and a wolf reduction rate of 72%. Since the start of predator removal in 2019, 100% of collared female caribou have survived. This result is expected to contribute positively to caribou population stability or growth notably in combination with the start of material penning project in spring 2022.

Columbia North

Wolf reduction has been underway for the Columbia North caribou population since 2017 as a recovery measure under the Mountain Caribou Recovery Implementation Plan and includes portions of the Columbia South and Frisby Boulder herds. Targeted, ground-based cougar reduction has been implemented more recently to further the recovery efforts. The winter of 2021-2022 was the sixth year of wolf reduction, and third year of cougar reduction. The program was approved for an additional 5 years in fall 2021. During this winter's reduction efforts, three wolves were removed through helicopter-based, aerial shooting from a 6,911 km² treatment area. Tracking conditions were favourable during the removal period and it was estimated that reduction rate within the treatment area was 100%. Additionally, five cougars were removed through ground-based, targeted removal within caribou habitat. The program incurred a total cost of \$130,000 primarily associated with helicopter services and dog handlers.

In 2019, 2020 and 2021 the survival rate of collared female caribou was 100%, 92%, 100%, respectively. Since 2018, annual population monitoring of caribou through recruitment surveys and censuses have documented consecutive years of population growth. The rate of predator reduction, and the resulting wolf density, in addition to the targeted removal of cougars, is expected to continue to contribute positively to caribou population stability or growth.

Hart Ranges

The Hart Ranges caribou population was selected as a recipient of wolf reduction treatments due rapid caribou population declines recorded over the past 10 years. The Hart Ranges is the largest population designated as Southern Group – Southern Mountain Caribou and is expected to yield the largest population returns in response to wolf reduction efforts. The winter of 2021-2022 was the third year of a seven-year program approval. During the winter's reduction efforts, 30 wolves were removed through helicopter-based, aerial shooting from a 13,730 km² treatment area. Winter weather conditions were excellent with frequent fresh snow and frozen rivers/creeks to support tracking and removal. The program incurred a total cost of \$179,900 primarily associated with helicopter services and radio collar purchase.

Average pack size was 3.4 wolves, ranging between 1–9 wolves per pack, with 10 packs detected. It is estimated that only four wolves remained within or immediately adjacent to the Hart Ranges treatment area, for a remaining wolf density of <0.1 wolves/1000 km² and a wolf reduction rate of 88%. The rate of reduction, and the resulting wolf density, is expected to contribute positively to caribou population stability or growth. The Hart Ranges (Parsnip and Hart South) was surveyed in March 2022. The Parsnip caribou subpopulation was estimated at 148 caribou in 2022 (up from ~120 caribou prior to 2020) with calves at 21%. The Hart South was estimated at 359 caribou (up from 282 since 2020) with calves estimated at 22% of population. Results from the 2022 survey indicate a positive response to wolf reduction which started in 2020. Overall, there are about 100 more caribou in the Hart Ranges following two years of wolf reduction representing a population increase of 26%.

North Cariboo Mountains

Wolf reduction was initiated in the North Cariboo Mountains subpopulation in 2022 in response to continued caribou population decline. The subpopulation declined from 284 to 187 individuals between 2002 and 2018. Only 145 caribou were estimated in the North Cariboo in 2020. The North Cariboo Mountains herd is one of the larger remaining subpopulations in DU 9, with over 100 animals and is adjacent to ongoing wolf reduction areas in the Hart Ranges. A total of 46 wolves in six packs were estimated in the North Cariboo range (7.7 wolves/1000 km²) based on results of a winter snow track survey in 2020. In 2022, seven wolves in four different packs were removed reducing the density to 5.5

wolves/1000 km². However, it is possible that some wolves moved out of the zone since 2020 as we estimated only 22 wolves in six packs in 2022. Average pack size was 3.6 wolves and ranged in size from 2–6 wolves per pack. A minimum of 11 wolves were estimated to remain within or immediately adjacent to the range and a radio-collared wolf observed in a pack of five wolves left the zone in April 2022. The program incurred a total cost of \$50,000 primarily associated with helicopter services and radio-collar purchase.

Conclusion

Ongoing monitoring continues to show the utility of predator reduction as an effective management action for recovering at-risk caribou populations. Public engagement and consultation with Indigenous communities were conducted in the fall of 2021 to seek an additional five-year approval to continue predator reduction efforts across 13 of BC's 54 caribou herds. The BC Caribou Recovery Program is committed to implementing and monitoring a rigorous and adaptive predator reduction program to support caribou recovery while other, longer-term solutions are applied. Despite suboptimal weather conditions in some treatment areas, the predator reduction activities undertaken during the winter of 2021-22 were largely successful and are expected to contribute positively to caribou population stability or growth.

Literature Cited

- B.C. Ministry of Forests, Lands, Natural Resource Operations and Rural Development. 2021. Caribou recovery program interim aerial wolf reduction procedure. Government of BC, Victoria, BC: https://www2.gov.bc.ca/assets/gov/environment/natural-resource-policy-legislation/fish-and-wildlife-policy/4-7-0406_-_aerial_wolf_reduction_procedure_-_september_16_2021.pdf
- Bridger, M. 2019. South Peace Caribou Recovery following Five Years of Experimental Wolf Reduction. BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development. https://www2.gov.bc.ca/assets/gov/environment/plants-animals-and-ecosystems/wildlife-wildlife-habitat/caribou/south_peace_caribou_recovery_following_five_years_of_experimental_wolf_reduction.pdf
- Canada, and Environment Canada. 2014. Recovery strategy for the woodland caribou, southern mountain population (*Rangifer tarandus caribou*) in Canada.
- Demars C., and R. Serrouya. 2019. Recommendations for implementing and evaluating predator management within the Tweedsmuir-Entiako and Hart ranges caribou herds: Predator feasibility project phase II. Caribou Monitoring Unit, Alberta Biodiversity Monitoring Institute. Prepared for British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development. Edmonton, AB. 38 pp.+ appendix
- Dickie, M., R. Serrouya, R.S. McNay, and S. Boutin. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology* 54: 253–263.
- Ehlers, L. P., C. J. Johnson, and D. R. Seip. 2016. Evaluating the influence of anthropogenic landscape change on wolf distribution: implications for woodland caribou. *Ecosphere* 7.
- Kinley, T. A., and C. D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. *Wildlife Society Bulletin*: 158–164.

- McNay, R.S., C. T. Lamb, L. Giguere, S. H. Williams, H. Martin, G. D. Sutherland, and M. Hebblewhite. 2022. Demographic responses of nearly extirpated endangered mountain caribou to recovery actions in central British Columbia. *Ecological Applications*. Accepted Author Manuscript e2580. <https://doi.org/10.1002/eap.2580>
- Seip, D. R. 1991. Predation and caribou populations. *Rangifer*: 46–52.
- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70: 1494–1503.
- Serrouya, R., D. R. Seip, D. Hervieux, B. N. McLellan, R. S. McNay, R. Steenweg, D. C. Heard, M. Hebblewhite, M. Gillingham, and S. Boutin. 2019. Saving endangered species using adaptive management. *Proceedings of the National Academy of Sciences* 116: 6181–6186.
- Wittmer, H. U., A. R. Sinclair, and B. N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144: 257–267.