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Demographic responses of nearly extirpated endangered mountain caribou to recovery actions in Central British Columbia

R. Scott McNay¹ | Clayton T. Lamb^{2,3}  | Line Giguere¹ | Sara H. Williams³ | Hans Martin³  | Glenn D. Sutherland¹ | Mark Hebblewhite³ 

¹Wildlife Infometrics Inc, Mackenzie, British Columbia, Canada

²Department of Biology, University of British Columbia, Kelowna, British Columbia, Canada

³Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, Montana, USA

Correspondence

Clayton T. Lamb

Email: ctlamb@ualberta.ca

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Abstract

Recovering endangered species is a difficult and often controversial task that challenges status quo land uses. Southern Mountain caribou are a threatened ecotype of caribou that historically ranged in southwestern Canada and northwestern USA and epitomize the tension between resource extraction, biodiversity conservation, and Indigenous Peoples' treaty rights. Human-induced habitat alteration is considered the ultimate cause of caribou population declines, whereby an increased abundance of primary prey—such as moose and deer—elevates predator populations and creates unsustainable caribou mortality. Here we focus on the Klinse-Za and Quintette subpopulations, part of the endangered Central Group of Southern Mountain caribou in British Columbia. These subpopulations were trending toward immediate extirpation until a collaborative group initiated recovery by implementing two short-term recovery actions. We test the effectiveness of these recovery actions—maternity penning of adult females and their calves, and the reduction of a primary predator, wolves—in increasing vital rates and population growth. Klinse-Za received both recovery actions, whereas Quintette only received wolf reductions, providing an opportunity to test efficacy between recovery actions. Between 1995 and 2021, we followed 162 collared female caribou for 414 animal-years to estimate survival and used aerial counts to estimate population abundance and calf recruitment. We combined these data in an integrated population model to estimate female population growth, total population abundance, and recovery action effectiveness. Results suggest that the subpopulations were declining rapidly ($\lambda = 0.90\text{--}0.93$) before interventions and would have been functionally extirpated (<10 animals) within 10–15 years. Wolf reduction increased population growth rates by ~ 0.12 for each subpopulation. Wolf reduction halted the decline of Quintette caribou and allowed them to increase ($\lambda = 1.05$), but alone would have only stabilized the Klinse-Za

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($\lambda = 1.02$). However, maternity penning in the Klinse-Za increased population growth by a further ~ 0.06 , which when combined with wolf reductions, allowed populations to grow ($\lambda = 1.08$). Taken together, the recovery actions in these subpopulations increased adult female survival, calf recruitment, and overall population growth, more than doubling abundance. Our results suggest that maternity penning and wolf reductions can be effective at increasing caribou numbers in the short term, while long-term commitments to habitat protection and restoration are made.

KEYWORDS

adaptive management, Before–After, conservation effectiveness, conservation intervention, endangered species, juvenile mortality, maternity penning, natality, population dynamics, population recovery, predation, *Rangifer tarandus*

INTRODUCTION

Positionality statement

This statement shares the backgrounds and contributions of the authors to explain author contributions, relationship to Indigenous collaborators, and relationship to related papers. We are an international group of eight scientists and wildlife practitioners with experience collecting field data, analyzing quantitative data, and working with Indigenous Peoples. The authors were tasked by two First Nations with analyzing, from a western science perspective, the past and recent demographic trends of a nearly extirpated caribou subpopulation that is the focus of an Indigenous-led conservation initiative. Specifically, two authors, R. Scott McNay and Line Giguere, own a western Canada wildlife science consulting firm (Wildlife Infometrics) retained by West Moberly First Nations and Sauteau First Nations to carry out conservation actions (maternal penning and habitat restoration) as well as collect and analyze data. Glenn D. Sutherland also works for Wildlife Infometrics, where he develops study designs and conducts quantitative analyses. Clayton T. Lamb, Sara H. Williams, Hans Martin, and Mark Hebblewhite are quantitative wildlife scientists at universities in Canada and the United States, and conducted the modeling presented here.

West Moberly First Nations and Sauteau First Nations, and partners, have been leading recovery of a culturally-important caribou subpopulation, guided by both Indigenous and Western Knowledge systems. A subset of authors on the present paper, together with Indigenous authors from West Moberly First Nations and Sauteau First Nations, have co-produced an overview of these recovery efforts in a related scientific paper (Lamb et al., 2022). The authors on the present

paper represent the technical science team that supports the Indigenous-led conservation efforts, including the collection of technical data and quantitative analysis. In this case, West Moberly First Nations and Sauteau First Nations members have specifically chosen to not be represented as coauthors here. Appendix S1: Section S6 includes a letter from both Nations that explains their reasoning. With limited time available, their focus is on-the-ground and legal conservation of their homelands, and co-produced manuscripts that braid knowledge systems such as Lamb et al. (2022). The Nations prefer that technical manuscripts such as this are handled by the science team represented as authors here. As expressed in their letter, the Nations have read the present manuscript and support our submission of this paper for publication. We thank West Moberly First Nations and Sauteau First Nations for their continued and courageous efforts to restore caribou in their homelands and for their support as we developed this manuscript.

Background and purpose

Reversing species' declines and averting extirpation is a primary goal of conservation science and conservationists have successfully averted the near extirpation of many iconic species such as bald eagles (*Haliaeetus leucocephalus*), California condors (*Gymnogyps californianus*), gray wolves (*Canis lupus*), and humpback whales (*Megaptera novaeangliae*). Although such conservation efforts help to reduce the overall rate of biodiversity loss, many other species across the globe are accumulating increasingly poor conservation status (Johnson et al., 2017). For example, between 1996 and 2008, the conservation status of 171 mammal species deteriorated and justified a higher threat ranking on the International Union on

the Conservation of Nature (IUCN) Red List, whereas conservation status only improved for 24 species (Hoffmann et al., 2010). Although the cause of declines for many species is unknown, limiting effective conservation action, for some species there are additional challenges to their recovery such as perceived conflicts between their viability and economic needs such as resource extraction. For several species, a hesitation or unwillingness to act on what is known to be needed for species recovery is a primary limitation to improving the conservation status of more endangered and threatened species. Collectively, these challenges limit the accumulation of evidence on interventions that successfully avert extirpation of imperiled species, hindering species recovery (Williams et al., 2021).

In North America, the recovery of declining threatened woodland caribou (*Rangifer tarandus caribou*, from this point forwards “caribou”) has been characterized as one of the greatest terrestrial conservation challenges on the continent (Serrouya et al., 2019). Woodland caribou are among the most recently extirpated large mammals in the lower 48 states in the USA (Moskowitz, 2019), and population declines are ongoing across much of the extant caribou range in Canada (Serrouya, Dickie, et al., 2021). Caribou conservation is challenging because the species extends broadly across most boreal and mountain ecosystems in North America, which are also extensively exploited by industries to extract valuable resources such as oil, gas, coal, hydroelectricity, and wood (Apps et al., 2013; Johnson et al., 2015; Peters et al., 2013; Seip, 1992; Wittmer et al., 2007; Wittmer, Sinclair et al., 2005). Habitat disturbance resulting from resource extraction ultimately causes declines in caribou populations through disturbance-mediated apparent competition (Holt, 1977; Holt & Lawton, 1994; Wittmer et al., 2013), whereby disturbance creates favorable conditions for prey (other than caribou) and their predators that then incidentally prey on caribou (Serrouya, Dickie, et al., 2021). Caribou have low fecundity and are vulnerable to predators and predation, in particular by wolves (*Canis lupus*) (Seip, 1991; Seip & Cichowski, 1996). Bears (*Ursus* spp.), wolverines (*Gulo gulo*), and felids also prey on caribou, especially juveniles (Adams et al., 1995; Brockman et al., 2017; Gustine et al., 2006; Jenkins & Barten, 2005; Pinard et al., 2012). Overall, unsustainable predation rates have been identified as the proximate cause of caribou population decline (Wittmer, McLellan et al., 2005).

Recovery actions to halt caribou declines and avert extirpations have been numerous and efficacy—in terms of increasing caribou populations—has varied. Linear features such as roads and seismic lines have been treated to reduce predator hunting efficiency and use of caribou habitat (Dickie et al., 2021; Keim et al., 2021; Neufeld, 2006; Tattersall et al., 2020), wolves have been reduced to

mitigate unsustainable caribou mortality (Hayes et al., 2003; Hervieux et al., 2013; Wilson, 2009), maternity pens have been built to protect caribou adults and calves from predators (Adams et al., 2019; Serrouya, Bollefer, et al., 2021; Smith & Pittaway, 2011), caribou have been translocated to bolster declining populations (Cichowski et al., 2014), primary prey has been liberally harvested to indirectly reduce predators (Serrouya et al., 2017; Steenweg, 2011), and nutrition has been enhanced through supplemental feeding to improve calf production (Heard & Zimmerman, 2021). Despite these recovery actions, results have mostly been inadequate to reverse population declines and expeditiously recover caribou, aside from a few exceptions (Heard & Zimmerman, 2021; Hervieux et al., 2013; Serrouya et al., 2019). There are no examples of woodland caribou populations recovered to self-sustaining levels without ongoing recovery actions, especially given the lack of long-term habitat protection (e.g., Nagy-Reis et al., 2021; Palm et al., 2020). Even if habitat is appropriately protected, caribou living in areas that have been previously disturbed will require effective short-term recovery actions to avert extirpation while habitat is restored, a process that will take many years. In the last decade, the functional extirpation (<10 members) of 10 subpopulations of caribou in British Columbia (BC) and two in Alberta (AB), and the sole remaining US subpopulation in northern Idaho and Washington, stand as testament to the precarious position for woodland caribou (BC Caribou Recovery Program, 2020; ECCC, 2018; Seip & Jones, 2014; Sittler & McNay, 2017). There is an urgent need to test and implement recovery actions that will recover endangered subpopulations of woodland caribou while habitat can be protected, reconnected, and restored.

The effectiveness of recovery actions for caribou conservation remains uncertain. Although the reduction of wolf numbers can help to reduce caribou mortality (Hervieux et al., 2013; Serrouya et al., 2019), it raises functional and ethical issues: (1) in multipredator ecosystems, other predators may respond in a compensatory manner (Leblond et al., 2016; Zager & Beecham, 2006); (2) killing one species to improve conditions for another is contentious and raises concerns around the ethics of such approaches (Proulx et al., 2017; Wasser et al., 2012); and (3) wolf reduction is meant to be a short-term action, and is therefore unable to prevent declines in the long term without addressing the ultimate driver of habitat loss and fragmentation (Brook et al., 2015; Hervieux et al., 2015; Musiani & Paquet, 2004). Maternity penning has been demonstrated empirically and, through modeling, to have some potential for enhancing recovery (Adams et al., 2019; Johnson et al., 2019). Although field trials of penning has generally revealed positive results,

the magnitude of effectiveness has generally been lower than expected due to a variety of unanticipated challenges such as high mortality or starting populations that were larger than expected (Adams et al., 2019; Serrouya, Bollefer, et al., 2021; Smith & Pittaway, 2011). The effects of alternate prey reductions are mixed, where reducing moose abundance did not increase caribou survival or population growth rate consistently (Serrouya et al., 2017). Finally, there is growing evidence that translocations conducted to date have not been an effective strategy to prevent caribou declines (Grant et al., 2019; Serrouya et al., 2019).

Understanding the precise demographic drivers of caribou declines may reveal that different recovery actions have context-specific efficacy. While ungulate demography is generally driven by high, but constant adult survival and variable juvenile recruitment (Gaillard et al., 1998), contributions of different vital rates to population recovery often differs for endangered ungulates (Hebblewhite et al., 2007). If caribou declines are caused by unsustainable rates of predation primarily on neonate or juvenile caribou, then maternity penning designed to enhance juvenile survival may be the most expedient recovery action. Alternatively, if predation is primarily limiting adult female survival, declines may be rapid, and not effectively reversed by maternity penning. Unfortunately, the mixed success of previous maternity penning on threatened or endangered caribou in western Canada (e.g., Serrouya et al., 2019; Smith & Pittaway, 2011) hinders evaluating the efficacy of these two actions. For example, in the Little Smoky maternity penning in AB, penning only occurred for a single year and co-occurred with wolf reductions, confounding interpretation, although calf mortality peaked soon after release from the pen (Smith & Pittaway, 2011). While Serrouya et al. (2019) suggested that population growth rate (λ) of the sole subpopulation to receive two sustained recovery actions (the Klinse-Za subpopulation, which is also the focus of this work) was enhanced by 0.15 by maternity penning and by 0.22 by wolf reduction, they only focused on λ (male and female) not the specific demographic drivers of adult versus juvenile survival. Focusing on λ derived from population counts, as was done in Serrouya et al. (2019), is a common approach to estimate λ , which bypasses the often-complex analyses to account for unstable age distributions that arise from population declines and bias λ estimated from survival and reproduction (Koons et al., 2006). However, when possible, including survival and reproduction information can provide additional insights into the mechanisms promoting growth as a result of management actions, and focusing on female growth rate is preferable whenever possible, given that their importance to overall population growth. Finally,

the wolf reduction effect estimated in Serrouya et al. (2019) was general across subpopulations, and not specific to the Klinse-Za. Therefore, it remains unclear that recovery action enhanced population growth rates and the specific demographic vital responses that drove population recovery in this subpopulation. Answering these questions will help to resolve uncertainty about the relative efficacy and demographic mechanisms fostering recovery in other imperiled caribou populations.

Despite the challenging nature of woodland caribou recovery across Canada, two First Nations communities (West Moberly First Nations and Saulteau First Nations, from this point forwards referred to as the Nations, while recognizing their distinct cultural identity) began a recovery program in 2013 to avert the pending extirpation of the Klinse-Za caribou subpopulation that is located within the endangered Central Group of Southern Mountain caribou central BC (Figure 1; Lamb et al., 2022). Caribou in this area were once as abundant as “bugs on the landscape” (West Moberly First Nations, 2009), and population counts in the 1990s suggested that there were at least 200 caribou in the Klinse-Za (Wood & Terry, 1999). By 2013, a minimum of 36 caribou persisted in the subpopulation. Extirpation was looming, following the extirpation of the neighboring Burnt Pine subpopulation in 2013 (Johnson et al., 2015). The Nation’s recovery program differed from previous recovery actions because it combined wolf reduction and maternity penning over multiple years, and sought to apply these recovery actions to avert extirpation while habitat protection and restoration was initiated (Lamb et al., 2022). Although the Nation’s recovery program has been lauded as a success—especially given that adjacent subpopulations not receiving recovery actions continued to decline and become extirpated (Serrouya et al., 2019; Lamb et al., 2022)—the effectiveness of the individual, short-term recovery actions applied has not been investigated.

Our objectives were to use a Before–After design that monitored the longitudinal fate of individual, radiocollared caribou and annual population surveys to: (1) assess the effectiveness of the Nation’s caribou recovery actions in the Klinse-Za and (2) partition the demographic effects of wolf reduction and maternity penning. To answer our questions, we used demographic data from the Klinse-Za subpopulation that received wolf reductions and maternity penning (two recovery actions), and contrasted trends with the adjacent Quintette subpopulation that received wolf reductions only (one recovery action). We predicted that if the wolf reduction and maternity pen components of the program were effective, annual rates of calf recruitment to 10-months, adult female survival, and population growth would all be higher in the following situations: (1) during post-

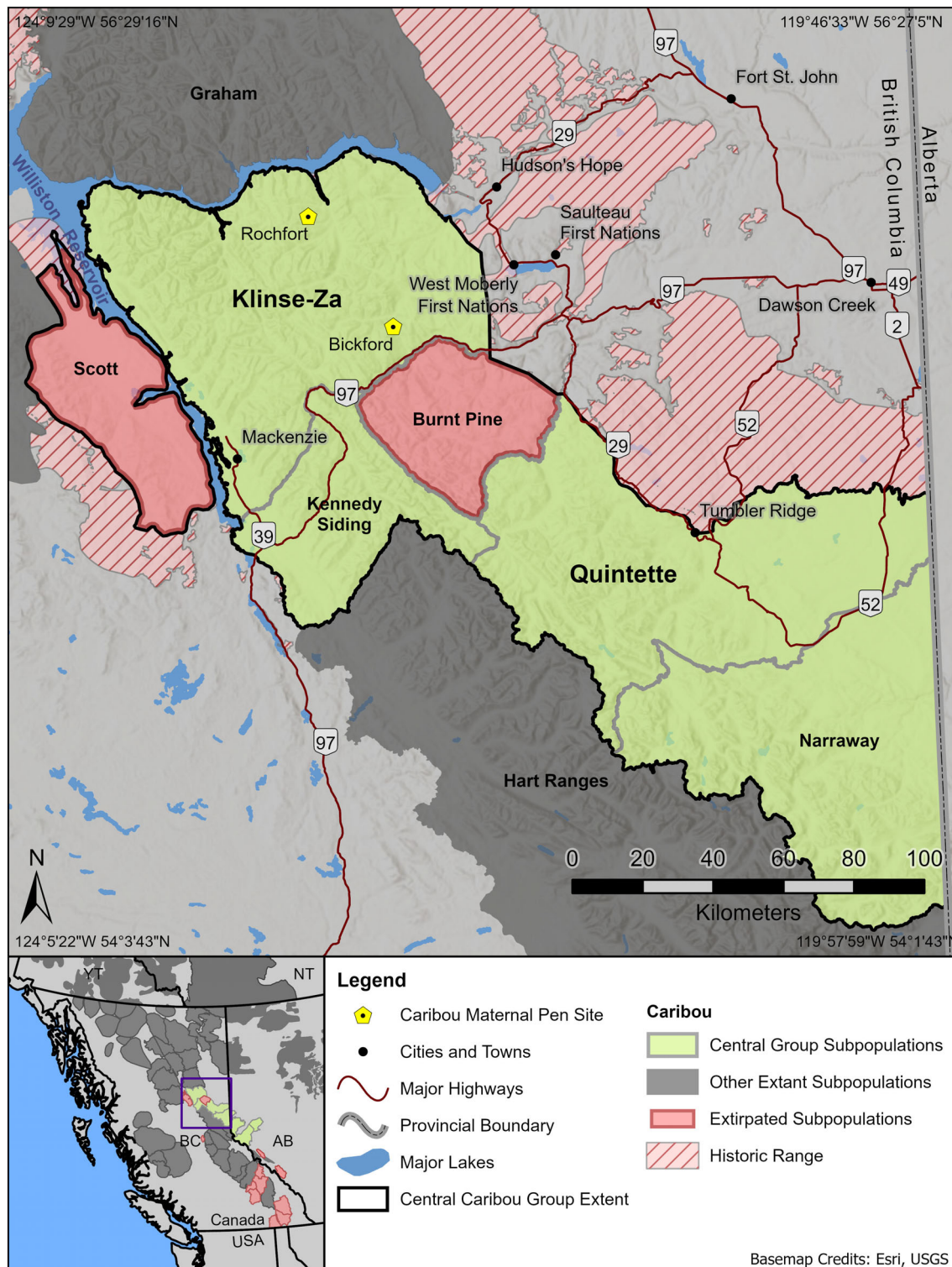


FIGURE 1 Study area figure of British Columbia's Central Group (bordered in black) of Southern Mountain woodland caribou (subpopulation boundaries 2020). The Klinse-Za and Quintette subpopulations are the focus of the demographic analysis considered here. Maternity penning was conducted at two sites, Bickford and Rochfort, within the Klinse-Za subpopulation. West Moberly First Nations and Saulteau First Nations communities are found on the shores of Moberly Lake. Boreal and mountain caribou subpopulations not considered here are filled with dark gray. Extirpated caribou subpopulations are filled with red. The 12 functionally extirpated subpopulations are shown in red (please refer to ECCC, 2018). Historic caribou range adjacent to the current distribution of Central Group caribou is shown in a hatched red (West Moberly First Nations, 2014)

recovery versus pre-recovery action years within the Klinse-Za and Quintette subpopulations, (2) for those animals that were penned for the natal period (affected by the pen and wolf reduction) versus those left free ranging (affected only by wolf reduction) during the period of recovery action implementation, and (3) for those in the Klinse-Za (two recovery actions) versus those in the adjacent Quintette subpopulation (one recovery action). We also predicted that population abundances would increase in both subpopulations during the period of recovery action implementation. These predictions suggest that penning and wolf reduction would have a significant additive contribution and improve the population demographics and that the simultaneous application of wolf reduction and maternity penning would improve population responses more than wolf reduction alone. However, if caribou declines were driven predominantly by low juvenile survival, for example, then we predicted that maternity penning would have a greater recovery effect on population growth rate (and vice versa with adult survival for wolf reduction). We sought to confront these predictions with long-term demographic information to assess recovery effectiveness, the demographic mechanisms promoting recovery, and to provide robust evidence to inform caribou survival and recovery.

METHODS

Study area

The study area (11,584 km²) is delineated by the Klinse-Za and Quintette caribou subpopulations (Figure 1; henceforth Klinse-Za and Quintette), and is characterized by mountainous terrain and rolling hills, with mountain peaks rising to 2100 m. Most of the higher elevation (>1400 m) is Engelmann Spruce–Subalpine Fir (ESSF) and Alpine Tundra (AT) biogeoclimatic zones (DeLong et al., 1994). The Sub-boreal Spruce (SBS) zone occurs at lower elevations below ~1000 m and the Boreal White and Black Spruce (BWBS) zone is found below the SBS in the eastern portion of both areas (DeLong, 2003, 2004; DeLong et al., 1990). Forest cover in the ESSF is mostly subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*) and hybrid white spruce (*P. glauca* × *engelmannii*). The SBS is dominated by hybrid white spruce with some lodgepole pine (*Pinus contorta*) occurring on drier sites. Tree cover in the BWBS consists of primarily trembling aspen (*Populus tremuloides*) due to disturbance by fires, with white and black spruce (*P. mariana*) occurring in wetter areas (DeLong et al., 1990). Fire disturbance is rare or infrequent in most of

the study area, except for in the eastern portions where fires occur, on average, every 100–150 years (DeLong, 2003). Other natural disturbances include the relatively recent outbreak of mountain pine beetle (*Dendroctonus ponderosae*), which was classed as moderate to severe in the eastern portion of the study area in 2010 (Westfall & Ebata, 2010). Recent forest health inventories and analyses have indicated an increased prevalence of the spruce bark beetle in BC (*D. rufipennis*) (Nicholls, 2020). The western portion of the study area is wetter and has more snow in winter than the eastern side. Alpine slopes in the eastern portions of the area tend to be windswept and have less snow than alpine slopes in the western portions of the area (Backmeyer, 1991).

Prominent within Quintette are six coal-mine sites situated mostly within high-elevation mountain ridges running southwesterly from Highway 29 toward the Rocky Mountains. Forest harvesting (cutblocks and roads) and oil and gas exploration (seismic lines) are industrial activities contributing predominantly to total disturbance (please refer to Lamb et al. [2022] Figure 2 for disturbance mapping on each subpopulation). Measuring disturbance consistent with Canada's Recovery Strategy (Environment Canada [EC], 2014), in which human-caused disturbance is buffered by 500 m, the Quintette is 79% disturbed and the Klinse-Za is 49% disturbed (Seaton, 2020). In Quintette, there are 22,221 km of linear features (roads and seismic lines) and 21% of the area is permanently disturbed by irreparable changes such as paved roads, electric transmission lines, and gas pipelines (Seaton, 2020). Klinse-Za is comparatively less disturbed, the length of linear features is 5658 km and permanent disturbance accounts for 12% of the area (Seaton, 2020).

Caribou in our study area are classified as the Central Group of Southern Mountain Woodland Caribou, Designatable Unit No. 8, under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2014; Ray et al., 2015). Yet, they are managed under the Southern Mountain caribou recovery strategy and associated recovery documents (EC, 2014). Central Group caribou have a variety of life-history strategies, including partial migration between seasonal allopatric ranges (Jones et al., 2007; McDevitt et al., 2009). Central Group caribou winter in habitats at higher elevations on wind-swept mountain ridges where they feed on terrestrial lichen, and lower elevation coniferous forests where they forage on both terrestrial and arboreal lichen (Ray et al., 2015). Anthropogenic risks are especially high for individuals that adopt the lower elevation wintering strategy in the Central Group (Williams et al., 2021). Currently, most caribou summer at higher subalpine and alpine habitats.

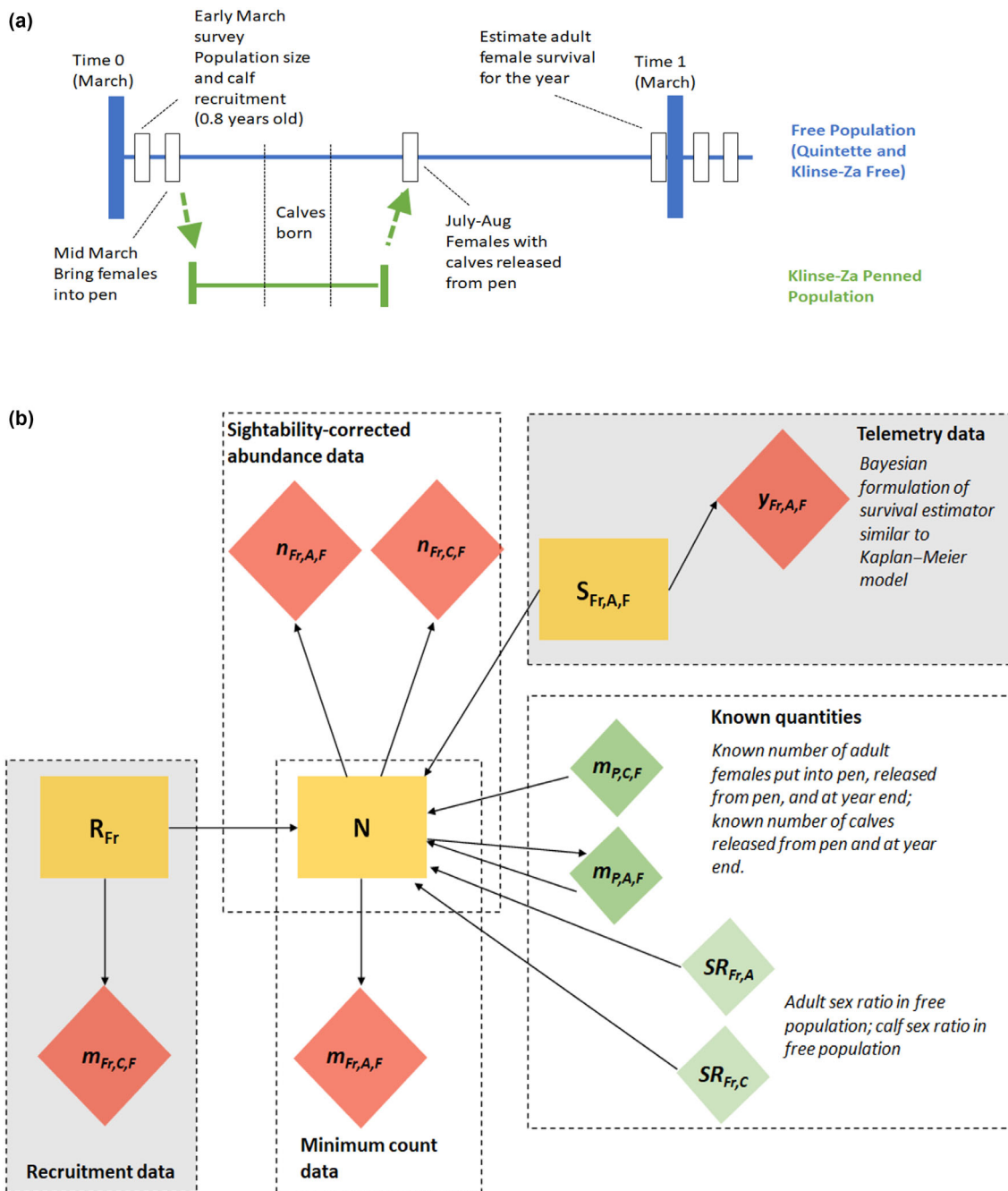


FIGURE 2 (a) Annual timeline for the Klinse-Za, depicting the data collection and cycle of movement between the pen and (b) directed acyclic graph representing data streams used in model fitting for Quintette and Klinse-Za integrated population models (lower). Red diamonds represent data inputs, green diamonds represent known quantities and yellow rectangles represent estimated parameters. A = adult, C = calf, F = female, Fr = free population, N = estimated abundance, P = penned population, SA = subadult. Gray shading indicates data and parameter estimates that are used in the first stage of the two-stage approach. Note that the penned population is only relevant to the Klinse-Za herd. Figure adapted from Moeller et al. (2021)

Large mammals in addition to caribou in the study area include grizzly bears (*U. arctos*), black bears (*U. americanus*), wolves, wolverines (*Gulo gulo*), lynx (*Lynx canadensis*), moose (*Alces americanus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), Stone's sheep (*Ovis dalli stonei*), mountain goats (*Oreamnos americanus*), and occasionally cougars (*Felis concolor*) (Johnson et al., 2015).

Study design and approach

We used a Before–After study design to assess the effectiveness of recovery actions to avert the extirpation of the Klinse-Za and Quintette caribou. We contrasted population size, growth rate, and vital rates for each subpopulation before and after implementation of recovery actions

to assess effectiveness. The Quintette received wolf reductions only between 2015 and 2020, while the Klinse-Za received wolf reductions from 2013 to 2020 and maternity penning from 2014 to 2020. We expected that the demographic signal of the actions would accrue 1 year after the actions, therefore the “After” period when recovery actions were implemented extended, and over which we summarized demographic data, occurred from 2014 to 2021 in the Klinse-Za, and 2016–2021 in the Quintette. The “Before” period extended from 1995 to 2013 in the Klinse-Za, and 2002–2015 in the Quintette. Beyond assessing recovery action effectiveness, we also sought to contrast the influence of wolf reduction alone with the combination of wolf reduction and maternity penning and to partition action-specific effectiveness when applied concurrently.

Recovery actions

Maternity penning

In collaboration with the Nations, we developed and implemented maternity penning facilities in the Klinse-Za subpopulation to enhance subpopulation recovery subpopulation through improvements to survival of adult and calf caribou. The maternity pen was initiated and supported by the Nîkanêse Wah tzee Stewardship Society (NWSS)—Nîkanêse is “future” in Cree and Wah tzee is “caribou” in Dunne-Za—a collaborative non-profit initiative between West Moberly First Nations (Dunne-Za) and Sauteau First Nations (Cree) and technical advisers supporting caribou recovery. We designed the maternity penning facilities in consultation with those who conducted previous maternity penning efforts (Little Smoky in AB, Smith & Pittaway, 2011; Revelstoke in BC, Serrouya et al., 2020; and Chisana in Yukon, Adams et al., 2019). One difference in the Klinse-Za pen was that we placed it at high elevations matching caribou summer life-history strategies consistent with a summer release from the pen. We moved the original pen (Bickford, Figure 1, 2014–2017) to a new site (Rochfort, Figure 1) in 2018 because of declining abundance of natural forage and to proactively reduce the probability of disease transmission (e.g., parasites). Both pen sites were >1200 m above sea level (asl), near treeline with average annual snow accumulations of ~1.5 to 2.5 m and with vegetation cover dominated by Engelmann spruce, sub-alpine fir, and wetland meadows with scattered black spruce. These sites offered trees for use as *in situ* fence posts, abundant sources of arboreal lichen (*Bryoria* spp., *Usnea* spp., and *Alectoria* spp.) forage, protection from the elements, access to free-running water in snow-free

months, and frequent winds for partial relief from flies during the calving season. The Bickford pen (2014–2017) encompassed 5.0 ha in 2014 and was enlarged to 7.0 ha for 2015–2017. The Rochfort pen (2018–2020) was 15 ha.

We captured adult females for the pen during March, following animal welfare guidelines (please refer to permits, Appendix S1: Section S1) and under veterinary oversight during capture, transport, and handling. We often selected females without a calf at heel to reduce invasiveness. It is possible that females without calves at heel might be more likely to successfully raise a calf in the pen, if they were in better nutritional status having been unsuccessful in raising a calf to recruitment in the previous year (Denryter et al., 2017) and vice versa for females with calves at heel left to be free ranging. We tested for this effect and found no evidence that the probability of rearing a calf to recruitment age (10 months) differed whether females had reared a calf to recruitment age the previous year (Appendix S1: Section S2). Therefore, we considered our approach to capturing females an unlikely contributor to any reproductive differences between penned and free animals.

When first penned, and prior to release, we fed caribou a diet of terrestrial lichens, *Cladina* spp. and *Cladonia* spp. at a rate of ~0.5 kg/adult caribou/day. We gradually transitioned this diet to an *ad libitum* diet of a commercial pelleted ration (Barboza & Parker, 2006; ~3 kg/adult caribou/day). Caribou also consumed freely available arboreal lichen, terrestrial lichen (*Cladina* spp. and *Cladonia* spp.), and other vegetation such as mushrooms, flowers (*Aster* spp.), willows (*Salix* spp.), shrub birch (*Betula glandulosa*), and bog bilberry (*Vaccinium uliginosum*). Indigenous Guardians lived at the pen during its operation to monitor individual caribou health and welfare and provide pelleted rations during mornings and evenings. Indigenous Guardians conducted daily patrols around the inside and outside perimeter of the pen to ensure fence integrity and assisted in the capture of calves prior to release. While the date of releasing animals from the pen varied among years (5 July 2014, 24 July 2015, 15 July 2016, 27 July 2017, 31 July 2018, 29 July 2019, and 5 August 2020), the process was generally the same. On the release date we opened a section of the pen fence, allowing animals to exit at their own pace. The process of exiting did not happen immediately but rather took a few hours for the animals to wander out.

Predator reduction

Wolf predation has been established as a leading proximate cause of caribou declines (Bergerud & Elliott, 1998;

EC, 2014; Seip, 1992; Serrouya et al., 2019), especially when wolf predation is a leading cause of adult female caribou mortality, although also an important cause (but not a leading cause compared with bears or wolverines) of juvenile mortality (Gustine et al., 2006). Therefore, reducing wolves was expected to increase adult female survival and, secondarily, caribou calf survival (e.g., please refer to Hayes et al., 2003). Wolf population estimates within the study area were provided by two approaches. First, Kuzyk and Hatter (2014) predicted 10–14 wolves/1000 km² based on wolf–prey biomass models for BC. Second, Seip (2014) used repeated observations of collared wolf packs to estimate approximately 5–8 wolves/1000 km² in the Quintette caribou subpopulation. Both estimates were greater than the density thresholds of 3–5 wolves/1000 km² recommended for caribou persistence by previous studies (Bergerud & Elliott, 1998; Hebblewhite et al., 2007) and by the Federal caribou recovery plan (EC, 2014), so the wolf reduction goal was to meet the recommended threshold by achieving reduction efficiencies of at least 50%–80% in annual wolf densities.

Beginning in 2013, wolves were reduced in the Klinse-Za using ground-based methods by First Nations trappers and hunters to rekindle traditional land use practices and in support of the maternity pen and caribou recovery. Wolves were also removed using aerial-based methods in Klinse-Za and Quintette in the broader study area through an aerial-based program initiated by the BC Government in 2015 (Bridger, 2019). The aerial-based removals began by following direction of the Federal recovery strategy (EC, 2014), and were modeled after the AB wolf reduction recovery actions (Hervieux et al., 2014), and are detailed in Bridger (2019) along with estimation of the degree of reduction conducted. BC Government biologists or contractors conducted winter aerial surveys in rotary-wing aircraft to search for radiocollared wolves (also deployed by BC Government) to facilitate full pack removal (please refer to also Hervieux et al., 2014). Please refer to permits and ethics approvals in Appendix S1: Section S1 for the legal and permitting authorities used in the recovery actions by the Nations, provincial government, contractors, and universities. Following Bridger (2019), we also consider a refined wolf reduction period, 2017–2020 where the first year of government-run wolf reduction was removed due to low effort and success

Caribou captures, care, and demographic monitoring

Capture and care

We (or BC Government biologists or contractors; from this point forwards, referred to as “we” for this section)

caught caribou with a net gun fired from a helicopter (either Bell 206B Jet Ranger or A-star 350 B2) mostly during March. Attempts were made to ensure an even spatial distribution of radiocollared animals in the free-ranging portions of the subpopulations and in Klinse-Za between 2014 and 2020, so that all known free-ranging groups of caribou would have at least one radiocollared female after selection of animals to be transported to the pen. After restraining the netted caribou, we applied a blindfold and hobbles. Caribou were collared with either VHF (Lotek, Model LMRT-4; Newmarket, Ontario, Canada) or GPS (Televilt GPS-Simplex; Televilt/TVP Positioning AB, Lindesberg, Sweden; Advanced Telemetry Systems, Iridium model G2110E, Isanti, Minnesota, USA; Vectronic Aerospace, Survey-2D, Iridium tear drop, Berlin, Germany) radiocollars. Pregnancy of adult females in Klinse-Za after 2013 was estimated based on blood parameters sampled at capture (positive pregnancy indicators: progesterone exceeding 1.2 mg/ml [2014–2017], and pregnancy-specific protein B levels exceeding 0.21 mg/ml [2018–2019]) (Russell et al., 1998; Sasser et al., 2009).

Caribou captured for maternity penning were first intranasally administered medetomidine (10–15 mg/caribou) for sedation (Cattet et al., 2004). We then placed caribou in a custom-made restraining bag before loading into a helicopter for transport to the maternity pen, which increased caribou and crew safety while in the helicopter. Transport helicopters landed near (~1 km distance) the pen and unloaded caribou into a sled and snowmobile that we used to tow the animal to the pen. Once in the pen, we processed caribou and obtained weights, blood, and other health samples while fitting collars. We then reversed the sedating effect of the medetomidine with atipamezole hydrochloride (30–50 mg/caribou), removed the hobbles and blindfold, and monitored caribou until mobile.

Demographic monitoring

To assess demographic parameters of Klinse-Za and Quintette caribou, we compiled multiple sources of data consisting of adult female survival, abundance, and recruitment of 10-month-old calves. These data were acquired from the BC Government for Quintette between 2002 and 2021 and for Klinse-Za between 1995 and 2013. We supplemented these data with additional demographic data that we collected in the Klinse-Za during 2014–2021.

Survival of adult females and penned calves was monitored using accelerometer-based mortality sensors. Prior to 2014, VHF and GPS collars were monitored weekly in winter and spring, and bimonthly in summer and fall, to directly detect mortality signals (Jones et al., 2007).

Mortality events from GPS collars after 2014 were received through remote communication (SMS text or email). When a mortality alert was detected, a mortality investigation was conducted usually within 48 h of the mortality event after 2014 but ranging up to 1–2 weeks after mortality in years prior to 2014.

Recruitment and abundance surveys were conducted by helicopter in each subpopulation during March of most years. When conditions and funding allowed, both a recruitment and abundance survey were conducted. However, prior to 2014, often only a recruitment survey was feasible and abundance surveys were done every 2–5 years. Recruitment surveys focused on enumerating cow: calf ratios, or cow: adult ratios.

When able to conduct an abundance survey, systematic flights were conducted on a designated high-elevation winter range (Price, 2018) in Quintette between 2002 and 2021, and in Klinse-Za prior to 2015 (please refer to Seip & Jones, 2008 and Seip, 2014 for survey details and flight lines). Although abundance surveys in Quintette extended beyond the winter range in some years, we focused only on the count from the winter range portion to be consistent with previous survey effort. Sightability was used to correct for animals not seen and was calculated as the number of collared females observed, divided by the number of active collars available to be seen. When no sightability information was available, but a full count was conducted, we used the mean sightability across years for each subpopulation. In Klinse-Za between 2014 and 2021, we enumerated caribou by counting all caribou within groups of radiocollared females (McNay et al., 2020). Although we attempted to maintain at least one collar in each group of caribou in the Klinse-Za, males tend to segregate at that time of year and so, coincident to searching for radiocollared animals, we found isolated groups of males that contributed to the total minimum number of caribou found in the subpopulation area. Minimum counts between 2014 and 2021 in Klinse-Za usually matched with, or were within 1–2 animals of, the number of caribou expected each year (average difference of 0.9 caribou, $n = 6$ surveys, $SD = 0.9$) where expected number was based on independent calculations using previous year population less estimates of current year adult mortality plus current year known recruits and, in 1 year, known additions resulting from an enlarged survey area (McNay et al., 2020).

Population dynamics

Integrated population modeling

To test the effectiveness of recovery actions, we estimated population demographic vital rates, population growth

(λ), and population abundances before and after implementation of recovery actions using an integrated population model (IPM; Besbeas et al., 2002; Brooks et al., 2004; Messmer et al., 2020; Schaub & Kéry, 2012) adapted from a recently developed model for caribou in Jasper National Park that uses a two-stage approach (Moeller et al., 2021). Integrated population models provide a statistical framework to integrate a combination of demographic data types with varying levels of certainty to estimate population growth and demographic parameters (Schaub & Abadi, 2011). The IPM consisted of a biological process model for survival, recruitment, and abundance that incorporated ecological variation, and observation models that related the observed data to the biological process while accounting for variance associated with sample error. In the two-stage approach, point estimates and uncertainty for survival, recruitment, and abundance are estimated in the first stage and used as the data inputs for the biological process models in the second stage within the IPM. Two-stage approaches are often used to improve computation efficiency and reduce model complexity. The results from these models closely reproduce a one-stage analyses (e.g., for meta-analysis; Lunn et al., 2013).

Integrated population models are less sensitive to biases in any one data source, information is shared between data types, variance from the imperfect data sources from the first stage of the analysis are accounted for within population estimates, and missing data can be accommodated within observation models (Royle & Dorazio, 2008). Therefore, an IPM produces more robust demographic estimates than a model using one data source alone. Overall, the IPM framework provides a powerful statistical approach that allows for efficient use of available data to create accurate estimates of population trends and vital rates.

We used the following data sources to simultaneously estimate female survival, recruitment of female 10-month-old calves, and female abundance per life-stage for each year (Figure 2a): (1) population surveys that consisted of either the number of animals seen (a minimum abundance) or sightability-corrected estimates of abundance, the number of calves and adults (the latter being all animals >1.75 years old), and in some, but not all, cases, sex; (2) the sex, age, and number of animals that went into the Klinse-Za maternity pen, as well as recruitment and sex of calves born in the pen; (3) annual survival of adult females estimated within the Eacker et al. (2019) application that employed a Bayesian formulation of a survival estimator similar to the standard Kaplan–Meier estimator; and (4) recruitment rate of 10-month-old female calves (calves/non-calf females), assuming a 50:50 sex ratio of

these calves (following Serrouya et al., 2019; Eacker et al., 2019). When comparing the influence of treatment effects on population dynamics we focused on female-only population growth and vital rates for three main reasons: (1) females are the demographic engine of the population and their population growth is therefore the most important parameter, (2) the survival data were for females only and we also did not bring any adult male animals into the pen, and (3) females are less transient, so immigration and emigration were less likely to be a concern for our annual female abundance estimates than for pooled male and female estimates.

The IPM structure allowed us to incorporate the varying types of population surveys while correctly accounting for sampling variances associated with each survey type. Instead of relying on population surveys or calf recruitment surveys and radiocollar mortality data alone to estimate population growth rates and demographic parameters, the IPM allowed us to use information from all data sources to obtain the most parsimonious estimates. This is most evident in the IPM's ability to incorporate age structure into the population model. Although we detected no bias from the capture protocol used to bring adult females to the pen (please refer to section *Capture and care* and Appendix S1: Section S2), we were able to account for potential effects of age structure on population responses in the IPM. When small populations are growing, the pulse of nonreproductive juveniles may be counted as reproductive adults during recruitment surveys, incorrectly decreasing estimates of reproduction. The IPM approach allowed us to account for the known age of individuals that were captured and brought into maternity pens, which was subsequently changing the ratio of adult females to unproductive juveniles outside the pen.

We adapted the IPM used in Moeller et al. (2021) to evaluate the single- and multiple-recovery action subpopulations (please refer to Appendix S1: Section S3 for equations, and Figure 2 for data timeline and IPM structure). In Klinse-Za, we estimated separate, annual, female-only population parameters, for the animals that experienced wolf removal only, and for the animals that experienced maternity penning and wolf removal. We also estimated pooled (total) population estimates for Quintette and Klinse-Za. We used a three-stage structured model: (1) recruited calves (0.75 years old), (2) subadults (1.75 years old) and, (3) adults (at least 2.75 years old; Figure 2a). The demographic process model for movement through stages was straightforward for the single-recovery action population. However, the process model for the multiple-recovery action population required us to address the removal of

adult females to the maternity pen for a portion of the year (Figure 2a). We achieved this by dividing the population into two units ("Control" and "Penned") and allowing survival and recruitment to vary between the units (as recruitment for the "Penned" unit was known through repeat surveys of collared females and collars on penned calves, it did not need to be estimated). We estimated total population size by applying annual sex ratios to the estimated female-only abundance. Sex ratios as observed on annual flights were generally used, but when no sex ratio data were available we used an average adult sex ratio of 0.64 (adult females : total adults), which was similar to sex ratios observed in nearby subpopulations (0.62–0.8; McNay, unpublished data). For both the single- and multiple-recovery action populations, we applied a random effect of year for the survival and recruitment rates to allow for annual variation in these parameters, such as when wolf reduction and/or maternity penning was applied.

Following Moeller et al. (2021), we used vague priors for survival and recruitment rate estimates using a normal distribution set to the mean of all rate values from the input data sources and a large variance. These priors were truncated between -10 and 10 such that they led to reasonable values for the intercept of the linear predictor on the logit scale. We also used a vague prior for the year one abundance estimate for each stage using a normal distribution with a mean of the first year of adults count data and a large variance. Because subadults and adults were not differentiated during survey counts, we assumed that adults accounted for 90% of the first-year survey count and subadults accounted for 10% of the first-year survey count to calculate mean values to be used in prior distributions. The proportion of subadults and adults assumed for the priors was based on an average calf recruitment of ~10%–20% of non-calf female population (Seip & Jones, 2008), therefore the proportion of calves that would survive to become yearlings in the following March would be slightly lower than calf recruitment. We assessed model sensitivity to this assumption by varying the % subadults between 5% and 20%. Models were fitted in R (ver. 4.0.3) using the "jagsUI" package (ver. 1.5.1). We ran each model for 50,000 iterations with a 5000 iteration adaptive phase. We discarded the first 8000 iterations after adaptation and used a thinning rate of three. We assessed convergence using the Gelman–Rubin diagnostic (r-hat; Gelman & Rubin, 1992), using a threshold of r-hat <1.1 , and we visually inspected posterior distribution traceplots using the "mcmcplots" package. To ensure reproducibility, our R and JAGS code and data have been posted on GitHub (https://github.com/ctlamb/KZ_QT_IPM, Zenodo DOI: 10.5281/zenodo.5772880). We

report 90% credible intervals (90% CrI; Jaynes, 1976) for all estimated parameters.

Partitioned management effects

We used a population simulation approach to disentangle the recovery action effects of wolf removal and maternity penning in the Klinse-Za. We used the estimated annual vital rates from each group and then projected a population forward assuming each population was fully under that recovery action. To do this we projected the 2013 population abundance forward using each of three sets of vital rates (wolf, wolf + pen, and control [pre-2013]), and compared the population growth and resulting population abundances for females.

RESULTS

Recovery actions

Maternity penning

We captured and penned 36 adult females (87 animal-years) at an average rate of 12 animals per year ($SD = 2.93$) representing 46% ($SD = 7\%$) of the non-calf, female portion of the Klinse-Za subpopulation each year from 2014 to 2020. One female was penned six times and two females were penned five times. Two penned females died in the pen, one 10 days after capture in 2016 from unconfirmed cause and another in 2019 from gastrointestinal complications. A third animal died from capture myopathy enroute to the pen in 2020. We included all these mortalities in the survival estimates for the pen. There were 65 calves born in the pen, three of which died in the pen; two were entangled in tree branches a day after birth (2014 and 2020) and another died from an unconfirmed cause 2 days after birth in 2015. There were four stillborn calves (one in 2015, two in 2017, and 1 in 2018) and four apparent aborted pregnancies (two in each of 2015 and 2016). In 2014, wolves found the penned animals 7 km from the pen 4 days after they were released, killing one adult female and three calves, and injuring another female but not fatally. Three females and two calves escaped the predation event to low elevation where one female was later killed by a cougar and a calf was killed on a highway after collision with a vehicle. The remaining female and calf that escaped to low elevation reunited with other penned animals 3 months later. Overall, 84 of 87 adult female captures for the pen resulted in successful penning and eventual release. In total, 62 calves were released from the pen with these females.

Predator reductions

In Klinse-Za, in total, 156 wolves were removed through the First Nations trap/hunt program from 2013 to 2020 (mean = 21/year, $SD = 14$) and 228 additional wolves were removed through the provincial aerial removal program from 2015 to 2020 (mean = 39/year, $SD = 19$). In Quintette, in total 200 wolves were removed through the provincial aerial removal program from 2015 to 2020 (mean = 42/year, $SD = 14$). These levels of wolf removal were thought to correspond with at least 70%–80% removal efficiency, with post wolf removal wolf densities estimated each year in late winter of ~ 2 wolves/1000 km² (Bridger, 2019), below the recommended management threshold (EC, 2014) for caribou persistence. In addition to the wolf reduction programs by the First Nations and BC Government, an additional 29 predators were removed by Indigenous Guardians and pen staff as part of pen security, most of which were black bears ($n = 21$). The other predator removals around the pen included coyote ($n = 2$), lynx ($n = 2$), wolf ($n = 1$), wolverine ($n = 2$), and grizzly bear ($n = 1$).

Caribou captures, care, and demographic monitoring

In total, 162 radiocollared female caribou were captured and monitored for 414 animal-years. Of these, the BC Government monitored 93 females for survival (211 animal-years) and conducted seven abundance counts and annual recruitment surveys in Quintette between 2002 and 2021. Between 1995 and 2013, the BC Government monitored the survival of 32 females (62 animal-years) and conducted seven abundance counts and annual recruitment surveys in Klinse-Za. We monitored an additional 45 females for 141 animal-years, and conducted eight minimum count and recruitment surveys between 2014 and 2021 in Klinse-Za. Further information on the historic demographic data and provincially collected data for these subpopulations can be found in Appendix S1: Section S4.

We sampled pregnancy rates (105 animal-years, female caribou >2 years old) in March in Klinse-Za between 2014 and 2020. Of these, 88% ($SE = 6.5\%$) of animals we brought into the pen were pregnant, while 100% of the free-ranging animals were pregnant.

Population dynamics

Integrated population modeling

Overall the IPM fitted the raw, observed data well, which suggests that this approach re-created what we had

observed but also was effective at informing population estimates when we had incomplete or insufficient data (Appendix S1: Section S5). Recruitment of female calves to 10 months old (female calves/non-calf female) in both areas was low before recovery action (Klinse-Za: 0.15 [90% CrI 0.13–0.17], Quintette: 0.13 [0.12–0.15]), and rates improved after recovery action in the Klinse-Za (0.22 [0.21–0.23]) and Quintette (0.18 [0.16–0.21]) (Table 1). Prior to recovery action, annual adult female survival was low in both population areas, but lower in Klinse-Za (0.78 [0.75–0.81]) compared with Quintette (0.85 [0.82–0.88], Table 1). Female survival rates improved in both areas after recovery action began, by a larger margin over pre-recovery action rates in Klinse-Za (0.89 [0.86–0.91]) compared with Quintette (0.88 [0.83–0.91]) (Table 1). Model results were not sensitive to our starting population assumption of subadults when we varied the percentage between 5% and 20%.

Over the 13-year period (1996–2013) prior to the application of recovery actions, IPM estimates suggested that both subpopulations exhibited an average annual female population growth rate (λ) below 1.0 (Figure 3, Table 1). The average λ for Klinse-Za between 1996 and 2013 was 0.90 (0.89–0.91), or a decline of ~10% per year. Between 2002–2015, average λ for Quintette was 0.93 (0.90–0.96), or a decline of ~7% per year. The total estimated abundance (male and female) for the Klinse-Za fell from a high of 254 animals in 1995 to 38 by 2013. Similarly, the Quintette abundance fell from a high of 163 animals in 2001 to 45 by 2016.

In the eight-year period (2014–2021) during recovery actions, average annual, female population growth in Klinse-Za increased over pre-recovery action levels by 0.18 (0.16–0.20) to 1.08 (1.06–1.10), allowing the population to grow at 8% per year. Similarly, female population growth during the 6-year recovery action period (2016–2021) in Quintette increased by 0.12 (0.03–0.20) over pre-recovery action levels, and grew at 1.05 (0.98–1.11), or an increase in abundance of 5% per year. The total estimated abundance of the Klinse-Za subpopulation grew from a low of 38 animals in 2013 to 98 animals by 2021. Similarly, the total estimated abundance of the Quintette subpopulation increased from a low of 45 animals in 2016 and totaled 78 animals in 2021.

Partitioned management effects

Annual female survival and recruitment rates of caribou that benefited from penning and wolf reductions led to a larger λ estimate compared with that of the free-ranging (wolf reduction only) portion of the Klinse-Za subpopulation (1.09 vs. 1.01, respectively; Table 1), but both were an improvement over the pre-recovery action growth rate of 0.90.

We estimated the realized effects of wolf reduction and maternity penning by parsing out the individual effects (Figures 4 and 5). The realized effect of wolf reduction (Figure 4) in Klinse-Za was estimated as an increase in female population growth of 0.12 (0.06–0.17),

TABLE 1 Annual population vital rates (female only) for groups (penned, free ranging, and pooled) of radiocollared caribou from two population areas (Klinse-Za and Quintette) observed pre- and post-management in Central British Columbia (90% credible intervals in parentheses)

Parameters female only	Klinse-Za				Quintette	
	Pre-management		Post-management		Pre-management	Post-management
	Pooled (1996–2013)	Penned (2015–2021)	Free ranging (2014–2021)	Pooled (2014–2021)	Pooled (2002–2015)	Pooled (2016–2021)
Recruitment 10-months (r , calves/non-calf adult)	0.15 (0.13–0.17)	0.28 (0.28–0.28)	0.16 (0.14–0.19)	0.22 (0.21–0.23)	0.13 (0.12–0.15)	0.18 (0.16–0.21)
Recruitment 10-months (r_3 , calves/adult >2 years)	0.19 (0.15–0.24)	0.30 (0.30–0.30)	0.21 (0.17–0.26)	0.25 (0.23–0.28)	0.15 (0.12–0.20)	0.28 (0.22–0.36)
Adult survival (S_a)	0.78 (0.75–0.81)	0.90 (0.90–0.90)	0.88 (0.83–0.92)	0.89 (0.86–0.91)	0.85 (0.82–0.88)	0.88 (0.83–0.91)
Population growth (λ)	0.90 (0.89–0.91)	1.09 (1.08–1.09)	1.02 (0.96–1.07)	1.08 (1.06–1.10)	0.93 (0.90–0.96)	1.05 (0.98–1.11)
Delta growth ($\Delta\lambda$)	...	0.06 (0.02–0.11) ^a	0.12 (0.06–0.17)	0.18 (0.16–0.20)	...	0.12 (0.03–0.20)

^aThe pen-only effect size, removing the wolf reduction effect.

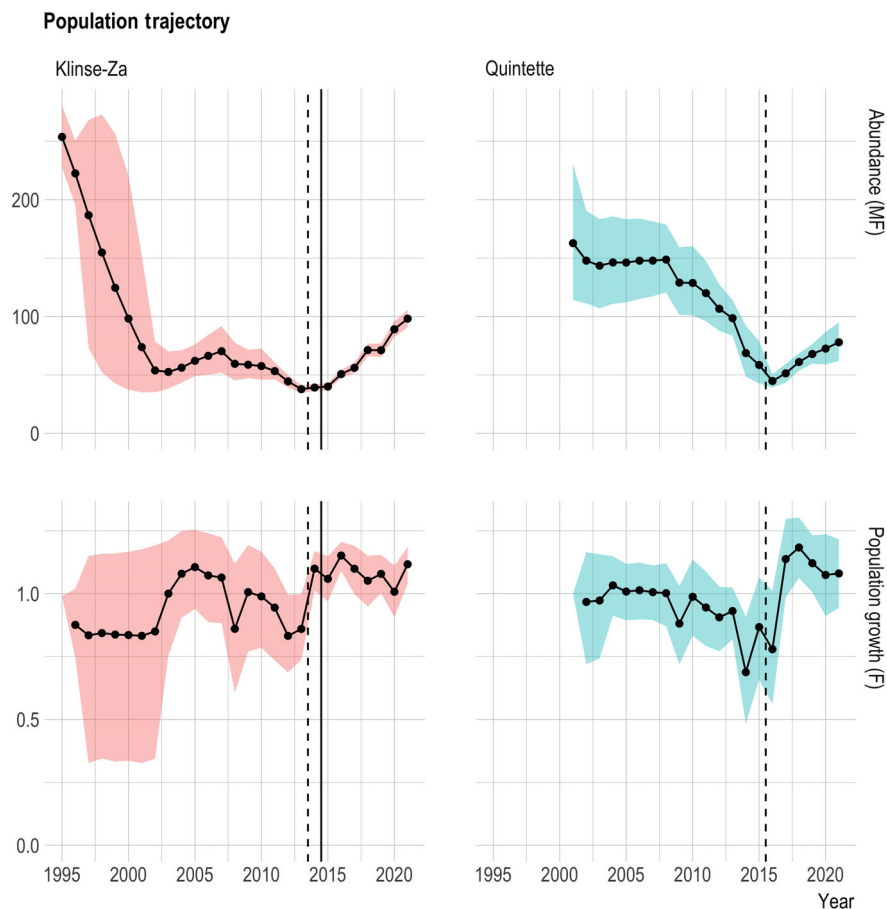


FIGURE 3 Abundance (male and female) and annual female population growth rate (λ) for caribou observed pre- and post-implementation of wolf reduction (dashed vertical lines) and maternity penning (solid vertical line) within the Klinse-Za (left) and Quintette (right) population areas in Central British Columbia. Error bands represent 90% credible intervals

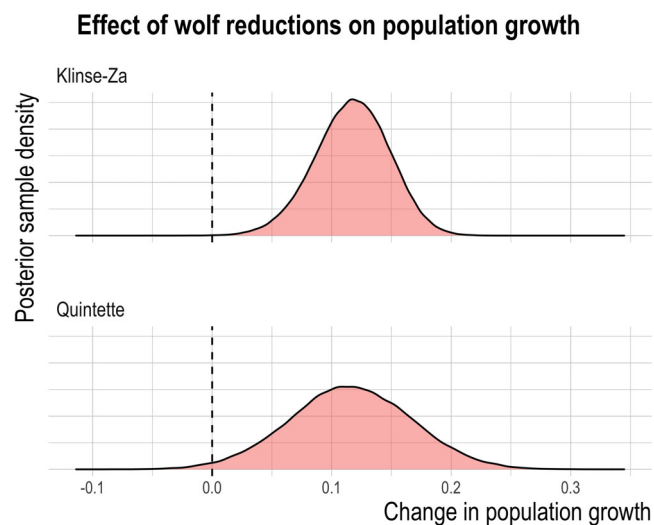


FIGURE 4 The estimated effect of wolf reduction on female caribou population growth ($-\lambda$) in Central British Columbia. Posterior distributions centered on the dashed line indicate no effect of the recovery actions on λ . Distributions to the right of the dashed line indicate a positive effect of wolf reduction on female caribou population growth

while maternity penning added a further 0.06 (0.02–0.11) increase (Figure 5a). Together, these actions generated the change in female population growth from 0.90 to 1.08. Wolf reduction also appeared to have a positive effect on female caribou population growth in Quintette. Population growth increased by 0.12 (0.03–0.20), in Quintette, compared with baseline. The efficacy of wolf reductions varied year to year, and the most effective wolf reduction years were believed to be 2016–2020 (Bridger, 2019). We re-estimated the effect of wolf reduction on female caribou population growth using only these refined years. In Quintette, the effect increased from 0.12 to 0.18 (0.12–0.24) during the refined period, while in Klinse-Za the effect remained similar at 0.10 (0.02–0.16). Similarly, excluding the first year of penning in the Klinse-Za, when some females and calves died soon after release due to high levels of wolf predation, the 2015–2020 penned animals had a higher growth rate ($\lambda = 1.11$) than 2014–2020 penned animals ($\lambda = 1.09$).

Had all Klinse-Za animals only received wolf reduction as a recovery action, we predict that the female

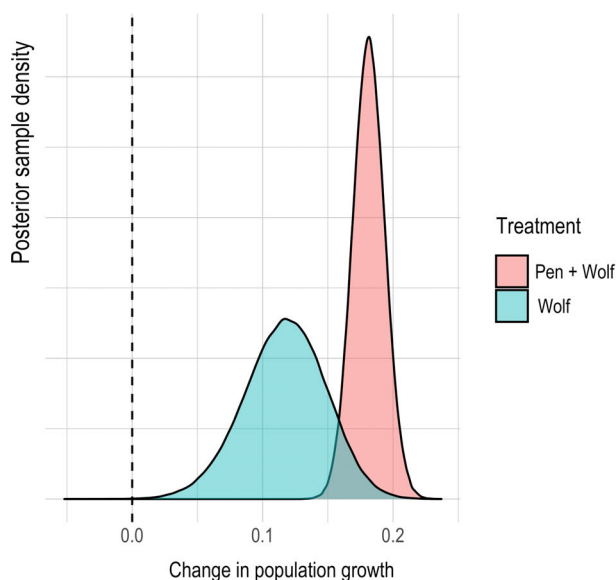
population would have been stable to slightly increasing, at a rate of $\sim 2\%$ per year ($\lambda = 1.02$, Figure 5b). We annually penned $\sim 46\%$ of females but, had we penned them all, while simultaneously reducing wolf abundance, the female population could have grown at 9% per year ($\lambda = 1.09\text{--}1.11$). If we only used the maternity pen, but not wolf reductions, the female population would probably not have increased and rather declined at 4% per year ($\lambda = 0.96$); which is an improvement over the baseline λ of 0.9 , but insufficient to halt the decline.

The success of the Klinse-Za maternity penning sent a pulse of young animals into the population and consequently skewed age ratios. For example, prior to management actions the average female age ratios in the Klinse-Za were 76% adult (>2 years old), 10% subadult (2 years old), and 13% juvenile (1 year old) (Appendix S1: Section S5). Following management, the overall population was composed of 72% adults, 12% subadults, and 15% juveniles. This altered age structure was created through two processes: (1) increased calf production due to maternity penning and wolf reductions, and (2) a non-random sample of adult animals brought in the pen (only 3% of which were subadults). Together, these processes created an age structure in the free-ranging population post-management of 67% adults, 20% subadults, and 13% juveniles. Although there were many benefits to our IPM approach, being able to appropriately account for these differences in an age-structured IPM model was an important aspect of our approach.

DISCUSSION

Southern mountain caribou are declining across their range and immediate action is required to avert the looming extirpation of many subpopulations (EC, 2014; Environment and Climate Change Canada [ECCC], 2018; Serrouya et al., 2019). Indeed, 12 subpopulations of Southern Mountain caribou have been functionally extirpated to less than 10 remaining animals during the 21st century (ECCC, 2018; Sittler & McNay, 2017; Wittmer, McLellan, et al., 2005b) and extant subpopulations without short-term recovery actions are declining an average rate of 14% per year (range -35% to -3%) (Serrouya et al., 2019). During the period of recovery actions we consider here, the adjacent Graham subpopulation did not receive significant recovery actions and declined by 33% from 347 animals in 2015 to 230 in 2021 (British Columbia, unpublished data). Here, we provide evidence of a collaborative effort that was successful in averting the near extirpation of the Klinse-Za and Quintette Southern Mountain caribou subpopulations. Through immediate, and effective actions, First Nations, Provincial Governments, and scientists were successful in nearly doubling these subpopulations from a combined low of 83 animals on winter range in 2013–2015 to over 176 in 2021. Without action, these caribou would have been functionally extirpated within 15 years or less, exacerbating the loss of caribou and First Nations' cultural connections to them (Muir & Booth, 2012).

(a) Klinse-Za treatment effects



(b) Simulated female abundance

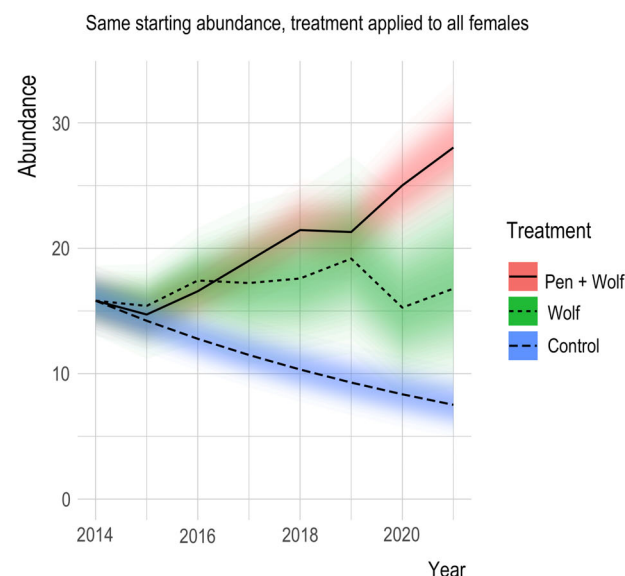


FIGURE 5 (a) The estimated effect, compared with pre-recovery action, of wolf reduction and the combined effect of maternity penning and wolf reduction on Klinse-Za caribou population growth. (b) Simulated abundance of female caribou under three scenarios, (1) control: do not apply any recovery actions to increase abundance, caribou retain mean vital rates from 1995–2012 period, (2) wolf reduction only, (3) wolf reduction and maternity penning

We leveraged the statistical rigor and flexibility of an IPM to elucidate the demographic responses of declining caribou subpopulations to short-term recovery actions: wolf reductions and maternity penning. While the vital rate or abundance estimates provide support for the effectiveness of these actions on their own, combining these multiple lines of evidence into a single analysis provided an integrated and robust assessment of caribou responses to recovery actions. Our results provide strong statistical support for the positive influence of wolf reductions and maternity penning on Quintette and Klinse-Za caribou. Consistent with our predictions, the calf survival, calf recruitment, and adult female survival generally increased in the following situations: (1) in both subpopulations following recovery actions, (2) in the Klinse-Za penned group (wolf + pen) versus the Klinse-Za free-ranging group (wolf), and (3) in the Klinse-Za as a whole (wolf + pen) compared with the Quintette (wolf). These results are consistent with Serrouya et al. (2019), who highlighted the additive benefit of applying more than one management action simultaneously to increase caribou populations. Here we provide further statistical support for the additive benefits of multiple actions, whereby maternity penning and wolf reductions increased Klinse-Za λ by 0.18, changing the 10% per year decline to an 8% per year increase. On their own, wolf reductions carried out by First Nations and Provincial governments increased λ in the Quintette and Klinse-Za by 0.12. Wolf reduction on its own would not have substantially increased the Klinse-Za caribou due to the steep decline observed before recovery actions ($\lambda = 0.90$), whereas wolf reductions served to stabilize and begin recovery in the Quintette subpopulation largely due to the lesser initial declines ($\lambda = 0.93$). These results suggest that the number and intensity of recovery actions need to match the severity of the pre-management decline to ensure actions can reverse declines and begin recovery.

The Klinse-Za and Quintette population trajectories provide new insights into the science of caribou recovery. Not all predator reductions or maternity pens have historically worked as expected. Predator reductions are not a panacea for effective prey recovery, due to context-dependent effectiveness (Clark & Hebblewhite, 2020; Serrouya et al., 2019) as well as ethical and social concerns surrounding heavy-handed interventions directed at proximate causes of decline (i.e., not directed at protecting and recovering habitat, Brook et al., 2015; Muir & Booth, 2012). Nevertheless, predator reductions appear to have stabilized or increased multiple caribou subpopulations on the brink of extirpation (Hervieux et al., 2015; Serrouya et al., 2019), but the statistical rigor of such inferences have been called into question (Harding et al., 2020). For the two subpopulations and

time periods we studied here, we believe that our results provide compelling evidence that wolf reductions carried out by First Nations and Provincial governments benefited these nearly extirpated caribou subpopulations, increasing λ by ~12%. To exemplify the significance of a 12% increase in λ , a hypothetical population of 50 animals declining at a similar rate of 8% per—as observed here before intervention—would be functionally extirpated within 20 years. However, a 12% increase in this λ would not only stabilize this population, but it would also increase by 4% per year to 101 animals within 20 years (i.e., increase by 110%).

Maternity pens have been used at least four times in North America with the goal of recovering declining populations of caribou. The pens have been deployed in the eastern slopes of the Wrangell and St. Elias Mountains in the Yukon (2003–2008, Adams et al., 2019), the Selkirk Mountains of BC (2014–2017), the Rocky Mountains of AB (2006, Smith & Pittaway, 2011), and the Rocky Mountains of BC (2014–2020, this study). The effectiveness of each pen varied and generally the effects on the population were not as distinctly positive as in our case. The reasons for subdued pen effectiveness elsewhere were not consistent. Adams et al. (2019) penned 146 female caribou over 4 years in the Chisana caribou subpopulation, which added 54 yearling recruits to the population. The Chisana maternity pen tripled neonatal calf survival compared with free-ranging rates (0.950 and 0.376, respectively). However, due to the Chisana population being twice as large as expected (~720 animals instead of ~300), the pen-only produced modest increases of 1%–2% growth to an already-stable and large population that diluted the effect of the 54 yearlings added. At the Revelstoke maternity pen (Serrouya, Bollefer, et al., 2021), 70 female caribou from the Columbia North subpopulation were penned, which added 29 yearling recruits to the population by nearly doubling calf survival. The Revelstoke pen did not have large population-level benefits, however, due to multiple in-pen mortalities of adult females that counteracted the positive effects of elevated calf recruitment. Finally, female caribou were penned in the Little Smoky subpopulation for a single year (Smith & Pittaway, 2011) and the efficacy of penning was difficult to measure due to a small sample size and concurrent predator reductions confounding the study design that was used. The varied responses suggest that maternity penning can be effective, as demonstrated here, but the proportion of the population penned and female survival in the pen can influence the magnitude of population benefits.

The Klinse-Za pen effectively generated large population-level benefits partly due to improvements in

the penning approach that were based on lessons learned elsewhere. We brought 36 female caribou into the high-elevation Klinse-Za pen that spanned 87 animal-years. We released 62 calves that resulted in the addition of 48 yearling recruits to the population between 2015 and 2021; approximately double the number that would have been recruited without maternity penning. During this period the estimated population increased from 38 to 98 animals, aided by the nearly doubling of calf recruitment compared with baseline vital rates, and slightly elevated adult female survival in the pen. Our approach to penning appears to have yielded the clearest population-level benefits of penning to date due to a combination of application to a nearly extirpated population, penning location, concurrent predator reductions, and a well designed monitoring and analytical approach. Even if all maternity pens had identical benefits to their occupants, the proportion of animals penned is bound to dictate the overall influence penning has on the population. Previous penning efforts brought 5%–20% of the female population into the pen a year, largely due to their starting populations being 150–720 animals. In our case, we annually penned ~46% of the female population, which in concert with a doubling of calf recruitment generated over one-third of the increased abundance observed in the Klinse-Za during recovery actions. Our pens were located at high elevation in natural and historically used calving range (>1200 m), which is different from the other mountainous pens, such as the Revelstoke pen that was located at ~600 m. The importance of pen location is highlighted by the concerns from the Revelstoke pen in which low elevation penning contributed to poor female survival due to elevated ambient temperatures as well as poor survival post release while animals moved from low elevation penning habitat to preferred high-elevation summer range. Predator reductions by First Nations and Provincial governments also bolstered the positive effects of penning and facilitated positive growth rates. The evidence we provide here suggests that future penning efforts will be most effective when paired with predator reductions. We also worked with, and learned from, Indigenous Guardians from the West Moberly First Nations and Sauteau First Nations who resided on site full time and were an important part of the pens' success. The Indigenous Guardians fed these caribou and monitored their health while ensuring the pen was physically secure and predators were not nearby. Finally, we were fortunate to learn about monitoring approaches from previous studies, and the recent development of IPM's, which together allowed us to decompose the individual effects of maternity penning and wolf reduction, use all the available count and vital rate data efficiently, and account for changing age and sex ratios appropriately.

Age structures can greatly influence the trajectory and the fate of endangered species. In 2014 when we started penning in the Klinse-Za, we noticed that all 10 females captured were of older age classes based on our subjective assessment of tooth wear. Low recruitment of calves in the years before management began contributed to the declining population abundance, and therefore the age structure would have tended toward older animals as fewer new calves were added to the population. Older age structure may partially explain why some caribou populations have become rapidly extirpated—at a rate that outpaces the decline in years previous—when the population size becomes low (Clutton-Brock & Coulson, 2002; Komers & Curman, 2000). Following our interventions, the Klinse-Za age structure began to shift toward younger animals as recruitment increased. Our approach of using an age-structured IPM was critical to generate accurate population trends with these shifting age distributions. Without the IPM, our estimates from the commonly used Hatter-Bergerud recruitment-mortality estimator (HB Hatter & Bergerud, 1991, as estimated in the Eacker application, Eacker et al., 2019), which is sensitive to age structures and sex ratios, produced λ values that diverged from IPM estimates. The HB estimates were overly optimistic for penning (HB = 1.18 vs. IPM = 1.09), pessimistic for wolf reductions (HB = 0.90 vs. IPM = 1.01), and overall underestimated the average annual λ in the Klinse-Za post-recovery action (HB = 1.02 vs. IPM = 1.08). Furthermore, the IPM provided additional insight, and a more accurate assessment of *in situ* population growth for the Klinse-Za compared with previous assessments using male and female abundance combined. Serrouya et al. (2019) reported $\lambda = 1.14$ for the Klinse-Za, while we reported $\lambda = 1.08$ here for the same period using female vital rates and abundances. Although our male and female combined growth rate ($\lambda = 1.13$) corroborated the findings of Serrouya et al. (2019), we believe that our focus on female growth rates provides a more accurate assessment of *in situ* population growth, given that females are the demographic engines of the population, and they disperse shorter distances than males, reducing the influence of immigration and emigration on their demographics. We suspect that the differences between the total and female-only growth rates stems from the relatively poor survival of the older-aged females remaining during the recovery action period and the fact they were replaced by an equal sex ratio of juveniles, and potentially some increases in males due to immigration. Looking forward in the Klinse-Za, the pulse of young animals into the population may create some demographic momentum that has yet to be realized in the numbers presented here. This demographic momentum may come about as these recently

recruited females age to prime-reproductive age (3–14 years old; Adams & Dale, 1998) and could produce greater population growth in the future than we have report here.

The increased intensity of wolf reductions between 2016 and 2020 appeared to benefit the caribou in the Quintette more than those in the Klinse-Za. We observed improved demographics in the Quintette caribou during the period of refined wolf reduction ($\lambda = 1.12$) compared with the entire wolf reduction period ($\lambda = 1.05$). In comparison in the Klinse-Za we observed $\lambda = 1.07$ during refined wolf reduction compared with the entire wolf reduction period ($\lambda = 1.08$). The source of this difference is likely to be due to the elevated density of other predators in the Klinse-Za compared with the Quintette (Lamb, 2019), and we also observed splintered and remaining wolf packs in the Klinse-Za still having a sizable impact on the population (generally <10 animals remaining per year (Michael Bridger, personal communication August 9, 2021). The additional wolf removal in Klinse-Za by First Nations may have also buffered any impacts during years of less effective areal reductions. Finally, this difference is likely to be also influenced by the persisting influence of those older female animals we started with in the Klinse-Za, and the not yet prime-aged young animals that are slowly becoming prime aged now. Taken together, this highlights the logistic and ecological complexity in recovering caribou.

The recovery actions, and resulting increases in caribou populations, took place on a heavily industrialized landscape, the ultimate reason the caribou declined to the point of needing these recovery actions. The disturbance threshold for self-sustaining subpopulations derived for neighboring boreal caribou suggests that no more than 35% of the area can be disturbed (EC, 2014; Johnson et al., 2020). No comparable threshold has been calculated for mountain caribou. But the disturbance in both subpopulations studied here exceed the boreal threshold with 49% disturbance in the Klinse-Za and 79% in the Quintette. To date there has been no instances of positive and persisting caribou demographic responses to management actions on such a disturbed landscape as seen here. The norm has been little to no effective and coordinated intervention and eventual subpopulation extirpation. At its heart, this effort owes its success to the courage and decisive actions of West Moberly First Nations and Sauteau First Nations who were committed to averting further extirpation of caribou in this region after the Burnt Pine subpopulation (neighboring the Klinse-Za) was extirpated in 2013 (Lamb et al., 2022). In addition to these short-terms efforts to avert extirpation, West Moberly First Nations, Sauteau First Nations, the Government of BC, and Government of Canada signed a

landmark Partnership Agreement to protect ~8000 km² of the Central Group caribou habitat (Intergovernmental Partners, 2020). The agreement adds modest habitat protection in the Quintette (20%, up from 3%) and substantial protection in the Klinse-Za (64% up from 7%). To date, there have been no examples of disturbed landscapes being sufficiently restored to create self-sustaining caribou populations. We view the Central Group caribou and the Partnership Agreement as the leading National example to create a successful case study of caribou recovery through the short-term recovery measures and forthcoming restoration in the newly protected caribou habitat (Lamb et al., 2022).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and code (Lamb, 2021) are available on Zenodo at <https://doi.org/10.5281/zenodo.5772880>.

ORCID

Clayton T. Lamb  <https://orcid.org/0000-0002-1961-0509>

Hans Martin  <https://orcid.org/0000-0003-2523-2548>

Mark Hebblewhite  <https://orcid.org/0000-0001-5382-1361>

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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