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Effectiveness of population-based recovery actions for threatened southern mountain caribou

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Abstract

Habitat loss is affecting many species, including the southern mountain caribou (*Rangifer tarandus caribou*) population in western North America. Over the last

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half century, this threatened caribou population's range and abundance have dramatically contracted. An integrated population model was used to analyze 51 years (1973–2023) of demographic data from 40 southern mountain caribou subpopulations to assess the effectiveness of population-based recovery actions at increasing population growth. Reducing potential limiting factors on threatened caribou populations offered a rare opportunity to identify the causes of decline and assess methods of recovery. Southern mountain caribou abundance declined by 51% between 1991 and 2023, and 37% of subpopulations were functionally extirpated. Wolf reduction was the only recovery action that consistently increased population growth when applied in isolation, and combinations of wolf reductions with maternal penning or supplemental feeding provided rapid growth but were applied to only four subpopulations. As of 2023, recovery actions have increased the abundance of southern mountain caribou by 52%, compared to a simulation with no interventions. When predation pressure was reduced, rapid population growth was observed, even under contemporary climate change and high levels of habitat loss. Unless predation is reduced, caribou subpopulations will continue to be extirpated well before habitat conservation and restoration can become effective.

KEYWORDS

adaptive management, bottom-up, endangered species, population dynamics, small populations, top-down

INTRODUCTION

During the last century, wildlife populations have declined by over 50% across the globe (Murali et al., 2022). Although climate change represents a current and accelerating threat to many wildlife populations, habitat loss from human activities continues to be the primary cause of population decline for most threatened and endangered species (Caro et al., 2022; Williams et al., 2022). As a result, most conservation strategies place an emphasis on protecting and restoring habitat (Geldmann et al., 2019; Maxwell et al., 2020). The contemporary shift to habitat restoration is highlighted by the United Nations (UN) Decade on Ecosystem Restoration (2021–2030), which is focused on preventing, halting, and reversing the degradation of ecosystems. However, habitat restoration alone may not be enough to support species residing in highly impacted areas because rapid population decline may result in extirpations before sufficient habitat for self-sustaining populations can be restored and protected (Schrott et al., 2005).

For species requiring expansive areas of undisturbed habitat or for habitats requiring complex successional processes to regenerate, it can take many decades to restore enough habitat for populations to recover (Schrott et al., 2005). In this situation, it will likely be

necessary to use population-based management actions like translocation, supplemental feeding, or predator reductions to support the species until sufficient habitat is restored (Batson et al., 2015; Oro et al., 2008; Reynolds & Tapper, 1996; Shea, 1998). However, like habitat restoration, implementing population-based actions can be difficult when they are expensive, complex, or controversial (Dubois et al., 2017; Johnson et al., 2019). Understanding the efficacy of population management actions is therefore critical to developing conservation strategies that recover populations and foster support among stakeholders, rightsholders, and the general public.

The recovery of woodland caribou (*Rangifer tarandus caribou*) and their habitat is one of the greatest conservation challenges in North America (Hebblewhite, 2017). Human-caused habitat loss—defined here as the human-caused degradation of caribou habitat that eliminates resources required for caribou persistence, such as predator refugia, food, and shelter from elements—has contributed to declines of woodland caribou across much of their distribution. As a result, two populations (boreal and southern mountain) have been listed as Threatened in Canada (Environment and Climate Change Canada, 2020; Environment Canada, 2014) and two as Endangered; one in the contiguous United

States (Fish and Wildlife Service, 2019) and one in Atlantic Canada (Environment and Climate Change Canada, 2022a). Human-caused habitat loss, hereafter “habitat loss,” can impact caribou in several ways, though the primary process is thought to be through disturbance-mediated apparent competition (Fortin et al., 2017; Frenette et al., 2020; Holt, 1977; Serrouya, Dickie, et al., 2021; St-Laurent et al., 2022). In this process, anthropogenic and natural alteration of the landscape increases the extent of early seral conditions that support increased densities of moose (*Alces alces americana*) and deer (*Odocoileus* spp.), which in turn support increased populations of their generalist predators, primarily wolves (*Canis lupus*) and cougars (*Puma concolor*). These generalist predators incidentally prey on caribou at unsustainable rates (Bergerud et al., 2007; Ehlers et al., 2016; Hebblewhite et al., 2007; Wittmer, Sinclair, & McLellan, 2005). Linear features such as roads and pipelines further contribute to increasing predation of caribou by altering predator movement and spatial behaviors, resulting in increased caribou–predator encounters (Barker et al., 2023; DeMars & Boutin, 2018; Dickie et al., 2022; Dickie, Serrouya, McNay, & Boutin, 2017). Federal recovery strategies for woodland caribou have identified habitat restoration and protection as key management actions for recovering self-sustaining populations (Environment and Climate Change Canada, 2020; Environment Canada, 2014). Habitat restoration that reduces the overall amount of early seral habitats should reduce the numeric response of moose and deer, and thus reduce the abundance of their predators (Fryxell et al., 2020; Serrouya et al., 2017; Serrouya, Dickie, et al., 2021). Linear feature restoration involves combinations of road removal and re-vegetation which is expected to interrupt the behavioral functional response of predators and reduce predator-caribou encounters (Dickie et al., 2021, 2022; Dickie, Serrouya, DeMars, et al., 2017; Serrouya et al., 2020). However, restoring caribou ranges with extensive habitat loss back to mature forest conditions will take decades, notwithstanding the logistical challenges, costs, threats of wildfire, and socioeconomic considerations associated with restoring the large spatial extents typical of caribou ranges. Consequently, few caribou ranges have seen a net gain in suitable habitat since the release of the federal recovery strategies (Environment Canada, 2012, 2014; Nagy-Reis et al., 2021), and caribou populations have generally continued to decline (Johnson et al., 2020).

Among the populations of woodland caribou, southern mountain caribou are the most imperiled (Environment and Climate Change Canada, 2018; Johnson et al., 2015). Over the last two decades, multiple southern mountain caribou subpopulations have been extirpated, and most

that remain are small (<100 individuals) and have been rapidly declining for years (Johnson et al., 2015; Moskowicz, 2019; Serrouya et al., 2019). In response to the dire state of southern mountain caribou and the inherent time lags in restoring habitat loss, five population-based management actions (hereafter “recovery actions”) have been implemented to stabilize and recover the population (Hervieux et al., 2014; Serrouya et al., 2019). Recovery actions include (1) maternal penning, which involves placing pregnant female caribou in fenced areas that exclude predators during the birthing and neonatal periods (Adams et al., 2019; McNay et al., 2022); (2) translocation to directly increase abundance (Compton et al., 1995; Leech et al., 2017); (3) supplemental feeding to reduce potential nutritional deficiencies (Heard & Zimmerman, 2021); (4) reduction of predator densities (Hervieux et al., 2014); and (5) reduction of apparent competitor density (e.g., moose [Serrouya et al., 2017]). Under the guiding principles of adaptive management (Walters & Holling, 1990), an evaluation of recovery actions provides an opportunity to adjust future efforts to recover southern mountain caribou.

Although the causes of caribou decline have been established, at least two major challenges impede caribou recovery. First, during the last half century most southern mountain caribou subpopulations have consistently declined, with many subpopulations now functionally extirpated (<10 adult females or total population <20) (Johnson et al., 2015; Moskowicz, 2019). Second, current knowledge indicates habitat-based solutions that facilitate low predator density are required to ultimately regain self-sustaining status for southern mountain caribou subpopulations, but the recovery of these habitats is expected to take decades. Given the slow rate of caribou habitat recovery and the rate of caribou population declines without intervention, recovery actions are needed in the interim to avoid ongoing extirpations.

Serrouya et al. (2019) synthesized the results of several recovery actions applied to southern mountain caribou. They concluded that wolf reductions and combinations of multiple measures, such as wolf reductions and maternal penning, were effective at increasing caribou population growth. Since then, a greater amount of caribou data, advanced analytical techniques, and information from additional recovery actions have become available. In addition, critiques of Serrouya et al. (2019) suggested that there was no evidence effectiveness of any of the recovery actions and that statistical anomalies and environmental gradients confounded or nullified results (Harding et al., 2020; Wilson et al., 2021).

In response to these critiques and to elevate the role of evidence in caribou recovery, we collated available data on southern mountain caribou demography to assess

trends in abundance across over 51 years (1973–2023) and measure population trajectories with and without recovery actions. We leveraged the statistical rigour of an integrated population model (IPM) to make efficient use of multiple data sources, account for uncertainty, and increase knowledge regarding the effectiveness of recovery actions. Our focus was on recovery actions directly affecting the mechanistic pathways of disturbance-mediated apparent competition. Such measures included decreasing predation directly by reducing wolf numbers, indirectly via moose reductions, or by using maternal penning to reduce predation on neonates. We also examined supplemental feeding, a recovery action hypothesized to alleviate risk-sensitive foraging and increase adult female survival (Heard & Zimmerman, 2021). All recovery actions were implemented with the recognition that habitat-based solutions are required for populations to ultimately achieve self-sustaining status. Because current efforts to protect and restore habitat have not yet reached scales expected to impact caribou demography (Nagy-Reis et al., 2021), we could not assess the efficacy of these longer-term recovery actions, but such an assessment will be necessary in the future to evaluate additional hypotheses of population decline and inform effective conservation strategies.

MATERIALS AND METHODS

Study area and caribou ecology

The study occurred across the range of southern mountain caribou in western Canada and the USA (Figure 1). Southern mountain caribou occupy mountainous areas and adjacent lower-elevation forests in British Columbia (BC) and Alberta, Canada, and were extirpated in Idaho and Washington, USA in 2018 (Serrouya et al., 2019). Southern mountain caribou are divided into southern, central, and northern groups (Environment Canada, 2014, Appendix S1: Section S1). Anthropogenic impacts vary across the extent of southern mountain caribou range (5%–86% disturbed, as defined by [Environment Canada, 2014]), but are primarily from forest harvesting, resource roads and other linear developments, hydroelectric reservoirs, oil and gas developments, and mining (Figure 2).

Data

We assembled available caribou data from government agencies, such as abundance and recruitment surveys, survival outcomes for radio-collared adult caribou, and recovery actions applied across the southern mountain

caribou range. For subpopulations located in BC, we obtained data from the Knowledge Management Branch of BC Environment and Climate Change Strategy, independent scientists, and regional government biologists. For populations located in Alberta, data were provided by Alberta Environment and Protected Areas and by Parks Canada. We compiled the raw data into a standardized format for subsequent population modeling, in collaboration with government biologists. These raw data are available at Lamb (2024). We used the abundance estimates from a previously completed IPM for the Tonquin subpopulation of Jasper National Park (Parks Canada, 2022).

Translocations were attempted to supplement caribou numbers in four declining or extirpated subpopulations (Kinley, 2010; Warren et al., 1996; Young et al., 2001) (Appendix S1: Section S1). We controlled for the influence of translocation by including this recovery action in the model. We report on the estimated effects of translocation, but evaluating this recovery action was not a focus of our work because it does not address mechanisms of disturbance-mediated apparent competition. Further, translocation is not a recovery action currently used by either province due to limited efficacy of past attempts (Kinley, 2010; Leech et al., 2017).

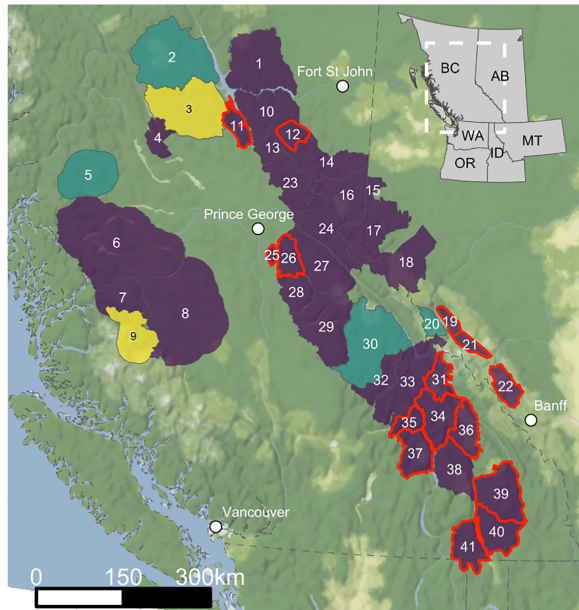
Abundance surveys

Caribou abundance was estimated through caribou aerial counts in BC or genetic capture–recapture in Alberta. Aerial surveys were primarily conducted in March when caribou sightability was high (>80%) in most subpopulations. When radio collar data were available for the subpopulation, we estimated abundance by dividing the number of animals observed during aerial counts by a sightability correction factor generated using the proportion of radio-collared animals (radio collared with either very high frequency [VHF] or Global Positioning System [GPS] collars; see below) observed relative to the radio collared sample within the subpopulation during the survey. During the survey, the location of radio-collared animals was unknown to surveyors. The sightability correction factor is assumed to equal the proportion of the subpopulation that would have been seen on the survey, as is typical of a mark–resight design using a Lincoln–Peterson estimator (Barker, 2008). We estimated uncertainty in the sightability correction based on a binomial distribution, which used the sightability correction, and the number of collars available to be observed, to calculate a standard error (Moeller et al., 2021).

At the end of the survey, radio-collared animals not seen during the survey were found using their VHF

a) Southern Mountain Caribou

Population growth without intervention ■ increasing ■ stable
 ■ declining ■ functional extirpation



b) Population Trend

51% decline since 1991, +1548 caribou from recovery actions

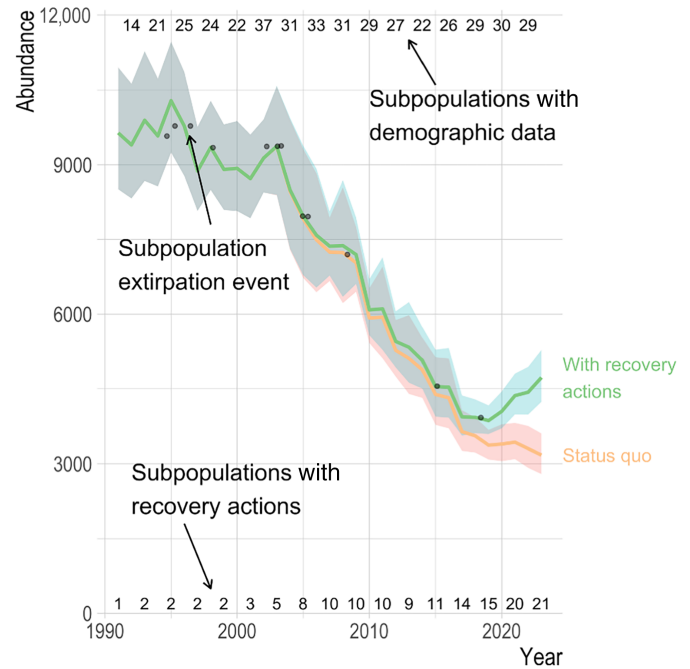


FIGURE 1 (a) Map of southern mountain caribou subpopulations in British Columbia and Alberta, Canada. Numbers for each subpopulation correspond to subpopulation identification numbers in Figure 2 and are numbered by Environment and Climate Change Canada (ECCC) recovery ecotype. Northern Group: 1–9, Central Group: 10–22, Southern Group: 23–41. Population growth trend for each subpopulation during the decade preceding recovery actions implementation (declining: $r < -0.01$, stable: $r > -0.01$ and $r < 0.01$, and increasing: $r > 0.01$) shown as choropleth. Because population growth estimates for individual subpopulations in (a) is based on the 10 years prior to recovery actions, it therefore does not necessarily reflect long-term or current population trends. Refer to Figure 2 for overall population trends for each subpopulation. Functionally extirpated subpopulations are outlined in red (<10 adult females or total population <20). (b) Overall southern mountain caribou population trend from 1991 to 2023. An observed (modeled) trajectory under the recovery actions implemented is shown in green as well as a counterfactual where no recovery actions were implemented (status quo) in orange. The number of subpopulations receiving recovery actions are shown along the bottom of the plot, with values for every second year shown. The number of subpopulations with demographic data (at least one of the following: abundance, recruitment, or survival) are shown along the top of the plot, with values for every second year shown. We display this restricted (>1990) temporal span instead of the full period (1973–2023) because relatively few subpopulations have demographic data before 1990, compared to after 1990, so predictions in these earlier periods heavily rely on information from prior distributions for most subpopulations. Demographic data were available for at least half (>20) the subpopulations by 1990, so we chose this more data-rich period as the beginning of our time frame to display the overall population trajectory. The timing of each documented subpopulation functional extirpation is shown as points along the trend. While 15 subpopulations are known to have been functionally extirpated between 1973 and 2023, three are not shown here because they occurred between 1973 and 1990, and one, Scott West, is not shown due to uncertain timing.

signal. These missed animals and any animals without collars that were with them were added to the number observed to create a minimum count. The animals found using VHF signals were not included as part of the sightability-corrected aerial abundance estimates. In cases where the minimum count exceeded the aerial abundance estimate, we used the minimum count as the best available abundance metric.

Three subpopulations in Alberta (À La Pêche, Redrock-Prairie Creek, and Narraway) had low sightability,

rendering aerial population enumeration methods impractical. Following the approach of McFarlane et al. (2020), DNA was collected and extracted from fecal material and used in a genetic spatial capture–recapture framework to estimate the size of each subpopulation.

We included only the abundance estimates generated from surveys where the entire caribou range was surveyed (or at least the portion known to have caribou occurrence) and when surveyors indicated that the weather and snow conditions were amenable to obtaining a reliable count.

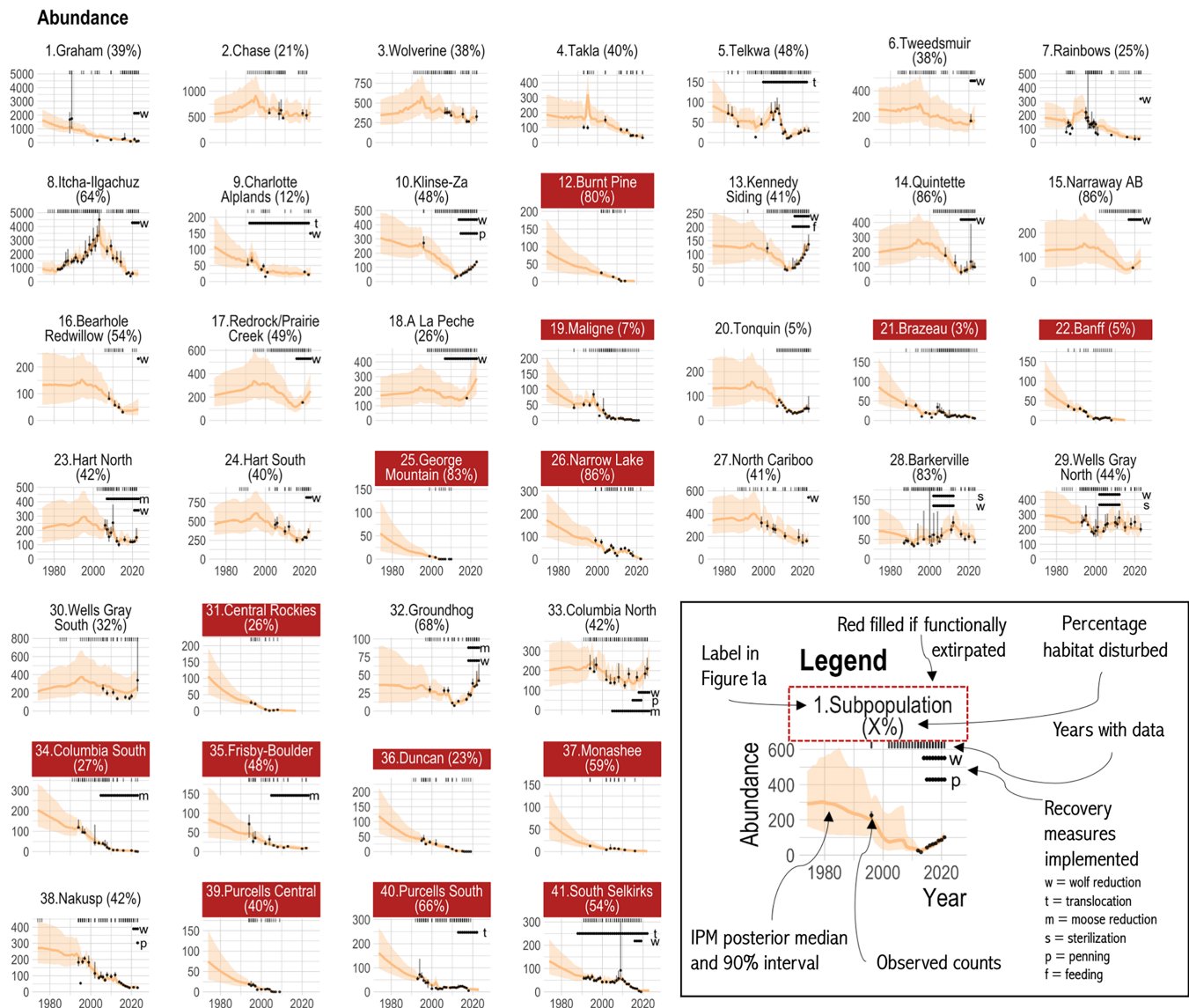


FIGURE 2 Median posterior estimates of abundance for each southern mountain caribou subpopulation from the integrated population model shown as orange line with 90% credible interval displayed as orange band. Extirpated and functionally extirpated subpopulations (<10 adult females or total population <20) highlighted in red. Observed minimum counts and abundance estimates shown as black dots with 90% CIs. Rug plots at top show years with survival, recruitment, or abundance data. Posterior estimates for years without demographic data rely on prior distributions as well as past and future population size. Posterior estimates before initiation of demographic data collection for each subpopulation should be interpreted cautiously. Percentage habitat loss (500 m buffered human-caused habitat loss [Environment and Climate Change Canada, 2022b]) shown by numerical labels for each subpopulation. Individual plots for each subpopulation can be found in Lamb (2024) under CaribouIPM?BCAB/plots/by_herd/with_treatments.

Recruitment surveys

Recruitment surveys were typically conducted in March to estimate the rate of calf recruitment when calves were ca. 9 months old. We used the number of calves per adult as our input for calf recruitment because it was not possible to identify the sex of adults safely and reliably in most surveys. If recruitment surveys were done earlier in the year, we noted the season, fall or spring, and included

these as variables in the IPM described in what follows. Our measure of recruitment encompasses pregnancy rates and calf survival for the first 9 months of life.

Survival monitoring

We monitored the fate of adult female caribou marked with GPS and VHF radio collars in a continuous-time

survival estimation framework with recurrent time horizons based on the biological year (e.g., DeCesare et al., 2016). For each animal, we collected information on the duration of monitoring and the outcome—censored or dead. Animals were censored when the collar was removed or stopped working. Animals monitored via aerial relocation of VHF whose status changed between flights were given a censored or dead date as the midpoint between last known live observation and the current observation. Radio collars with GPS generally provided an exact mortality date. Previous studies demonstrated low bias and high accuracy of the methods used to estimate caribou survival data using this study design (DeCesare et al., 2016).

Recovery actions

Recovery actions included predator reductions (wolf and/or cougar), predator sterilization (wolf), maternal penning, supplemental feeding, primary prey reductions (moose), and combinations of these recovery actions applied together. All recovery actions ultimately attempted to reduce predation mortality on caribou. We collected information on when and which recovery actions were implemented for each subpopulation. These recovery actions have been described elsewhere (Hervieux et al., 2014; McNay et al., 2022; Serrouya et al., 2017, 2019), and we briefly outline them here. Recovery actions were conducted under the authority of the respective provincial wildlife acts and the authority enshrined in treaty rights on traditional territory (see Appendix S1: Section S2 for additional details on permits and approvals). The university-affiliated authors of the current work were not directly involved in the activity or permits associated with recovery actions, thereby obviating the need for university animal care review or approvals.

Predator reduction

Predator reduction focused on reducing wolf abundance, as wolves were the primary predator in most southern mountain caribou ranges. In two southern subpopulations, Columbia North and Nakusp, predator reductions also included the removal of cougars using hounds and shooters. Hereafter, we refer to this measure as wolf reduction because wolves made up >99% of the predators removed (Appendix S1: Figure S1).

The goal of wolf reduction was to reduce the annual abundance of wolves to levels that would increase caribou survival and population growth (e.g., <3 wolves/1000 km² [Environment Canada, 2014]). Wolf reduction was carried out by provincial government biologists or their contractors, primarily through aerial tracking and shooting. Toxicant application was used in some years to reduce wolves in a

portion of the À La Pêche winter range in Alberta. Wolves were also reduced in Klinse-Za through trapping and shooting by Indigenous trappers and hunters (McNay et al., 2022). Although bear (*Ursus* spp.) and wolfers (*Gulo gulo*) are known to predate on caribou (Wittmer, McLellan, et al., 2005), especially calves (Gustine et al., 2006; Leclerc et al., 2014), no measures were taken to reduce their abundance except around the Klinse-Za maternity pen (McNay et al., 2022).

Wolf sterilization

Wolves were captured and surgically or chemically sterilized with the intention of reducing reproductive success and, thus, the abundance of wolves (Hayes, 2013).

Moose reduction

Moose reduction focused on reducing the abundance of moose using licensed hunting to levels expected under a natural forest age class distribution in areas where their abundance was inflated due to forest harvest (Serrouya et al., 2011). Efforts to substantially reduce other primary prey such as white-tailed deer (*Odocoileus virginianus*) or elk (*Cervus canadensis*) were not conducted.

Maternal penning

Maternal penning sought to increase neonatal survival by protecting calves during their first weeks of life. Maternal pens are 4–12 ha enclosures situated within caribou ranges, which protect female and calf caribou from predators. Pregnant adult female caribou were transported into the enclosures in March and kept until their calves were 6–10 weeks of age, at which point the adults and their calves were released (McNay et al., 2022). Caribou were fed while in the pen. Hereafter we refer to this measure as penning.

Supplemental feeding

Free-ranging caribou were fed a supplemental diet of pellets in the fall (Heard & Zimmerman, 2021). Hereafter we refer to this measure as feeding.

Integrated population model

We classified the application intensity of each recovery action as “standard” or “low” to identify subpopulation-years where the application was limited in spatial extent (i.e., applied only to a portion of a caribou range), application effort was low, or for small caribou subpopulations. For example, three subpopulations had wolf reductions applied to only a portion of their ranges during the early years of application (Appendix S1: Section S3) and, hence, were considered low application intensity. For moose, when

<50% of the reduction target was met, low application was also assigned. Similarly, low application was assigned when less than 20% of the female population was penned or there were few (<30) caribou left in subpopulations and were thus close to extirpation at the time of recovery action application.

To assess the effectiveness of recovery actions, we developed an IPM using multiple data sets on caribou demography (Brooks et al., 2004; Schaub & Abadi, 2011; Schaub et al., 2007). Our IPM was built based on the structure of two previous IPMs focused on assessing caribou population status and response to recovery actions (McNay et al., 2022; Moeller et al., 2021). The goals of the model were to (1) combine multiple sources of demographic information (counts, demographic rates) to produce robust estimates of past caribou population size; (2) evaluate population responses to recovery actions; (3) incorporate the uncertainty from each source of demographic information into estimates of vital rates and population size, responses to recovery actions, and derived parameters such as population growth; and (4) estimate the demographic trajectory of caribou populations in the absence of recovery actions.

Model structure

Integrated population models provide a statistical framework to combine and simultaneously analyze multiple demographic data types to increase estimated precision and enable the estimation of parameters (and derived, latent parameters) over periods for which data were not collected (Besbeas et al., 2002; Kéry & Schaub, 2011). The IPM consisted of a latent biological process model for survival, recruitment, and abundance that incorporated annual variation and hierarchical state-space observation submodels that related the observed data to the corresponding biological process while accounting for variance associated with sampling error. We followed a two-stage approach where point estimates and uncertainty for survival, recruitment, sex ratios, and abundance were estimated in the first stage and then used as the data inputs for the biological process submodels for the second stage. Two-stage approaches are often used to improve computational efficiency and reduce model complexity, including for IPMs (McNay et al., 2022; Moeller et al., 2021; Saunders et al., 2019). The results from these models closely reproduce one-stage analyses, and such models enable the integration of historical data where only point estimates and measures of variance are available, not original data sets (e.g., Lunn et al., 2013).

We adapted the IPMs from Moeller et al. (2021) and McNay et al. (2022) to evaluate recovery actions. We used

an age-structured caribou population model with two classes, which consisted of recruited calves (generally 0.75 years old) and adults (generally 0.75+ years old). Previous models included a juvenile age class, which can provide additional insights when input data on juveniles are available. However, the southern mountain caribou data available in BC and Alberta contained limited details on juvenile survival, and juveniles could rarely be identified from aerial surveys with accuracy. For this reason and to reduce model complexity, we simplified our model to two age classes after confirming that the simplification produced results similar to those of a three-age-class model. We estimated a female-only population size by applying annual sex ratios to the estimated total abundance.

Survival and recruitment data were subpopulation specific. We accounted for environmental stochasticity and sampling variance by including a random effect for subpopulation and year in the linear predictor for each of these parameters. We estimated a random intercept for each subpopulation, which allowed variation in vital rates between subpopulations. We estimated annual random effects for each ecotype (southern, central, and northern [COSEWIC, 2011]) such that annual variation for each subpopulation was influenced by the survival and recruitment data from that specific subpopulation and also from the larger ecotype for which it was a part. In one case, the Itcha-Ilgachuz subpopulation, the population increased nearly fourfold and then declined, a dynamic that was not observed in adjacent subpopulations within the same ecotype. As such we included a fourth random effect for Itcha-Ilgachuz on its own so that this unique trajectory did not unduly influence adjacent subpopulations with different trajectories. We included an effect for each recovery action that was constant across subpopulations to explicitly estimate the effect on survival and recruitment rates when recovery actions were applied. We included a covariate to account for the increased recruitment rates observed during surveys that occurred when calves were younger (spring or fall) and, hence, had less exposure to mortality factors in comparison to calves counted later in the year (winter).

We used vaguely informative priors for survival and recruitment rate estimates using a normal distribution that generally covered the ecologically plausible values for the mean of each parameter. We set the prior for the mean annual survival at 0.85 and recruitment at 0.15. We logit transformed both values and created a normal distribution with a SD of 1 based on previous analyses of demography across populations (McNay et al., 2022; Wittmer, McLellan, et al., 2005). Because sex ratio data were sparse, we used an informative prior based on all sex ratios observed during surveys, which equated to a

mean of 0.64 with a SD of 0.12. We used a vague prior for the Year 1 abundance estimate for each stage using a normal distribution with a mean of the first 4 years of count data with a large variance ($\tau = 0.001$). We assumed that adults accounted for 85% and calves the remaining 15% of the first-year survey count. We previously assessed the sensitivity of results to these starting values and found posterior estimates to be insensitive to variation in these parameters (McNay et al., 2022).

We estimated the annual finite rate of increase (λ) as a derived parameter ($\lambda_t = N_t/N_{t-1}$), where N_t was the abundance at time t and N_{t-1} was abundance the year prior. We transformed annual λ into the instantaneous rate of increase (r) using $r = \log(\lambda)$ when assessing recovery actions because r is symmetric around 0 and provided symmetrical effect sizes for decreases and increases in abundance. This symmetry arises because r has no lower or upper bounds whereas λ is bounded between 0 and infinity. Hereafter, we report all changes in annual population growth as the instantaneous rate of increase (r), which we also refer to as the population growth rate.

Models were fit in JAGS via R (version 4.2.0 [R Core Team, 2021]) using the jagsUI package (version 1.5.2). We ran each model for 400,000 iterations with a 60,000-iteration adaptive phase and a thinning rate of 90. We assessed convergence using the Gelman–Rubin diagnostic (r-hat), using a threshold of r-hat < 1.1 , and we visually inspected posterior distribution traceplots using the mcmcplots package. R and JAGS code and data are available in Lamb (2024). We report 90% credible intervals (90% CIs) for all estimated parameters.

Recovery action effectiveness

We collated the posterior distributions of population growth rates for each subpopulation-year for postprocessing in R. We assessed the demographic influence of recovery actions in three ways: (1) comparisons among populations to compare population growth rates across recovery actions and combinations of recovery actions and against a reference condition when recovery actions were not implemented; (2) before–after recovery action application within each population to compare population growth before and after recovery ($\Delta r = r_{\text{after}} - r_{\text{before}}$) measures for each population and to account for local conditions and demography; we viewed this approach as a strong test of effectiveness and thus also included responses of survival and recruitment to recovery actions in our assessment; and (3) modeling the average effect of individual recovery actions when applied at standard treatment intensity. We partitioned

variation using the results from Item 2 for individual recovery actions and combinations of recovery actions applied with standard treatment intensity to each population using a linear regression model to partition the effects of individual recovery measures on Δr . We only considered demographic responses for caribou subpopulations during years in which the abundance was above the functional extirpation threshold due to unstable demography when populations become very small.

Harding et al. (2020) proposed that population trend and recovery action effectiveness might differ by ecotype. In addition, Wilson et al. (2021) noted a potential influence of selection bias, where the choice of subpopulations may have influenced the findings of Serrouya et al. (2019). To test whether effectiveness differed by ecotype, we assessed the before–after effectiveness of recovery actions by ecotype as well as a partitioned variation of each recovery action while including ecotype as a fixed effect (Appendix S1: Section S4). Caribou ecotypes have been defined elsewhere using two separate approaches, one based on arboreal versus primarily terrestrial lichen feeders (two groups [Heard & Vagt, 1998; Stevenson & Hatler, 1985]) and another based on behavioral adaptations, ecological distinctness, and genetic evidence (three groups, hereafter Environment and Climate Change Canada [ECCC] recovery ecotype [COSEWIC, 2011]). We therefore assessed both definitions of ecotype to further evaluate if the results were sensitive to how ecotype was defined. The ECCC recovery ecotypes were used by Harding et al. (2020) to delineate ecotype in their critique. In addition, to minimize concerns about selection bias, we included subpopulations in a complete before–after–control–impact (BACI) analysis with spatiotemporally matched controls for each recovery action population from within the same ecotype (Appendix S1: Section S4).

Recovery action effects on population

To assess the overall effect of recovery actions for southern mountain caribou, we projected a counterfactual situation where recovery actions were not implemented and the population continued on unmitigated trajectories. For each subpopulation that received a recovery action, we averaged survival and recruitment rates across the 10 years prior to the implementation of recovery actions. We chose 10 years because it provided enough data to provide reasonably precise vital rates while providing temporally relevant rates with which to project the counterfactual. We used these averaged vital rates to project the population through time as if recovery action implementation did not happen. We compared the total

number of caribou (for the counterfactual and as observed with recovery action) that would be present in 2023.

RESULTS

Data

We compiled all available demographic data from 40 of the 41 subpopulations of southern mountain caribou collected between 1973 and 2023 (Figure 1). The one missing population, Scott West, was not rigorously monitored and thus not included in the IPM; however, this population was confirmed as being functionally extirpated in 2017 (Sittler & McNay, 2017). The demographic data available for southern mountain caribou consisted of 501 population-years of abundance estimates ($n = 424$ sightability-corrected estimates, $n = 77$ minimum counts), 589 population-years of recruitment estimates, and 556 population-years of survival rates that were estimated using known fate data from 1583 radio-collared caribou monitored for 4266 animal-years, with 604 recorded mortalities. A total of 179 population-years of sightability estimates were gathered, and 33 of 40 subpopulations had at least one sightability estimate.

Recovery actions were applied in 344 population-years for 25 subpopulations between 1988 and 2023, with most actions applied after 2004 ($n = 297$ population-years, Figure 2). Multiple recovery actions were applied concurrently to a subpopulation during 62 population-years (Figure 2). Recovery actions were applied with low intensity during 55 population-years. Wolf reductions were applied to 22 subpopulations across 121 population-years between 2002 and 2023. All 21 subpopulations received wolf reductions ($n = 1986$ wolves removed), while two subpopulations also received cougar reductions, though few cougars were removed ($n = 20$, see Appendix S1: Table S2). Wolf sterilization was attempted for two subpopulations in conjunction with wolf reductions spanning 22 population-years between 2002 and 2012. Moose abundance was reduced for five subpopulations, spanning 80 population-years between 2005 and 2023. Supplemental feeding was only attempted for the Kennedy Siding subpopulation and spanned 9 years between 2015 and 2023. Feeding was only applied in isolation during 2015; subsequent years also included wolf reductions. Maternal penning was applied to three subpopulations spanning 15 population-years between 2015 and 2023. Maternal penning was never applied in isolation but rather was paired with wolf reductions and moose reductions and by design included supplemental feeding. Finally, four subpopulations received multiple translocations of caribou between 1984 and 2012, which

occurred over 1–6 years for individual subpopulations. These translocations were designed to increase abundance and buoy demographic rates and thus could have demographically affected these subpopulations for 99 population-years after translocation. A complete table of recovery action type and timing by subpopulation is provided in Appendix S1: Figure S1.

Integrated population model

We estimated annual demographic changes for 40 subpopulations of southern mountain caribou using the IPM (Figure 2). Although the earliest demographic data informing the IPM was collected in 1973, data collection began for most (>50%) subpopulations after 1991. We provide estimates for each subpopulation for the entire period (1973–2023) and highlight which portion of this period is informed by demographic data and which portion is primarily informed by priors and parameters shared with adjacent subpopulations (Figure 2). We summarize population size for the whole southern mountain caribou population (Figure 1) between 1991 and 2023 to capture the period where most subpopulations had demographic data available. In 1991 the entire southern mountain caribou population was estimated at 9639 (8507–10,953) caribou. In 2023, the population had declined to 4727 (4240–5280). Thus, between 1991 and 2023 the population declined by 51% (Figure 1). We provide estimates of population size for each group of caribou in Appendix S1: Section S5.

Recovery action effectiveness

Recovery actions increased the abundance of declining caribou subpopulations in most cases (Figure 3). There were 31 instances of recovery actions applied to subpopulations (subpopulation–treatment combinations), and of these, 26 resulted in positive median changes to the subpopulation's trajectory ($\Delta r > 0$). Although translocations initially increased population size and temporarily slowed population declines, there was no detectable increase in the growth of subpopulations in the years following augmentation ($\Delta r = 0.02$ [−0.03 to 0.08, 90% CI]). With the exceptions of moose reduction applied in isolation (which appeared to have low effectiveness) and maternal penning with moose and wolf reduction (which had a low sample size, population-years = 2), the recovery actions increased the growth rate of caribou subpopulations compared to their pre-recovery action trajectories by 7%–16% (Table 1). CIs of recovery actions that increased growth rates substantially overlapped with 0 for feeding, penning with moose reductions, and penning with moose and wolf reductions, all of which had low sample sizes

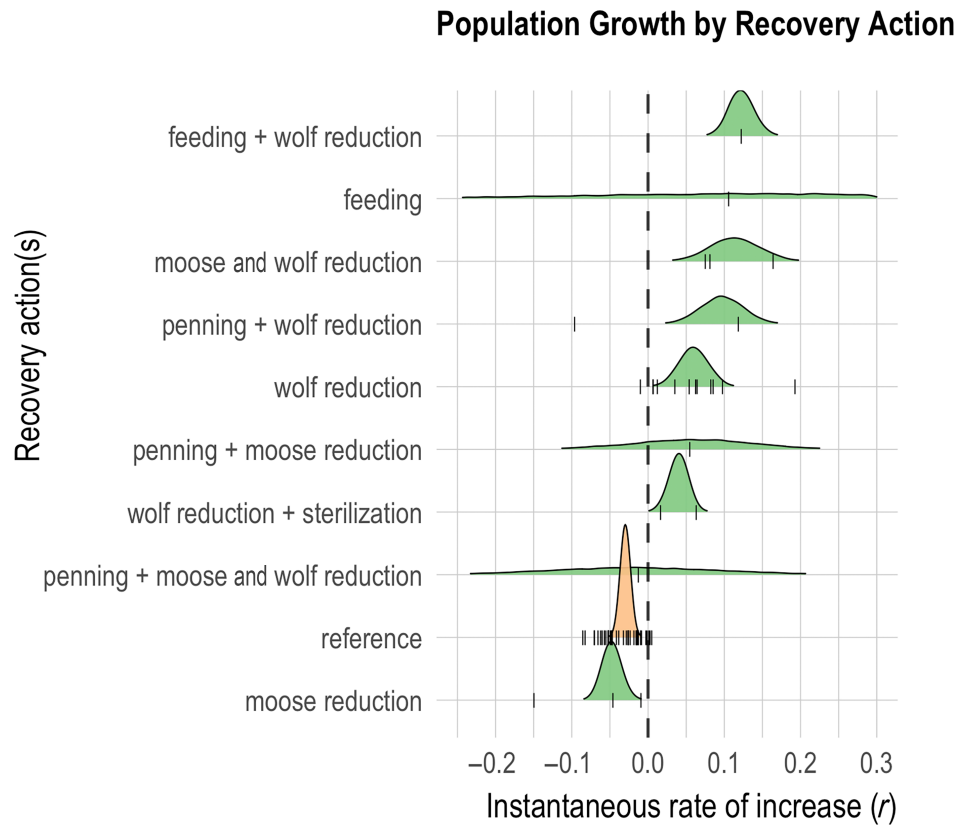


FIGURE 3 Posterior distribution of estimated annual instantaneous rate of increase (r) from integrated population model for each southern mountain caribou recovery action or combination of actions. Reference condition was estimated from herd-years when no recovery actions were applied. Rug plots along the bottom of the distributions show the average growth rate for each subpopulation the recovery action was applied to.

(population-years < 3). The 90% CIs of reducing wolves in isolation and the combination of wolf reduction with maternal penning, feeding, moose reduction, or wolf sterilization did not overlap with 0 (Table 1). For example, wolf reductions applied in isolation increased population growth by 0.08 (0.02–0.13, 90% CI), while the limited sample of one subpopulation application of wolf reductions together with feeding increased growth by 0.14 (0.09–0.20, 90% CI) (Figure 4). When wolf reductions were paired with feeding or maternal penning, the response of caribou growth rates was more beneficial than when wolf reductions were applied in isolation (Figures 3 and 4). Even small increases in population growth garnered through applying multiple recovery actions together produced large increases in total population size due to exponential growth (Figure 5).

We partitioned the effects of individual recovery actions applied at standard intensity using linear models. Results from this analysis indicated that wolf reductions, penning, and feeding were the most effective measures, although the feeding effect was imprecise (Figure 5). Assuming the effects were additive (i.e., when combined, individual recovery action effects summed to create the final effect), estimates of

TABLE 1 Posterior estimates of average change in southern mountain caribou annual instantaneous rate of increase (Δr) following recovery actions with 90% credible intervals.

Recovery action	Δr
Penning + wolf reduction	0.16 [0.12 to 0.2]
Feeding	0.15 [−0.27 to 0.49]
Feeding + wolf reduction	0.14 [0.09 to 0.2]
Moose and wolf reduction	0.11 [0.04 to 0.18]
Penning + moose reduction	0.07 [−0.17 to 0.30]
Wolf reduction	0.08 [0.02 to 0.13]
Wolf reduction + sterilization	0.07 [0.01 to 0.13]
Penning + moose and wolf reduction	−0.01 [−0.2 to 0.2]
Moose reduction	−0.04 [−0.1 to 0.01]

the average partitioned response suggested that r increased by 0.10 (0.03–0.17, 90% CI) with wolf reductions in isolation, by 0.10 (−0.14 to 0.31) with feeding in isolation, and by 0.08 (0.00–0.17) with penning in isolation. Wolf sterilization and moose reductions were less effective ($r = -0.01$ [−0.10 to 0.06] and 0.03 [−0.03 to 0.08], respectively).

Before-After Assessment of Effectiveness

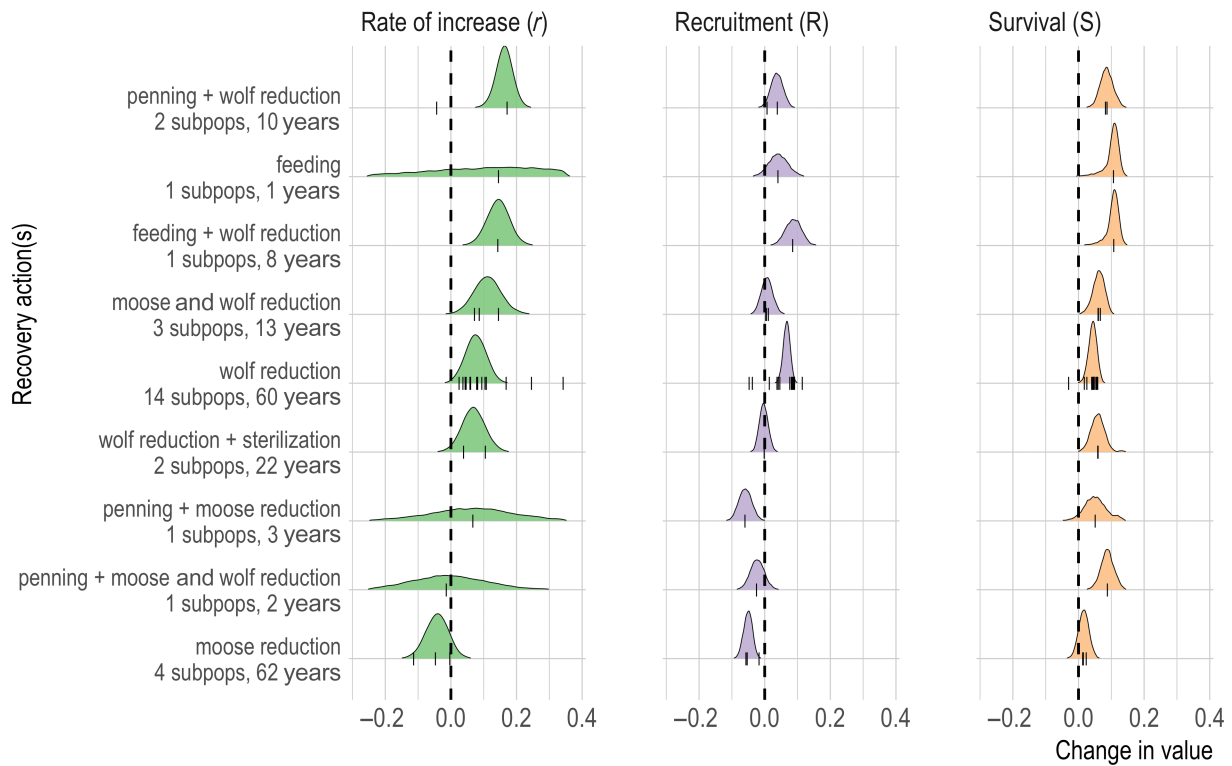


FIGURE 4 Posterior distributions of change in annual vital rates (after recovery action minus before) from the integrated population model for each southern mountain caribou recovery action. Rug plots along the bottom of the distributions show the average change in the rate for each subpopulation the recovery action was applied to.

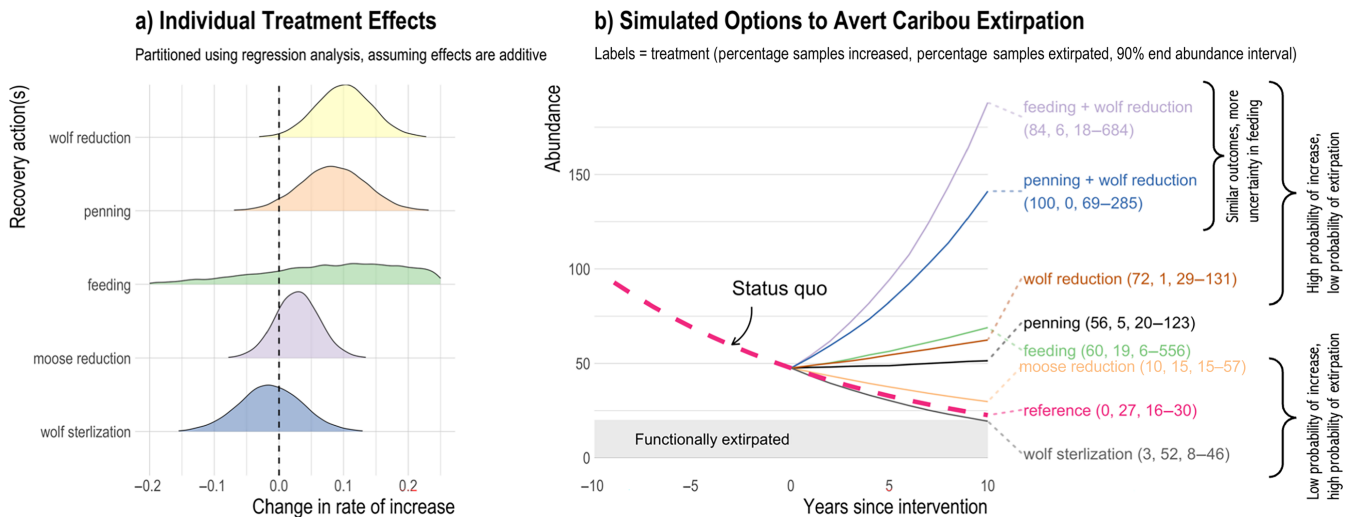


FIGURE 5 (a) Effectiveness of individual southern mountain caribou recovery actions at standard application intensity assessed via generalized linear models and (b) simulated outcomes of each recovery action compared to a status quo (no recovery action) scenario. Only wolf and moose reductions were applied in isolation across multiple subpopulations and years. The remainder of the estimates is primarily derived from partitioning the individual treatment effect from a combination of actions applied concurrently and assuming effects were additive. Note that combinations of recovery actions achieve greater abundances than the sum of individual effects due to the effects of exponential growth, so small increases in population growth can yield large returns in abundance over the long term.

We evaluated the robustness of our results by examining alternative analytical approaches and addressing past criticisms regarding statistical anomalies, selection bias, and environmental confounds. We employed two additional methods to assess our findings: (1) a BACI approach, stratified by caribou ecotype, to determine effectiveness with spatiotemporally matched controls; and (2) inclusion of caribou ecotype in partitioned effects analyses. Although we briefly outline the results of these analyses, we found no compelling reason to include these more complex approaches in the main manuscript and instead provide them in detail in Appendix S1: Section S4. The BACI analysis stratified by ecotype produced estimates of recovery action effectiveness that were similar to those from the before–after estimates of effectiveness. In fact, some effects were slightly stronger, and overall, none of the differences were large or suggested alternate conclusions from the data. Therefore, we retained the simpler before–after approach, with its more conservative effect sizes, that does not include ecotype or spatiotemporal controls. The partitioned effects models with ecotype did not show a strong influence of ecotype, likely due to limited sample sizes available for partitioning effectiveness by recovery action and ecotype. For example, for the fixed effect of ecotype (as defined by COSEWIC [2011]), the northern group effect was estimated at 0.02 (−0.09 to 0.11) and the southern group at −0.04 (−0.14 to 0.07) compared to the central group. These results suggest that changes in population growth rate following recovery actions were not well explained by ecotype or, at the very least, the effect was uncertain given the parameters' substantial coverage of zero (no effect).

Comparison to simulations without recovery actions

In 2023 there were 1548 (1175–1942, 90% CI) more caribou within the threatened southern mountain caribou population because of the application of recovery actions (Figure 1). Recovery actions increased the population through the recruitment of 1552 (1140–1934 90% CI) additional calves and increased adult female survival.

DISCUSSION

Over the last half century, southern mountain caribou abundance has declined by over 50%, but recovery actions have helped to stimulate population growth in many subpopulations. Prior to recovery actions, the intrinsic growth rate for southern mountain caribou subpopulations was below 0, and CIs did not overlap with 0. This means that without the observed recovery actions, many southern mountain caribou subpopulations would

have been on an unequivocal trajectory to extirpation. Indeed, many subpopulations were declining and became extirpated before these recovery actions took place. However, delivery of recovery actions, especially wolf reductions and wolf reductions together with other actions, has increased the abundance of southern mountain caribou by more than 1500 individual caribou. In other words, recovery actions have added approximately 52% additional southern mountain caribou to the landscape today compared to what likely would have occurred without interventions. Our work demonstrates that multiple population recovery actions can contribute to caribou recovery and avert caribou extirpation while habitat protection and restoration are underway.

Our IPM combined multiple, sometimes disparate, data sets in a statistically rigorous manner to provide cohesive results (Schaub & Abadi, 2011). No single source of demographic data can always provide a complete and unbiased account of population size and change, and each type of demographic data has varying degrees of precision. For instance, as populations decline, precise counts may be achievable, but precise survival estimates become difficult when few animals are monitored. By integrating multiple sources of demographic data through the IPM, we effectively utilized all the available data, transparently included and propagated uncertainty, and provided integrated results based on the information provided by each data set.

Our results reinforce the central paradigm of southern mountain caribou recovery: There is a need to curtail elevated mortality from predators resulting from human-caused habitat loss. From the perspective of process-based restoration (Ford, 2021), a caribou landscape is restored when rates of predator-caused mortality allow for caribou persistence. This condition arises from fewer encounters between wolves and caribou, due to there being fewer wolves, or from reduced access for wolves into caribou habitat. Indeed, wolf reductions have played a central role in provincial and Indigenous-led recovery efforts (Lamb et al., 2022) and have helped halt the decline of caribou populations (Hervieux et al., 2014; McNay et al., 2022). Although predator reductions are not a panacea for all species or situations (Clark & Hebblewhite, 2021), reducing predators to protect species affected by apparent competition is considered the most suitable conservation strategy (reviewed in Wittmer et al., 2013). Multiple species of conservation concern have benefitted when the limiting effects of predation have been addressed, such as the increased abundance of endangered Channel Island foxes following the removal of eagles (Coonan et al., 2014), increased hatching success, fledgling success, and breeding populations for multiple species of vulnerable birds after predators were

reduced (Smith et al., 2010), and increased abundance of critically endangered lizards following the removal of introduced mammalian predators (Reardon et al., 2012).

Our results show that wolf reductions alone increased the growth rate of southern mountain caribou subpopulations by ~11% with standard application intensity, resulting in stabilization or increasing abundance for most declining subpopulations where this recovery action was applied. Additionally, our results corroborate Serrouya et al. (2019), whereby pairing wolf reductions with additional recovery actions, especially feeding (Kennedy Siding single trial—wolf reduction and feeding) and maternal penning (Klinse-Za—wolf reduction and penning), further increased rates of population growth (Heard & Zimmerman, 2021; McNay et al., 2022). The Kennedy Siding and Klinse-Za subpopulations went from declining at ~3%–5% per year to increasing at 12% per year. Maintaining caribou in the wild is vital to ensure that development and application of habitat conservation and restoration (e.g., Lamb et al., 2022) will ultimately provide the ecological conditions that caribou need (i.e., low predator density) to maintain self-sustaining populations and recolonize extirpated areas.

The positive demographic responses to reduced wolf abundance further support evidence that elevated predation is causing southern mountain population declines (Hebblewhite et al., 2007; Hervieux et al., 2014; McNay et al., 2022; Seip, 1992; Serrouya et al., 2019; Wittmer, McLellan, et al., 2005; Wittmer, Sinclair, & McLellan, 2005). Reducing wolf abundance allowed caribou populations to grow even in very disturbed habitats and under contemporary climate change (Figure 2). We note that grizzly bears, black bears, coyotes, wolverines, and cougars (with the exceptions noted in *Materials and methods*) were not subject to population reductions as part of caribou recovery actions, even though those species are known to prey upon adult and, especially, calf caribou (Apps et al., 2013; Gustine et al., 2006; McNay et al., 2022). The effects of some recovery actions may thus have been dampened by ongoing, nonwolf predation of caribou. For example, in Klinse-Za, bear and wolverine predation on calf and adult caribou reduced population growth, yet populations still tripled under wolf reductions and maternal penning (McNay et al., 2022). Caribou populations in the less disturbed areas of northern British Columbia and Alaska are large and thought to be self-sustaining—although data are limited in many places (Cichowski et al., 2022). Caribou in these northern populations are often consumed by the same predators that cause declines in southern mountain caribou (Adams et al., 1995; Gustine et al., 2006; Young & McCabe, 1997), indicating that caribou can be self-sustaining under natural levels

of predation but not the elevated rates of predation associated with human-caused habitat loss (Cichowski et al., 2022).

Maternal penning was deployed in three subpopulations (Klinse-Za, Nakusp, and Columbia North) of southern mountain caribou, but never in isolation. Penning appeared to contribute to increased calf survival and population growth, especially in Klinse-Za, accounting for approximately one-third of the population growth observed (McNay et al., 2022). The Nakusp pen was only in operation for a single year (April–July 2022) during the course of our study. Early results showed the pen likely increased calf survival but predation on adult females outside the pen caused continued population declines in 2022–2023. In Columbia North, penning doubled calf survival but had no positive effect on population growth because it was never scaled up to include enough adult females to affect population growth and had high mortality of adult caribou inside the pen, likely due to the pens' location at an elevation lower than typical calving habitat (Serrouya, Bollefer, et al., 2021). Results from the Chisana maternal pen on the east slopes of the Wrangell and St. Elias Mountains in the Canadian Yukon (2003–2008) encountered similar challenges (Adams et al., 2019). The Chisana maternal pen successfully tripled calf survival; however, the overall population effect was muted due to a small proportion of the population being penned. The results from Klinse-Za, Nakusp, Columbia North, and Chisana projects suggest that pen location, the proportion of the population penned, predation risk outside the pen, and animal husbandry practices all affect maternal penning effectiveness.

Our simulations show that combining recovery actions can increase small, rapidly declining subpopulations. For example, starting with a declining subpopulation of 50 caribou, we estimated that maternal penning and wolf reductions increased caribou abundance by ~10% within 10 years, and wolf reductions alone would likely increase the subpopulation by 32% in the same time (Figure 5). Alternatively, following the status quo for this hypothetical declining subpopulation, the population would be functionally extirpated within 10 years. Combining recovery actions can increase caribou abundance quicker than single recovery actions alone, largely due to exponential growth yielding large returns in abundance with even small increases in positive population growth.

Supplemental feeding was only applied in isolation for 1 year to one population, so we had limited evidence that added nutrition increased caribou population growth rates. More feeding trials are needed to confirm the efficacy and viability of supplemental feeding as a recovery action. The feeding trial reported here occurred in the

Kennedy Siding caribou population, which is relatively small ($n = 50\text{--}100$ animals) and unique in that the entire subpopulation uses an early winter range of ~ 3000 ha that is accessible by road, making feeding practical. It would likely be impractical to deliver supplemental feeding across large caribou ranges that have greater numbers of caribou and more diffuse home ranges. It is also important to consider how supplemental feeding could concentrate caribou and increase close contact between individuals, which may have implications for vulnerability to predation and disease transmission, especially chronic wasting disease (Arifin et al., 2020). Nevertheless, the positive demographic response at the Kennedy Siding feeding trial suggests nutritional supplementation warrants further investigation, possibly through additional replicates where feasible.

Assessing potential nutritional limitations as a factor influencing southern mountain caribou declines would, as an initial inquiry, require an understanding of any possible changes to the quantity and/or quality of forage over the multidecade period that coincides with observed caribou declines, particularly during the sharp decline of southern mountain caribou in the early 2000s. Research has indicated that winter forage is not limiting caribou abundance (McLellan et al., 2012; Wittmer, McLellan, et al., 2005); however, others have raised the possibility that availability of or access to summer/autumn forage has changed (Denryter et al., 2022) and may be limiting (Cook et al., 2021). Caribou sampled in boreal and arctic populations suggests that body fat is high during the winter and lowest over the summer, which roughly coincides with the period of peak mortality (spring–fall) (Cook et al., 2021). Demonstrated links between nutrition and caribou demography remain weak but warrant further research. Evidence from western Canada suggests caribou foraging strategies can increase overlap with predators (bears in this case) and increase predation on caribou (Rioux et al., 2022). An alternate nutritional mechanism, as proposed by Heard and Zimmerman (2021), invokes declining forage availability due to risk-sensitive foraging by caribou, whereby the increased abundance of predators has impacted caribou caloric intake. These hypothesized mechanisms warrant further investigation.

Moose reductions were designed to reduce wolf abundance and therefore indirectly reduce predation pressure on caribou. The intent was to reduce moose densities consistent with natural forest age structure (i.e., pre-industrial development) when caribou populations would have been self-sustaining (Serrouya et al., 2011). Southern mountain caribou would not exist today if they had not been self-sustaining under a natural disturbance regime, which has been largely interrupted in the last two centuries following the European colonization of North America. Moose

reduction was applied in the mid-2000s, a period when wolf reductions were not widely applied in BC, and in areas with moose populations that greatly exceeded historic densities. Considering all caribou subpopulations where this recovery action was applied, reducing moose, as a recovery action on its own, did not produce a strong or consistent response by caribou populations. Closer scrutiny revealed that of the four caribou subpopulations where it was applied, moose reduction did stabilize the decline of one subpopulation (Columbia North), which was relatively large (~ 150 caribou) and had intensive removal of moose ($>70\%$ reduction). Moose reductions did not affect caribou demography in Columbia South, likely due to the subpopulation being too small when moose reductions began (~ 30 caribou), and did not appear to work in Hart North due to too few moose being harvested (Serrouya et al., 2019). In the context of these results, we do not recommend reducing moose as an isolated action to recover caribou. There is also potential for prey reductions alone to induce prey switching, whereby wolves may switch from their reduced primary prey to caribou (Frenette, 2017). However, theoretical predictions and empirical validation suggest that prey switching is much less likely to occur if the primary prey are reduced gradually via intentional management, but when a severe weather event suddenly reduced primary prey (deer), predator switching did occur, to the detriment of caribou (Serrouya et al., 2015). Where wolf reductions are ongoing, attempts to maintain stable populations of primary prey species like moose and, importantly, prevent their eruption, is expected to contribute to caribou conservation and recovery by limiting the rate and extent of annual wolf population recovery. The Government of Alberta is currently applying this approach to moose stabilization for the Redrock-Prairie Creek, A La Pêche, and adjacent boreal ecotype Little Smoky caribou subpopulations through increased licensed harvesting of moose, elk, and white-tailed deer. Stabilizing primary prey in national parks will remain challenging due to limited hunting opportunities in these areas. Given that increased abundance of apparent competitors is a central tenet of the disturbance-mediated apparent competition hypothesis (Serrouya, Dickie, et al., 2021), we recommend the delivery of a triad approach of (1) conserving and recovering habitat immediately to support an environment that has lower wolf and primary prey density and is conducive to self-sustaining caribou subpopulations in the long-term, (2) maintaining stable prey abundance and preventing eruptive prey population growth, and (3) mitigating predation of caribou by maintaining low wolf density through wolf reductions.

Recovery actions have increased the abundance of southern mountain caribou by over 1500 animals but have also attracted criticism based on views that these

approaches are acting only as “band-aids” in the face of ongoing habitat loss (Johnson et al., 2022). This critique has legitimacy given that the underlying causes of caribou population declines—disrupted predator–prey dynamics due to human-caused habitat loss—remain largely unresolved, and the habitat conditions over the duration of this study have not been conducive to population persistence. Moreover, habitat loss continues to worsen for most subpopulations (Nagy-Reis et al., 2021), locking caribou into a long-term situation of diminishing habitat, elevated predator densities, and disrupted predator–prey dynamics. Today, industrial tenures and operating approvals for forestry, oil and gas developments, and mining continue to be granted within or adjacent to critical caribou habitat (Collard et al., 2020; Palm et al., 2020), and full recovery of those developments (if/when restoration is initiated) back to suitable caribou habitat will take decades (Dalerum et al., 2007). Meanwhile, fire has also increased, affecting some southern mountain caribou ranges without a commensurate reduction in industrial resource extraction, creating a potentially additive disturbance regime. With continued and mounting threats to caribou habitat, immediate action to conserve and restore habitat is needed.

There have been cases where caribou population recovery actions helped to avert extirpation while habitat conservation and restoration actions were being developed, but such cases are limited. For example, an Indigenous-led recovery program by West Moberly First Nations and Sauteau First Nations used maternal penning and wolf reductions to avert the imminent extirpation of Klinse-Za caribou (McNay et al., 2022), while the government of BC and partners used wolf reductions and feeding to support neighboring caribou populations (Heard & Zimmerman, 2021; McNay et al., 2022). While these recovery actions were being applied, provincial, federal, and Indigenous governments negotiated an agreement to protect and restore 8000 km² of caribou habitat (ECCC et al., 2020). A landmark agreement for caribou and the signatories. Even in this situation where significant habitat protection commitments have been made by three levels of government, recovery actions will be needed for many years until habitat has been restored to the ecological conditions consistent with self-sustaining caribou populations.

Habitat restoration is expected to take decades to create the ecological conditions—low density of predators and their primary prey—needed for caribou population persistence. This vision of restoration focuses on the functional restoration of processes that sustain caribou populations (Ray, 2014). Evaluations of recent work to initiate habitat restoration have provided mixed results,

with evidence of reduced use by wolves in some studies but not others (Dickie et al., 2021, 2022; Keim et al., 2021; Tattersall et al., 2020). It is likely that habitat restoration has not been conducted at sufficient scales of intensity, space, or time to adequately evaluate effectiveness to achieve caribou demographic outcomes. The high cost and delayed efficacy of habitat restoration activities compared to population-based recovery actions have likely limited the scaling up of habitat restoration. For example, an analysis of population recovery options in the boreal forest of BC suggested that wolf reductions would cost orders of magnitude less (\$25,000–\$55,000 per additional caribou) than habitat restoration (\$531,000–\$4,426,000 per additional caribou) or other population-based recovery actions such as maternal penning (\$163,000–\$336,000 per additional caribou) (Johnson et al., 2019; similar results were independently derived by Nagy-Reis et al. [2020]). Feeding in Kennedy Siding has proven to be a highly economical option (<\$10,000 per additional caribou), but it does require a unique situation as discussed earlier and notwithstanding the uncertainties associated with efficacy. Although the population-based recovery actions are economically attractive on their own, it is imperative to recognize the fundamental role of habitat in effective species recovery and invest in caribou habitat conservation and restoration across broader spatial extents. Large-extent habitat measures would provide an opportunity for investigators to assess the demographic outcomes for caribou.

Habitat restoration implementation and evaluation ought to be an important component of southern mountain caribou conservation in the coming decades, and we provide recommendations for how to implement habitat restoration to provide the required data for an assessment of effectiveness in the future. First, restoration needs to occur at the subpopulation level, rather than in small areas within a subpopulation, to allow for an appropriate scale of evaluation. Second, restoration needs to be sufficiently extensive, whereby most features are restored across all habitats of caribou and alternative prey (Serrouya et al., 2020). Finally, better inference will be possible if sample size (i.e., number of subpopulations) is higher, so restoration should ideally be implemented both intensively and extensively across multiple candidate subpopulations. With these sampling-design and treatment parameters in mind, an evaluation of habitat restoration should be possible in the future. We recommend targeting subpopulations with sufficient landscape protection to ensure investments in habitat restoration are secure, allowing for an appropriate assessment of restoration effects on caribou demography in the long term. Study designs will have to be carefully implemented

to isolate effects of habitat restoration from other treatments (Dickie et al., 2023).

A singular focus on habitat conservation and restoration is unlikely to enable the near-term survival of many southern mountain caribou subpopulations due to the human-altered predator–prey communities that will linger for decades. However, a risk-averse and data-driven approach to caribou recovery would integrate the effectiveness of population recovery actions that increase adult female and calf survival through predator reductions, apparent competitor management, maternal penning, and, possibly, feeding, while simultaneously focusing on habitat-based solutions to restore predator–prey dynamics. Building off the results from this analysis and the collective experience of members of the author group who have applied or studied many of the recovery actions, we suggest that the intensity of application must be considered when delivering future recovery actions and habitat measures. Efforts will be most successful when applied at a broad spatial extent (i.e., across an entire subpopulation or multiple subpopulations), with sufficient intensity to achieve the desired ecological response and to subpopulations of sufficient size (~30 animals or more) that are less subject to Allee effects and demographic stochasticity. Ultimately, the long-term goal of this dual “habitat and population” approach is that eventually the active reduction of predation will no longer be needed once sufficient caribou habitat and linked predator–prey dynamics have been restored.

In the absence of habitat conservation and restoration, predator reductions would be required indefinitely to avoid the extirpation of southern mountain caribou. The application of effective predator reductions may become increasingly impractical and unsustainable if landscapes continue to be subject to ongoing loss of caribou habitat. It will likely be challenging to achieve caribou population growth in the face of ever-increasing populations of moose, deer, and their predators. In addition, it will become difficult to maintain social license for the application of predator reductions as an ongoing interim measure without progress on caribou habitat conservation and restoration. Opponents of recovery actions to avert caribou extirpation often cite habitat protection and restoration as the only solution. Calls to focus on habitat are valuable; however, condemning interim population recovery actions in favor of only pursuing habitat measures is a false choice. If interim recovery actions are eliminated, in many cases the long-term outcome will be landscapes devoid of southern mountain caribou.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Lamb, 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.10437005>.

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REFERENCES

- Adams, L. G., R. Farnell, M. P. Oakley, T. S. Jung, L. L. Larocque, G. M. Lortie, J. McLelland, M. E. Reid, G. H. Roffler, and D. E. Russell. 2019. “Evaluation of Maternal Penning to Improve Calf Survival in the Chisana Caribou Herd.” *Wildlife Monographs* 204: 5–46.
- Adams, L. G., F. J. Singer, and B. W. Dale. 1995. “Caribou Calf Mortality in Denali National Park, Alaska.” *Journal of Wildlife Management* 59: 584–594.
- Apps, C. D., B. N. McLellan, T. A. Kinley, R. Serrouya, D. R. Seip, and H. U. Wittmer. 2013. “Spatial Factors Related to Mortality and Population Decline of Endangered Mountain Caribou.” *Journal of Wildlife Management* 77: 1409–19.
- Arifin, M. I., A. Staskevicius, S. Y. Shim, Y.-H. Huang, H. Fenton, P. D. McLoughlin, G. Mitchell, C. I. Cullingham, and S. Gilch. 2020. “Large-Scale Prion Protein Genotyping in Canadian Caribou Populations and Potential Impact on Chronic Wasting Disease Susceptibility.” *Molecular Ecology* 29: 3830–40.
- Barker, K. J., E. Cole, A. Courtemanch, S. Dewey, D. Gustine, K. Mills, J. Stephenson, B. Wise, and A. D. Middleton. 2023. “Large Carnivores Avoid Humans while Prioritizing Prey Acquisition in Anthropogenic Areas.” *Journal of Animal Ecology* 92: 889–900.
- Barker, R. 2008. “Theory and Application of Mark—Recapture and Related Techniques to Aerial Surveys of Wildlife.” *Wildlife Research* 35: 268.
- Batson, W. G., I. J. Gordon, D. B. Fletcher, and A. D. Manning. 2015. “REVIEW: Translocation Tactics: A Framework to Support the IUCN Guidelines for Wildlife Translocations and

- Improve the Quality of Applied Methods.” *Journal of Applied Ecology* 52: 1598–1607.
- Bergerud, A. T., W. J. Dalton, H. Butler, L. Camps, and R. Ferguson. 2007. “Woodland Caribou Persistence and Extirpation in Relic Populations on Lake Superior.” *Rangifer* 27: 57.
- Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. “Integrating Mark-Recapture-Recovery and Census Data to Estimate Animal Abundance and Demographic Parameters.” *Biometrics* 58: 540–47.
- Brooks, S. P., R. King, and B. J. T. Morgan. 2004. “A Bayesian Approach to Combining Animal Abundance and Demographic Data.” *Animal Biodiversity and Conservation* 27: 515–529.
- Caro, T., Z. Rowe, J. Berger, P. Wholey, and A. Dobson. 2022. “An Inconvenient Misconception: Climate Change Is Not the Principal Driver of Biodiversity Loss.” *Conservation Letters* 15: e12868.
- Cichowski, D., R. S. McNay, and J. C. Ray. 2022. *Caribou in Northern British Columbia: An Assessment of Range Condition and Population Status*. Prepared for the Habitat Conservation Trust Foundation, Victoria, B.C., and BC Ministry of Forests, Smithers, B.C. Wildlife Conservation Society Canada Conservation Report No. 16. Toronto, Ontario, Canada. <https://doi.org/10.19121/2022.Report.44066>.
- Clark, T. J., and M. Hebblewhite. 2021. “Predator Control May Not Increase Ungulate Populations in the Future: A Formal Meta-Analysis.” *Journal of Applied Ecology* 58: 812–824.
- Collard, R., J. Dempsey, and M. Holmberg. 2020. “Extirpation Despite Regulation? Environmental Assessment and Caribou.” *Conservation Science and Practice* 2: e166.
- Compton, B. B., P. Zager, and G. Servheen. 1995. “Survival and Mortality of Translocated Woodland Caribou.” *Wildlife Society Bulletin* 23: 490–96.
- Cook, J. G., A. P. Kelly, R. C. Cook, B. Culling, D. Culling, A. McLaren, N. C. Larter, and M. Watters. 2021. “Seasonal Patterns in Nutritional Condition of Caribou (*Rangifer tarandus*) in the Southern Northwest Territories and Northeastern British Columbia, Canada.” *Canadian Journal of Zoology* 99: 845–858.
- Coonan, T. J., V. Bakker, B. Hudgens, C. L. Boser, D. K. Garcelon, and S. A. Morrison. 2014. “On the Fast Track to Recovery: Island Foxes on the Northern Channel Islands.” *Monographs of the Western North American Naturalist* 7: 373–381.
- COSEWIC. 2011. *Designatable Units for Caribou (Rangifer tarandus) in Canada* 89. Ottawa: Committee on the Status of Endangered Wildlife in Canada.
- Dalerum, F., S. Boutin, and J. S. Dunford. 2007. “Wildfire Effects on Home Range Size and Fidelity of Boreal Caribou in Alberta, Canada.” *Canadian Journal of Zoology* 85: 26–32.
- DeCesare, N. J., M. Hebblewhite, P. M. Lukacs, and D. Hervieux. 2016. “Evaluating Sources of Censoring and Truncation in Telemetry-Based Survival Data: Telemetry-Based Survival Monitoring.” *The Journal of Wildlife Management* 80: 138–148.
- DeMars, C. A., and S. Boutin. 2018. “Nowhere to Hide: Effects of Linear Features on Predator–Prey Dynamics in a Large Mammal System.” *Journal of Animal Ecology* 87: 274–284.
- Denryter, K., R. C. Cook, J. G. Cook, and K. L. Parker. 2022. “Animal-Defined Resources Reveal Nutritional Inadequacies for Woodland Caribou during Summer–Autumn.” *The Journal of Wildlife Management* 86: e22161.
- Dickie, M., A. T. Ford, R. Steenweg, and R. Serrouya. 2023. “Intervention-Forward Adaptive Management in the Face of Extinction.” *Trends in Ecology & Evolution* 38: 505–6.
- Dickie, M., R. S. McNay, G. D. Sutherland, G. G. Sherman, and M. Cody. 2021. “Multiple Lines of Evidence for Predator and Prey Responses to Caribou Habitat Restoration.” *Biological Conservation* 256: 109032.
- Dickie, M., R. Serrouya, C. DeMars, J. Cranston, and S. Boutin. 2017. “Evaluating Functional Recovery of Habitat for Threatened Woodland Caribou.” *Ecosphere* 8: e01936.
- 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.
- Dickie, M., G. G. Sherman, G. D. Sutherland, R. S. McNay, and M. Cody. 2022. “Evaluating the Impact of Caribou Habitat Restoration on Predator and Prey Movement.” *Conservation Biology* 37: 414004.
- Dubois, S., N. Fenwick, E. A. Ryan, L. Baker, S. E. Baker, N. J. Beausoleil, S. Carter, et al. 2017. “International Consensus Principles for Ethical Wildlife Control: Principles for Ethical Wildlife Control.” *Conservation Biology* 31: 753–760.
- ECCC, FLNRORD, Sauteau First Nations, and West Moberly First Nations. 2020. “Intergovernmental Partnership Agreement for the Conservation of the Central Group of the Southern Mountain Caribou.” 28. <https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/conservation-agreements/intergovernmental-partnership-conservation-central-southern-mountain-caribou-2020.html>.
- Ehlers, L. P. W., C. J. Johnson, and D. R. Seip. 2016. “Evaluating the Influence of Anthropogenic Landscape Change on Wolf Distribution: Implications for Woodland Caribou.” *Ecosphere* 7: e01600.
- Environment and Climate Change Canada. 2018. *Imminent Threat Assessment for Southern Mountain Caribou* 65. Ottawa: Environment and Climate Change Canada.
- Environment and Climate Change Canada. 2020. *Amended Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada* 157. Ottawa: Environment and Climate Change Canada.
- Environment and Climate Change Canada. 2022a. “Woodland Caribou (*Rangifer tarandus caribou*), Atlantic Gaspésie Population: Amended Recovery Strategy 2022.” Featured Articles. <https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/recovery-strategies/woodland-caribou-2022.html>.
- Environment and Climate Change Canada. 2022b. “Habitat Disturbance Mapping for Woodland Caribou, Southern Mountain Population (*Rangifer tarandus caribou*).” Canadian Wildlife Service—Pacific Region [Unpublished data set].
- Environment Canada. 2012. *Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada* 138. Ottawa: Environment Canada.
- Environment Canada. 2014. *Recovery Strategy for the Woodland Caribou, Southern Mountain Population (Rangifer tarandus caribou) in Canada* 103. Ottawa: Environment Canada.
- Fish and Wildlife Service. 2019. “Endangered and Threatened Wildlife; Endangered Species Status for Southern Mountain Caribou Distinct Population Segment Fish and Wildlife

- Service.” 260–261. Interior. <https://www.federalregister.gov/documents/2019/10/02/2019-20459/endangered-and-threatened-wildlife-endangered-species-status-for-southern-mountain-caribou-distinct>.
- Ford, A. T. 2021. “Operationalizing Process-Based Restoration for Terrestrial Communities.” *Restoration Ecology* 29: e13457.
- Fortin, D., F. Barnier, P. Drapeau, T. Duchesne, C. Dussault, S. Heppell, M.-C. Prima, M.-H. St-Laurent, and G. Szor. 2017. “Forest Productivity Mitigates Human Disturbance Effects on Late-Seral Prey Exposed to Apparent Competitors and Predators.” *Scientific Reports* 7: 6370.
- Frenette, J. 2017. *Démographie et viabilité de la population de caribous de la Gaspésie-Atlantique*. Université du Québec à Rimouski. https://semaphore.uqar.ca/id/eprint/1293/1/Jonathan_Frenette_mars2017.pdf.
- Frenette, J., F. Pelletier, and M.-H. St-Laurent. 2020. “Linking Habitat, Predators and Alternative Prey to Explain Recruitment Variations of an Endangered Caribou Population.” *Global Ecology and Conservation* 22: e00920.
- Fryxell, J. M., T. Avgar, B. Liu, J. A. Baker, A. R. Rodgers, J. Shuter, I. D. Thompson, et al. 2020. “Anthropogenic Disturbance and Population Viability of Woodland Caribou in Ontario.” *The Journal of Wildlife Management* 84: 636–650.
- Geldmann, J., A. Manica, N. D. Burgess, L. Coad, and A. Balmford. 2019. “A Global-Level Assessment of the Effectiveness of Protected Areas at Resisting Anthropogenic Pressures.” *Proceedings of the National Academy of Sciences* 116: 23209–15.
- Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. “Calf Survival of Woodland Caribou in a Multi-Predator Ecosystem.” *Wildlife Monographs* 165: 1–32.
- Harding, L. E., M. Bourbonnais, A. T. Cook, T. Spribille, V. Wagner, and C. Darimont. 2020. “No Statistical Support for Wolf Control and Maternal Penning as Conservation Measures for Endangered Mountain Caribou.” *Biodiversity and Conservation* 29: 3051–60.
- Hayes, B. 2013. *Quesnel Highland Wolf Sterilization Pilot Assessment 2012 an Independent Evaluation of the Response of Mountain Caribou* 31. Smithers: BC Fish and Wildlife Recovery Implementation.
- Heard, D. C., and K. L. Vagt. 1998. “Caribou in British Columbia: A 1996 Status Report.” *Rangifer* 18: 117.
- Heard, D. C., and K. L. Zimmerman. 2021. “Fall Supplemental Feeding Increases Population Growth Rate of an Endangered Caribou Herd.” *PeerJ* 9: e10708.
- Hebblewhite, M. 2017. “Billion Dollar Boreal Woodland Caribou and the Biodiversity Impacts of the Global Oil and Gas Industry.” *Biological Conservation* 206: 102–111.
- Hebblewhite, M., J. Whittington, M. Bradley, G. Skinner, A. Dibb, and C. White. 2007. “Conditions for Caribou Persistence in the Wolf-Elk-Caribou Systems of the Canadian Rockies.” *Rangifer* 17: 79–91.
- Hervieux, D., M. Hebblewhite, D. Stepnisky, M. Bacon, and S. Boutin. 2014. “Managing Wolves (*Canis lupus*) to Recover Threatened Woodland Caribou (*Rangifer tarandus caribou*) in Alberta.” *Canadian Journal of Zoology* 92: 1029–37.
- Holt, R. D. 1977. “Predation, Apparent Competition, and the Structure of Prey Communities.” *Theoretical Population Biology* 12: 197–229.
- Johnson, C. A., G. D. Sutherland, E. Neave, M. Leblond, P. Kirby, C. Superbie, and P. D. McLoughlin. 2020. “Science to Inform Policy: Linking Population Dynamics to Habitat for a Threatened Species in Canada.” *Journal of Applied Ecology* 57: 1314–27.
- Johnson, C. J., L. P. W. Ehlers, and D. R. Seip. 2015. “Witnessing Extinction—Cumulative Impacts across Landscapes and the Future Loss of an Evolutionarily Significant Unit of Woodland Caribou in Canada.” *Biological Conservation* 186: 176–186.
- Johnson, C. J., M. A. Mumma, and M. St-Laurent. 2019. “Modeling Multispecies Predator–Prey Dynamics: Predicting the Outcomes of Conservation Actions for Woodland Caribou.” *Ecosphere* 10: e02622.
- Johnson, C. J., J. C. Ray, and M.-H. St-Laurent. 2022. “Efficacy and Ethics of Intensive Predator Management to Save Endangered Caribou.” *Conservation Science and Practice* 4: e12729.
- Keim, J. L., P. D. DeWitt, S. F. Wilson, J. J. Fitzpatrick, N. S. Jenni, and S. R. Lele. 2021. “Managing Animal Movement Conserves Predator–Prey Dynamics.” *Frontiers in Ecology and the Environment* 19: 379–385.
- Kéry, M., and M. Schaub. 2011. “Introduction.” In *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*, 1st ed. Boston: Academic Press.
- Kinley, T. A. 2010. *Augmentation Plan for the Purcells-South Mountain Caribou Population* 51. Victoria: BC Ministry of Environment.
- Lamb, C. 2024. “ctlamb/CaribouIPM_BCAB: Lamb et al. 2024 Zenodo Commit for Ecological Applications Paper v3.” Zenodo. <https://doi.org/10.5281/zenodo.10437005>.
- Lamb, C. T., R. Willson, C. Richter, N. Owens-Beek, J. Napoleon, B. Muir, S. McNay, et al. 2022. “Indigenous-Led Conservation: Pathways to Recovery for the Nearly Extirpated Klinse- Za Mountain Caribou.” *Ecological Applications* 32: e2581.
- Leclerc, M., C. Dussault, and M.-H. St-Laurent. 2014. “Behavioural Strategies towards Human Disturbances Explain Individual Performance in Woodland Caribou.” *Oecologia* 176: 297–306.
- Leech, H., D. Jelinski, L. DeGroot, and G. W. Kuzyk. 2017. “The Temporal Niche and Seasonal Differences in Predation Risk to Translocated and Resident Caribou (*Rangifer tarandus caribou*).” *Canadian Journal of Zoology* 95: 809–820.
- Lunn, D., J. Barrett, M. Sweeting, and S. Thompson. 2013. “Fully Bayesian Hierarchical Modelling in Two Stages, with Application to Meta-Analysis.” *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 62: 551–572.
- Maxwell, S. L., V. Cazalis, N. Dudley, M. Hoffmann, A. S. L. Rodrigues, S. Stolton, P. Visconti, et al. 2020. “Area-Based Conservation in the Twenty-First Century.” *Nature* 586: 217–227.
- McFarlane, S., M. Manseau, R. Steenweg, D. Hervieux, T. Hegel, S. Slater, and P. J. Wilson. 2020. “An Assessment of Sampling Designs Using SCR Analyses to Estimate Abundance of Boreal Caribou.” *Ecology and Evolution* 10: 11631–42.
- McLellan, M., R. Serrouya, B. McLellan, K. Furk, D. Heard, and H. Wittmer. 2012. “Implications of Body Condition on the Unsustainable Predation Rates of Endangered Mountain Caribou.” *Oecologia* 169: 853–860.
- McNay, R. S., C. T. Lamb, L. Giguere, S. Williams, H. Martin, G. Sutherland, and M. Hebblewhite. 2022. “Demographic Responses of Nearly Extirpated Endangered Mountain Caribou to Recovery Actions in Central British Columbia.” *Ecological Applications* 32: e2580.
- Moeller, A. K., J. J. Nowak, L. Neufeld, M. Bradley, M. Manseau, P. Wilson, S. McFarlane, P. M. Lukacs, and M. Hebblewhite.

2021. "Integrating Counts, Telemetry, and Non-invasive DNA Data to Improve Demographic Monitoring of an Endangered Species." *Ecosphere* 12: e03443.
- Moskowitz, D. 2019. "The Contiguous United States Just Lost its Last Wild Caribou." *Science*. <https://doi.org/10.1126/science.aaw7110>.
- Murali, G., G. H. de Oliveira Caetano, G. Barki, S. Meiri, and U. Roll. 2022. "Emphasizing Declining Populations in the Living Planet Report." *Nature* 601: E20–E24.
- Nagy-Reis, M., M. Dickie, A. M. Calvert, M. Hebblewhite, D. Hervieux, D. R. Seip, S. L. Gilbert, et al. 2021. "Habitat Loss Accelerates for the Endangered Woodland Caribou in Western Canada." *Conservation Science and Practice* 3: e437.
- Nagy-Reis, M., M. Dickie, P. Sólymos, S. L. Gilbert, C. A. DeMars, R. Serrouya, and S. Boutin. 2020. "'WildLift': An Open-Source Tool to Guide Decisions for Wildlife Conservation." *Frontiers in Ecology and Evolution* 8: 564508.
- Oro, D., A. Margalida, M. Carrete, R. Heredia, and J. A. Donazar. 2008. "Testing the Goodness of Supplementary Feeding to Enhance Population Viability in an Endangered Vulture." *PLoS One* 3: e4084.
- Palm, E. C., S. Fluker, H. K. Nesbitt, A. L. Jacob, and M. Hebblewhite. 2020. "The Long Road to Protecting Critical Habitat for Species at Risk: The Case of Southern Mountain Woodland Caribou." *Conservation Science and Practice* 2: 219.
- Parks Canada. 2022. *2017–2020 Caribou Program Progress Report Jasper National Park*. Jasper, Alberta, Canada: Jasper National Park, Parks Canada Agency.
- R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Ray, J. C. 2014. *Defining Habitat Restoration for Boreal Caribou in the Context of National Recovery* 54. Ottawa: Environment and Climate Change Canada.
- Reardon, J. T., N. Whitmore, K. M. Holmes, L. M. Judd, A. D. Hutcheon, G. Norbury, and D. I. Mackenzie. 2012. "Predator Control Allows Critically Endangered Lizards to Recover on Mainland New Zealand." *New Zealand Journal of Ecology* 36: 141–150.
- Reynolds, J. C., and S. C. Tapper. 1996. "Control of Mammalian Predators in Game Management and Conservation." *Mammal Review* 26: 127–155.
- Rioux, È., F. Pelletier, and M.-H. St-Laurent. 2022. "Trophic Niche Partitioning between Two Prey and their Incidental Predators Revealed Various Threats for an Endangered Species." *Ecology and Evolution* 12: e8742.
- Saunders, S. P., M. T. Farr, A. D. Wright, C. A. Bahlai, J. W. Ribeiro, Jr., S. Rossman, A. L. Sussman, T. W. Arnold, and E. F. Zipkin. 2019. "Disentangling Data Discrepancies with Integrated Population Models." *Ecology* 100: e02714.
- Schaub, M., and F. Abadi. 2011. "Integrated Population Models: A Novel Analysis Framework for Deeper Insights into Population Dynamics." *Journal of Ornithology* 152: 227–237.
- Schaub, M., O. Gimenez, A. Sierro, and R. Arlettaz. 2007. "Use of Integrated Modeling to Enhance Estimates of Population Dynamics Obtained from Limited Data." *Conservation Biology* 21: 945–955.
- Schrott, G. R., K. A. With, and A. W. King. 2005. "Demographic Limitations of the Ability of Habitat Restoration to Rescue Declining Populations." *Conservation Biology* 19: 1181–93.
- Seip, D. R. 1992. "Factors Limiting Woodland Caribou Populations and their Interrelationships with Wolves and Moose in South-eastern British Columbia." *Canadian Journal of Zoology* 70: 1494–1503.
- Serrouya, R., K. Bollefer, R. C. Cook, S. Gilbert, R. Gill, C. Legebokow, B. Macbeth, H. Schwantje, and C. Thacker. 2021. "Revelstoke Caribou Rearing in the Wild Final Report." 62. <https://cmu.abmi.ca/wp-content/uploads/2021/11/RCRW-Final-Science-Report-Oct-2021.pdf>
- Serrouya, R., M. Dickie, C. DeMars, M. J. Wittmann, and S. Boutin. 2020. "Predicting the Effects of Restoring Linear Features on Woodland Caribou Populations." *Ecological Modelling* 416: 108891.
- Serrouya, R., M. Dickie, C. Lamb, H. van Oort, A. P. Kelly, C. DeMars, P. D. McLoughlin, et al. 2021. "Trophic Consequences of Terrestrial Eutrophication for a Threatened Ungulate." *Proceedings of the Royal Society B: Biological Sciences* 288: 20202811.
- Serrouya, R., B. N. McLellan, S. Boutin, D. R. Seip, and S. E. Nielsen. 2011. "Developing a Population Target for an Overabundant Ungulate for Ecosystem Restoration." *Journal of Applied Ecology* 48: 935–942.
- Serrouya, R., B. N. McLellan, H. van Oort, G. Mowat, and S. Boutin. 2017. "Experimental Moose Reduction Lowers Wolf Density and Stops Decline of Endangered Caribou." *PeerJ* 5: e3736.
- 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: 6181–86.
- Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015. "Using Predator-Prey Theory to Predict Outcomes of Broad-scale Experiments to Reduce Apparent Competition." *The American Naturalist* 185: 665–679.
- Shea, K. 1998. "Management of Populations in Conservation, Harvesting and Control." *Trends in Ecology & Evolution* 13: 371–75.
- Sittler, K. L., and R. S. McNay. 2017. "Conservation of Caribou in the Scott West Herd Area: Year 3 Final Report:25." https://wildlifeinfometrics.com/wp-content/uploads/2018/02/Sittler_and_McNay_2017_WII_Report572_Conservation_of_Scott_West_Caribou_PEAf17W1478.pdf.
- Smith, R. K., A. S. Pullin, G. B. Stewart, and W. J. Sutherland. 2010. "Effectiveness of Predator Removal for Enhancing Bird Populations." *Conservation Biology* 24: 820–29.
- Stevenson, S. K., and D. F. Hatler. 1985. *Woodland Caribou and their Habitat in Southern and Central British Columbia*. Information Services Branch, Ministry of Forests. Victoria: Queen's Printer Publications.
- St-Laurent, M.-H., Y. Boulanger, D. Cyr, F. Manka, P. Drapeau, and S. Gauthier. 2022. "Lowering the Rate of Timber Harvesting to Mitigate Impacts of Climate Change on Boreal Caribou Habitat Quality in Eastern Canada." *Science of the Total Environment* 838: 156244.
- Tattersall, E. R., J. M. Burgar, J. T. Fisher, and A. C. Burton. 2020. "Mammal Seismic Line Use Varies with Restoration: Applying Habitat Restoration to Species at Risk Conservation in a Working Landscape." *Biological Conservation* 241: 108295.

- Walters, C. J., and C. S. Holling. 1990. "Large-Scale Management Experiments and Learning by Doing." *Ecology* 71: 2060–68.
- Warren, C. D., J. M. Peek, G. L. Servheen, and P. Zager. 1996. "Habitat Use and Movements of Two Ecotypes of Translocated Caribou in Idaho and British Columbia." *Conservation Biology* 10: 547–553.
- Williams, J. J., R. Freeman, F. Spooner, and T. Newbold. 2022. "Vertebrate Population Trends Are Influenced by Interactions between Land Use, Climatic Position, Habitat Loss and Climate Change." *Global Change Biology* 28: 797–815.
- Wilson, S. F., T. D. Nudds, and A. de Vries. 2021. "A Causal Modelling Approach to Informing Woodland Caribou Conservation Policy from Observational Studies." *Biological Conservation* 264: 109370.
- Wittmer, H. U., B. N. McLellan, D. R. Seip, J. A. Young, T. A. Kinley, G. S. Watts, and D. Hamilton. 2005. "Population Dynamics of the Endangered Mountain Ecotype of Woodland Caribou (*Rangifer tarandus caribou*) in British Columbia, Canada." *Canadian Journal of Zoology* 83: 407–418.
- Wittmer, H. U., R. Serrouya, L. M. Elbroch, and A. J. Marshall. 2013. "Conservation Strategies for Species Affected by Apparent Competition." *Conservation Biology* 27: 254–260.
- Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005. "The Role of Predation in the Decline and Extirpation of Woodland Caribou." *Oecologia* 144: 257–267.
- Young, D. D., and T. R. McCabe. 1997. "Grizzly Bear Predation Rates on Caribou Calves in Northeastern Alaska." *The Journal of Wildlife Management* 61: 1056.
- Young, J. A., J. A. Youds, and N. L. Freeman. 2001. *Status of the Charlotte Alplands Caribou Herd A Successful Short Distance Caribou Transplant* 26. Cariboo Region: BC Wildlife Branch.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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