



No statistical support for wolf control and maternal penning as conservation measures for endangered mountain caribou

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Abstract

Mountain caribou, a behaviourally and genetically distinct set of ecotypes of the Woodland caribou (*Rangifer tarandus caribou*) restricted to the mountains of western Canada, have undergone severe population declines in recent decades. Although a broad consensus exists that the ultimate driver of these declines has been the reduction of habitat upon which mountain caribou depend, research and policy attention has increasingly focused on predation. Recently, Serrouya et al. (Proc Nat Acad Sci USA 116:6181–6186, 2019) analysed population dynamics data from 18 subpopulations in British Columbia and Alberta, Canada, subject to different treatments and ‘controls’, and concluded that lethal wolf control and maternal caribou penning provide the most effective ways to stabilize population declines. Here we show that this inference was based on an unbalanced analytical approach that omitted a null scenario, excluded potentially confounding variables and employed irreproducible habitat alteration metrics. Our reanalysis of available data shows that ecotype identity is a better predictor of population trends than any adaptive management treatments considered by Serrouya et al. Disparate behavioural characteristics and responses to industrial disturbance among ecotypes suggest it may be incorrect to assume that adaptive management strategies that might benefit one ecotype are transferable to another.

Keywords Adaptive management · Bottom-up processes · British Columbia · Canada · Conservation · Ecotype · Habitat · Mountain caribou · Rebuttal · Statistics · Wolf

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Introduction

The conservation of Caribou (*Rangifer tarandus*), one of the most iconic species in Canada, is now urgent and carries large economic, ecological, cultural and social implications. The species is now classified nation-wide as threatened or endangered, owing to severe population declines. Some of the steepest declines have occurred in ecotypes of the western Cordillera. Here, Environment Canada recognizes four “designatable units” of caribou (COSEWIC 2011): (1) the Boreal ecotype (woodland caribou), which is non-migratory; (2) the Northern Mountain ecotype, in northern British Columbia (BC) and the Yukon and a small portion of adjacent Alaska; (3) the Central Mountain ecotype, along the Rocky Mountain crest; and (4) the Southern Mountain ecotype, which occurs in eastern BC, and until 2017, extended southward into the United States (Wiles 2017). The Boreal, Northern, and Central Mountain ecotypes forage in winter predominantly on ground-dwelling lichens, accessible because of relatively shallow snow depths. The Southern Mountain ecotype, by contrast, lives in an ecosystem where winter snows are often 3–4 m deep, and has evolved an obligate dependence on arboreal lichens. This key winter forage only grows in suitable abundance in old forests and is accessible from atop the snowpack (Edwards et al. 1960). This ecological and evolutionary context, and its two annual elevational migrations (Edwards and Ritcey 1959), has led most authors to regard the Southern Mountain ecotype as distinctive, and prompted some to refer to it descriptively as the Deep-Snow Mountain caribou (Seip and McLellan 2008; Serrouya et al. 2012; Serrouya 2013). We adopt that naming convention here.

Deep-Snow Mountain caribou have experienced some of the steepest population declines of any caribou ecotype in the world. Declines began at the southern edge of the range, which once extended into Montana’s Bitterroot Mountains (Manley 1986). Nearly all U.S. populations had disappeared by 1980, except for one in the Selkirk Mountains of Idaho and Washington. In 1984, the Deep-Snow Mountain ecotype was listed as Endangered under the U.S. Endangered Species Act (as ‘Mountain Caribou’). A decline in BC began around the same time (Spalding 2000). Despite warnings that industrial resource extraction, primarily forestry, was detrimental to maintaining viable caribou populations, habitat modification, fragmentation and associated road-building increased over subsequent decades. By the early 2000s, population declines had accelerated across the Canadian mountain caribou ecotypes, with Deep-Snow Mountain caribou registering a reduction of 45% in 27 years (COSEWIC 2014). In 2014, Deep-Snow Mountain and Central Mountain caribou were classified as Endangered by the Committee on the Status of Endangered Wildlife in Canada, while the other ecotypes remained listed as Threatened (COSEWIC 2014).

Since the 1970s, biologists and governments identified clearcut logging as the likely primary cause for the decline of Deep-Snow Mountain caribou (BC Ministry of Environment 1979; Stevenson et al. 2001). Low recruitment was, however, widely attributed to predation, which is thought to be facilitated by two intertwined processes: first, the increase of other ungulates in early seral habitats that result from logging, which leads to increased predator densities (“apparent competition”: Seip 1992; Wittmer et al. 2007, 2010); and second, the greater accessibility for predators to caribou via clearcuts, roads, snow compacted by snowmobiles, and the loss of forested refuges (Environment Canada 2014). The recognition of the disturbance-mediated effects of predators has led to a shift in the types of “adaptive management” measures recommended to governments and land management stakeholders. For example, wolf culling by poison baits and shooting from helicopters was reinstated in the 1980s to slow caribou declines in Northern Mountain and Central Mountain ecotypes

(Bergerud and Elliot 1986) and later in the Deep Snow Mountain ecotype (Seip 1992). Additionally, pregnant caribou cows have been held in two experimental “maternity pens” to allow calving without risk of predation. Even so, biologists have expressed skepticism at the efficacy of these measures, especially for Deep-Snow Mountain caribou (Serrouya et al. 2017).

Against this background, Serrouya et al. (2019) analyzed the efficacy of four variants of “adaptive management” in slowing population declines of threatened and endangered caribou in BC and Alberta, Canada: wolf removal ($n = 6$ subpopulations), moose removal ($n = 4$), wolf removal + penning ($n = 1$), and translocation ($n = 1$), compared to controls (i.e., no intervention; $n = 6$). Using this approach, Serrouya et al. (2019) tested hypotheses regarding the potential efficacy of various treatments (factors) with reference to control conditions, while accounting for habitat alteration (using an index) as a covariate. The 18 populations were drawn from three mountain ecotypes (17) and one Boreal subpopulation. As a response metric, Serrouya et al. evaluated changes in the finite population growth rate, lambda (λ) between periods of various lengths before and after treatments. They combined a frequentist approach and information theoretic model selection to assess whether adaptive management or habitat alteration could account for changes in lambda. The authors found wolf removal and wolf removal + penning were associated with more positive values of lambda compared to controls. They noted, prominently and in the abstract, no effect of the habitat alteration covariate. In national media, the authors referred to their results as a “black and white” case for wolf culling and maternal penning (e.g. Weber 2019). BC government policy soon thereafter ruled out new habitat protections for Deep Snow Mountain caribou (Fletcher 2019) and BC government officials cited the research as justification for at least one new wolf culling program (Shore 2019).

Given the policy implications and ultimate costs of error related to this applied research, the work of Serrouya et al. (2019) warrants close examination. Drawing on principles of strong inference (Platt 1964), we evaluated their analytical approach and re-examined the authors’ own data to “stress-test” their conclusions. We identified several shortcomings, which we detail below under five broad headings.

The authors did not report the results of a null model, which performs equally as well as treatments

Serrouya et al. employed model selection based on net change relative to a top-performing model, as expressed as differences in their respective corrected Akaike Information Criteria ($\Delta AICc$)—an information theoretical approach that confronts a limited set of a priori models with data. This strategy can help scientists make inferences about biological processes, but the outcome of model selection relies on the candidate set of models considered (Burnham and Anderson 2002). Serrouya et al. reported only a subset of possible models (treatment + habitat, treatment, and habitat: their Tables S2, S3, Table 1) and omitted the important intercept-only model. The latter is crucial because it serves as a null scenario in which the response varies randomly, irrespective of any considered predictor. When including this null model, we found $\Delta AICc$ to differ little ($\Delta AICc < 2$; Table 1A) among the intercept-only, habitat alteration and treatment models (Table 1A). This finding alone indicates that the wolf culling and maternal penning treatments from Serrouya et al. (2019) explain population dynamics of caribou no better than either habitat alteration or random chance alone.

Table 1 Model comparison based on AICc for (A) predictors except ecotype and (B) predictors as in (A) plus ecotype

	df	logLik	AICc	Delta	Weight
A—predictors except ecotype					
Treatment	6	13.06	- 6.5	0	0.462
Intercept^a	2	5.25	- 5.7	0.78	0.313
Habitat	3	6.14	- 4.6	1.92	0.177
Treatment + habitat	7	13.58	- 2	4.51	0.048
Treatment + habitat + habitat × treatment	9	13.88	12.7	19.21	0
B—As in (A) plus ecotype					
Ecotype^a	5	12.81	- 10.6	0	0.726
Treatment	6	13.06	- 6.5	4.14	0.091
Habitat + ecotype ^a	6	12.81	- 6	4.64	0.071
Intercept ^a	2	5.25	- 5.7	4.92	0.062
Habitat	3	6.14	- 4.6	6.06	0.035
Treatment + habitat	7	13.58	- 2	8.66	0.01
Habitat + ecotype + ecotype × habitat ^a	8	16.23	- 0.5	10.15	0.005
Treatment + ecotype ^a	9	17.78	4.9	15.56	0
Ecotype × treatment + ecotype + treatment ^a	10	21.84	7.8	18.37	0
Treatment + habitat + ecotype + ecotype × treatment ^a	11	28.34	9.3	19.93	0
Treatment + habitat + ecotype ^a	10	19.5	12.4	23.04	0
Treatment + habitat + habitat × treatment	9	13.88	12.7	23.36	0
Treatment + habitat + ecotype + ecotype × habitat ^a	12	21.46	43.5	54.10	0
Treatment + habitat + habitat × treatment + ecotype ^a	12	19.85	46.7	57.32	0

Models are sorted based on lowest AICc

^aModels not considered in Serrouya et al. (2019)

Models with lowest AICc (Δ AICc < 2) are highlighted in bold

Owing to differences in behaviour and habitat use among ecotypes, we hypothesized that the change in lambda might be either ecotype-specific or that it depends on the interaction between ecotype and other predictors considered by Serrouya et al. Accordingly, we considered a broader candidate model set, which additionally included ecotype and its interactions with habitat alteration and treatments. We found that a model with ecotype as predictor outperformed all others (Δ AICc \geq 4.1, Table 1B), with significant differences between (i) Northern Mountain and Central Mountain and (ii) Deep-Snow Mountain and Central Mountain ecotypes, respectively (Fig. 1). The question why ecotype accounts for so much variation in the response variable is discussed below.

The study design was not balanced

Although Serrouya et al. (2019) referred to their work as a “replicated management experiment”, the study in fact drew from a patchwork of older and more recent studies across the four ecotypes. For example, the authors selected controls based on “matching ecological conditions as closely as possible to the treatment populations”, but wolf

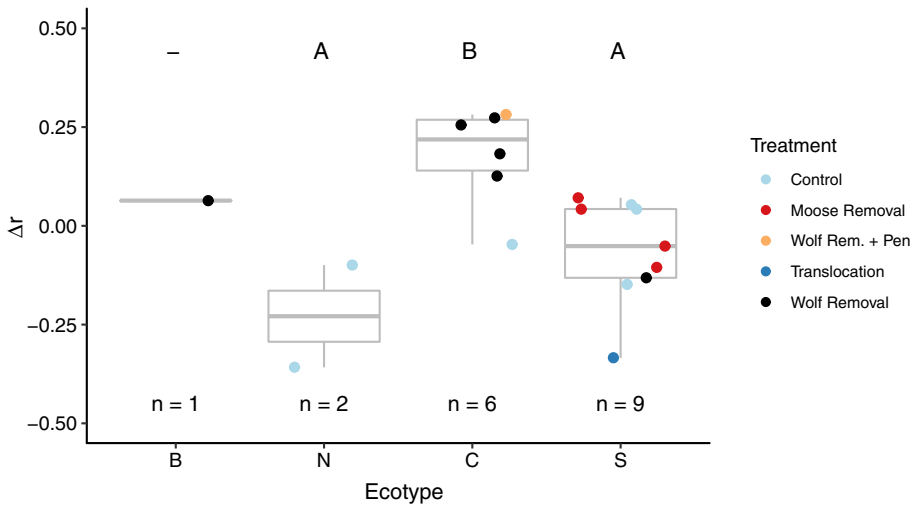


Fig. 1 Variation in Δr [$\log(\lambda_{end}) - \log(\lambda_{start})$] across ecotypes. Filled circles overlaying boxplots have a horizontal jitter and show lambda for individual populations within each treatment. Capital letters indicate the results of a pairwise *t*-test with a Bonferroni correction, with different letters indicating significant differences. The Boreal ecotype was excluded from the test due to insufficient sample size

reduction treatments were drawn from the Central Mountain ecotype ($n = 5$) and Boreal population ($n = 1$), whereas the six controls were drawn from Deep-Snow Mountain ($n = 3$), Northern Mountain ($n = 2$) and Central Mountain ($n = 1$) ecotypes. This unbalanced design challenges the ability to account for any potential effects of ecotype (Fig. 1). Another variable that could not be accounted for (neither in the original nor in this work) was wolf density associated with different ecotypes and populations, which for most areas is unknown in the absence of wolf census data. Collectively, these design considerations carry broad implications for the inference of cause and the assumption of transferability of results among ecotypes, which we discuss in more detail below.

More than half of the populations in the study area were omitted and not discussed

Serrouya et al. (2019) used only 18 of 42 mountain caribou populations in the study area (COSEWIC 2014; ECCC 2018). The 24 excluded populations (Supplementary Table 1) include: (a) two large Deep-Snow Mountain populations subjected to an 8-year wolf sterilization experiment; and (b) nine other populations—three Central Mountain, one Northern Mountain and five Deep-Snow Mountain—that became functionally extinct during the study (COSEWIC 2014; ECCC 2018). Population data were available for all 24 of these populations to calculate lambda over appropriate periods, both for those with treatments and those without (Supplementary Table 1). Several of the trajectories of the excluded populations appear to contradict the inference Serrouya et al. (2019) made. In the Quesnel Lake area, for example, lambda declined during or after a wolf cull while in Wells Gray Park, in the same years but with no such treatment, lambda increased (both of these are parts of the Wells Gray subpopulation; Wittmer et al. 2005b). In the North Cariboo Mountains, lambda decreased during or after wolf sterilization and moose reduction. In South Narraway, lambda declined markedly during or after a wolf cull. Finally, the

Charlotte Alplands subpopulation became extirpated altogether despite translocation of 52 caribou from the nearby Itcha-Ilgatchuz subpopulation (Supplementary Table 1). Including these and the other cases in the analysis might have allowed more comprehensive evaluation of the adaptive management approaches advocated by Serrouya et al (2019). At minimum, explicitly acknowledging the exclusion of these populations seems important.

Additional adaptive management measures were neither included in analyses nor discussed

Snowmobile and heliskiing harassment are pervasive across the range of Deep-Snow Mountain caribou (ECCC 2018) and impose potential harm during winter and spring calving (Environment Canada 2014; COSEWIC 2014). To mitigate potential effects, the BC government imposed closures of various spatial extents and periods across the study area, a source of variation not evaluated or discussed by Serrouya et al (2019). Another management intervention neither evaluated nor discussed is the habitat protections included in the 2008 provincial recovery plan (Mountain Caribou Recovery Implementation Plan 2008), which may have ameliorated downward trajectories of some populations. These additional management measures constitute additional potentially confounding variables not addressed in the original study.

Habitat alteration analysis cannot be replicated

Serrouya et al. (2019) found that changes in lambda were not associated with estimates of habitat alteration, defined as net forest loss from Global Forest Change (GFC) data derived from Landsat imagery (Hansen et al. 2013). GFC estimates forest loss annually from 2001 to 2019 and cumulative forest gain from 2001 to 2012. Serrouya et al. interpreted the forest loss as “early seral forest” and used estimates across each subpopulation’s range as the habitat alteration covariate. Following the methods described and using publicly available caribou population ranges for BC and Alberta with the same GFC data, we were unable to replicate the authors’ habitat alteration results. This suggests that further steps were taken in the geospatial analysis that are not specified in their methods.

Even if had we been able to replicate their habitat alteration estimates, GFC data carry limitations that restrict their usefulness for inferring habitat alteration. First, forest loss data do not match the temporal range of the before-treatment period for nine of the 18 populations. While the GFC will capture some pre-2000 disturbance, existing forest change products specifically developed for Canada (e.g., Hermosilla et al. 2015; Guindon et al. 2018) provide cumulative forest disturbance beginning in the 1980’s and thus would have been more suitable for characterizing forest loss in the before-treatment period. Second, forest change detection using Earth observation satellite data relies on inter-annual spectral change (Hermosilla et al. 2015) and does not fully account for roads and infrastructure that pre-date the reference year. Habitat fragmentation resulting from such features, which can influence lambda (Wittmer et al. 2007; Van Oort et al. 2011), would require the integration of other geospatial data sources.

Finally, the spatial context of any forest loss is also important. Critical low and high elevation caribou habitat has in fact been mapped throughout the study area (Environment Canada 2014). Using the more broadly circumscribed subpopulation range, as Serrouya et al. did, likely further influenced estimates of forest loss by increasing the denominator (Jelinski and Wu 1996).

Discussion

The conclusions that can be drawn from our re-analysis of available data diverge from those offered by Serrouya et al. (2019). After inclusion of a null model—standard practice in information theoretic approaches (Burnham and Anderson 2002)—we found no difference in the relative performance of null, treatment, and habitat alteration models. A subsequent re-analysis of a yet broader set of candidate models revealed support for the additional hypothesis that vital rates simply differed by ecotype, and found no support for the efficacy of management treatments. As compelling as such results are, we urge caution. First, as detailed above, the original study design has severe constraints. It can be better described as a post hoc observational, not experimental, study. Second, the introduction of additional variables and models to model selection approaches often results in novel patterns (Mundry 2011).

From the standpoint of scientific hypothesis testing, these limitations call for richer data sets, a more balanced design, consideration of potential ecotype-specific responses to environmental change, and attention to environmental change itself across ecotypes. We cite here four well-documented ecotype factors that may mediate such differential responses. First, Deep-Snow Mountain caribou are obligately bound to forests old enough to support accessible arboreal hair lichens in quantities sufficient to offset the costs of locomotion and other physiological processes (Antifeau 1987), a habitat requirement incompatible with large-scale clearcut forestry (Stevenson et al. 2001). By contrast, the Boreal, Central Mountain, and Northern Mountain ecotypes occupy regions with shallower snow and use primarily terrestrial lichens in forests of various ages (COSEWIC 2014). Deep-Snow Mountain caribou can thus be expected to respond differently to cutting of old forests than those in other ecotypes. Second, Deep-Snow Mountain caribou are uniquely sensitive to year-over-year changes in snow depth (Kinley et al. 2007). A winter with especially deep snowpack can cause lichen dieback in the lower forest canopy (Goward 2003). If followed by a shallow-snow winter, caribou may be compelled to seek forage in secondary habitats at lower elevations. Third, although data are limited, the effects of predators likely differ among ecotypes. For example, wolves do not comprise the primary source of mortality for Deep-Snow Mountain caribou, constituting only 5–10% of verified cases of mortality (Furk et al. 2008; Apps et al. 2013)—in fourth place after cougars, bears and wolverines (Wittmer et al. 2005a). In Central and Northern Mountain caribou populations, wolves account for 50–55% of verified mortalities (Wittmer et al. 2005b). Finally, fourth, snowmobile harassment has been acknowledged as an increasingly important factor in Deep-Snow Mountain caribou winter ecology (Seip et al. 2007), but Northern and Central Mountain caribou follow the snow line to areas where they can paw through to terrestrial lichens in winter, which tend not to be winter recreation hotspots. These differences suggest that population dynamics across ecotypes can be expected to differ. As a corollary, adaptive management that might benefit one ecotype—e.g., reducing wolves, or curtailing snowmobiling—cannot be assumed to be effective in all.

Population declines in Mountain caribou, especially the Deep-Snow Mountain caribou, are now so rapid that many additional subpopulations will likely disappear in the time needed to design and execute a new study. Indeed, two subpopulations, both subjected to “treatments”, have been declared extinct in the short period since Serrouya et al. (2019) was published. Given the implications for ecological and human well-being, natural resource management requires the use of best available information and strong inference. Decades ago, Platt (1964) argued that strong inference emerges from experimental designs

that consider alternative hypotheses. Accepting less, he argued, can lead to interpretations that favour predetermined beliefs. Requirements for strong inference are particularly pronounced when potential conservation interventions could threaten economic activity, impose harm to animals and ecosystems, or elicit social opposition. The fact, demonstrated here, that the study by Serrouya et al. (2019) falls short of important benchmarks brings into serious question its utility as a guide to policy decisions. In addition to reporting seemingly irreproducible results, this study emphasized predator control to the exclusion of any meaningful consideration of the 'bottom-up' habitat requirements of caribou (Wasser et al. 2012; Proulx et al. 2017). It also comes at a time when regulatory safeguards to protect caribou habitat are already failing to translate to effective protection on the ground (Collard et al. 2020; Palm et al. 2020). If efforts to prevent the extinction of the Mountain caribou are to succeed, conservation biologists must make use of the whole spectrum of available data, and encourage government to design and implement ecotype-specific, evidence-based management plans. Critically, no management recommendation that could demonstrably strengthen efforts at caribou recovery should be taken a priori off the table.

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