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Movement ecology of endangered caribou during a COVID-19 mediated pause in winter recreation

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Keywords
anthropause; woodland caribou; recreation; heli-skiing; home range; movement ecology; disturbance; resource selection.

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Abstract

The long-term conservation of species at risk relies on numerous, and often concurrent, management actions to support their recovery. Generally, these actions are habitat-based while others are focused on a species' position within its ecological community. Less studied are the impacts from human presence, despite evidence that human activity may reduce the area functionally available for occupancy or resource acquisition. In the winter of 2020/2021, COVID-19-related travel restrictions led to a reduction in helicopter-assisted back-country skiing (heli-skiing). We examined how these reductions in heli-skiing (termed the anthropause) affected the movement ecology and resource selection of southern mountain caribou (*Rangifer tarandus caribou*) as compared to two prior years (2018/2019 and 2019/2020) and the following year when heli-skiing resumed (2021/2022). We found that home-range size was on average 80–120% larger during the anthropause than in years of normal heli-ski operations. Movement rates also varied among periods, with movement during the anthropause (11.9 km^2/day) being higher than in 2019/2020 (7.8 km^2/day) and 2021/2022 (8.7 km^2/day), though similar to 2018/2019 (12.2 km^2/day). Resource selection among periods did not differ, with caribou consistently selecting old forests, high elevations and gentle terrain. These results suggest that back-country recreation, specifically heli-skiing, may be limiting access to resources for southern mountain caribou. This limitation arises through reduced home-range size within suitable late-winter habitat, relative to when heli-skiing is reduced or not occurring – consistent with Encounter Theory. While the demographic effects of reduced home-range size and movement were not examined here, reduced access to resources likely compounds other stressors known to affect population viability of caribou. The results of this study demonstrate the impact that recreation can have on wildlife and highlight the need to consider heli-skiing and other forms of recreation when developing recovery plans.

Introduction

Human activity around the globe has triggered the Earth's sixth major episode of mass extinction (Barnosky *et al.*, 2011; Davis, Faurby, & Svenning, 2018). Although the ongoing biodiversity crisis has been caused by numerous factors (e.g. invasive species, pollution, overharvest and climate change), habitat loss is consistently recognized as the primary threat to species' survival (Venter *et al.*, 2006; Woo-Durand *et al.*, 2020). Indeed, a recent assessment by Plumptre *et al.* (2021) found that the human footprint on the natural environment was estimated to affect 97% of the planet's land surface. Importantly, however, the effects of this footprint can be manifested both directly, by physical changes through the loss and degradation of ecosystems (Williams *et al.*, 2020), or indirectly, through changes to ecological processes, biodiversity loss (Mu *et al.*, 2022), altered movement (Tucker *et al.*, 2018) or the displacement of wildlife (Larson *et al.*, 2016). Consequently, wildlife may not only be impacted by permanent habitat changes but also by the presence of humans on the landscape, despite the potential for some individuals to habituate to human presence (Altmann, 1958; Boyle & Samson, 1985; Taylor & Knight, 2003; Gaynor *et al.*, 2018). Individual responses to human presence can range from short-term flight behavior (Stankowich, 2008) to long-term changes in diet patterns (Gaynor *et al.*, 2018; Lamb *et al.*, 2020), movement patterns (Tucker *et al.*, 2018; Corradini *et al.*, 2021) and resource selection (Wisdom *et al.,* 2004; Whittington *et al.,* 2022). The presence of humans in those few remaining, undisturbed areas thus has the potential to make otherwise high-quality environments unavailable to species, exacerbating the negative impacts of habitat loss.

While the effects of habitat loss on wildlife are widely known (Fahrig, 1997; Nagy-Reis *et al.,* 2021), and the cumulative effects of human disturbance on this loss are becoming increasingly clear (Polfus, Hebblewhite, & Heinemeyer, 2011; Plante *et al.,* 2018), there is limited understanding of how human presence in-and-of-itself influences the value of habitat for wildlife. This is primarily because it is difficult to disentangle the effects of temporary human presence from human-wrought physical changes to the environment, as the two tend to be highly correlated (Tablado & Jenni, 2017; Nickel *et al.,* 2020). With the increasing human population size and concurrent rise in popularity of outdoor recreation (Bowker *et al.,* 2012), it is important to improve our understanding of how human presence itself might be impacting species. To this end, we can learn from a change that occurred in 2020, when efforts to contain COVID-19 infection rates resulted in dramatic restrictions on human travel across the globe (Abu-Rayash & Dincer, 2020). This sudden restriction on human movement, termed the 'anthropause', created a unique opportunity in which the effects of human presence on wildlife could be explicitly studied (Rutz *et al.,* 2020).

Within the southern interior mountain ranges of British Columbia, southern mountain caribou (SMC) are an ecotype of woodland caribou that commonly migrate between low-elevation old-growth forests (spring and early winter) and high-elevation forests (late-winter and summer; Apps *et al.,* 2001). Historically found as far south as the 46° parallel in Idaho (Spalding, 2000), this ecotype is the most recent large mammal to become extirpated from the contiguous US (Moskowitz, 2019). Due to range contraction, population declines and low population growth rates, SMC are federally designated in Canada as Threatened (ECCC, 2014), but since 2014 the southern group of southern mountain caribou have been recommended for designation as Endangered (SC, 2002 c.29, ECCC, 2014). These population declines continue throughout their range despite efforts to protect and maintain critical habitat (The Mountain Caribou Technical Advisory Committee, 2002; ECCC, 2014; Lamb *et al.,* 2022).

An important challenge for SMC conservation occurs during the period of their winter range residency, when they occupy high-elevation habitats that are also ideal for helicopter-assisted downhill skiing (heli-skiing). While the effects of heli-skiing on caribou are not well known (but see Freeman, 2007, Huebel, 2012, Wilson & Wilmshurst, 2019), aerial disturbance (Harrington & Veitch, 1992; Luick *et al.,* 1996), noise (Perra *et al.,* 2022) and encounters with humans (Nellemann *et al.,* 2000; Whittington & Mercer, 2004) have demonstrated the effects on caribou. For these reasons, the potential of heli-skiing activities to impact caribou recovery is substantial due to the large geographic area over which heli-skiing occurs (40 000 km^2) and the similarity of these activities to other known disturbances. Other forms of backcountry recreation also occur within SMC range, but they are either managed through closures (i.e. snowmobile management areas) or restricted to smaller areas (ground-based, mechanized [cat] skiing and non-mechanized ski-touring). The location, speed and noise-levels associated with heli-skiing means that they are likely the primary human disturbance to SMC during the late-winter period.

The COVID-19 outbreak was declared a pandemic in early 2020, leading to near-simultaneous global mandates to reduce disease transmission. Similar to directives from other countries, in March, 2020, Canada closed its borders to international travel, and, in November 2020, the province of British Columbia (BC) introduced regional travel restrictions (Canada, 2021). This resulted in a severe curtailment of international recreational visitors, a key demographic for the heli-ski industry (Cloutier, 2023). These travel restrictions resulted in an unprecedented 84% reduction in skier days at HeliCat Canada member operations in 2020/2021 compared to the previous years (Helicat Canada, 2022). This near absence of heli-skiing acts as a rare experimental manipulation, against which caribou movement ecology during years of normal heli-ski operation can be compared (Rutz *et al.,* 2020). In this study, we used GPS location data collected between 2018 and 2022 for 120 individuals to investigate the extent to which movement and resource selection were impacted by the reduction of heli-skiing during the anthropause.

We hypothesized that during normal heli-ski years, caribou exist in a Landscape of Fear (Brown, Laundré, & Gurung, 1999; Clinchy *et al.,* 2016), where exposure to anthropogenic disturbance is perceived as a predation threat. Responding to this threat, we propose two non-mutually exclusive potential mechanisms by which caribou may modify their movement when exposed to heli-skiing. The first is based upon encounter rates with predators, or in the case of caribou and helicopters, perceived predators. Under this theory, animals adjust the size and/or location of their home ranges to reduce the overlap with potential predators, thereby decreasing predator encounter rates (Martinez-Garcia *et al.,* 2020; Noonan et al., 2021; Fig. 1a; Encounter Theory). The realized home range then may be smaller than is required to adequately fulfill an individual's life requisites (Burt, 1943). The second is based on the principal that animals optimize their foraging behavior against local predation risk (Brown, 1988; Smith *et al.,* 2022). When the risk of predation is low, individuals spend more time extracting resources or fulfilling life requisites. When predation threat is high, in contrast, individuals are more likely to increase vigilance, forgo foraging opportunities and flee, or seek out security cover (termed giving-up-densities, or GUDs; Brown, 1988, Bedoya-Prez et al., 2013). Perceived or real predation risk can therefore impact the functionally available amount of resources, ultimately reducing habitat quality with implications for survival and recruitment (Losier *et al.,* 2015). Because of the negative relationship between habitat quality and home-range size (e.g. Ochiai *et al.,* 2010; Bjørneraas *et al.,* 2012; Viana *et al.,* 2018), caribou foraging under the risk of predation would be forced to range over larger areas to meet their resource requirements (Fig. 1b; GUD). Both of these responses can have demographic

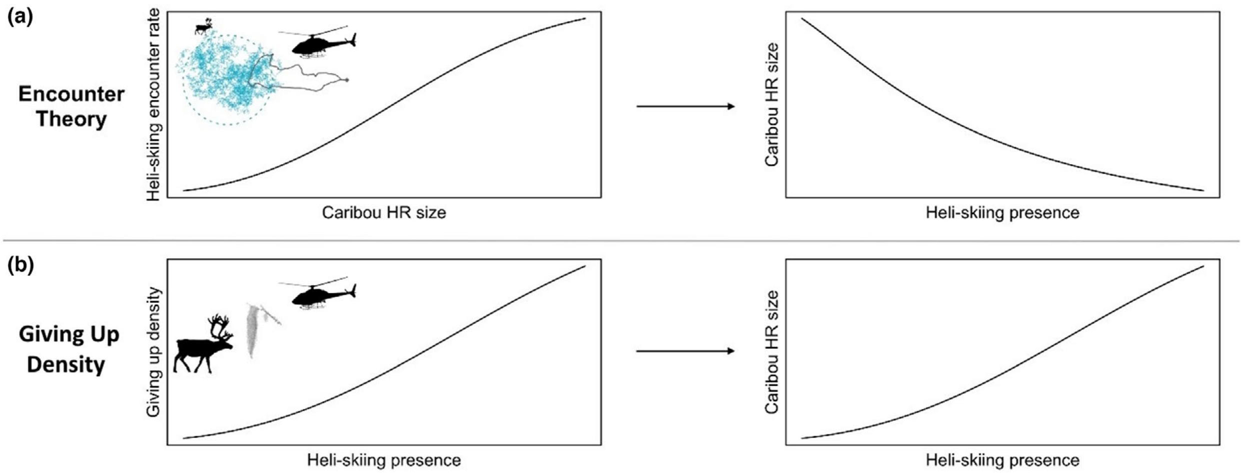


Figure 1 Conceptual diagram showing how Encounter Theory (a) and Giving Up Density (GUD) Theory (b) make counter predictions on how caribou may respond to helicopters during late-winter residency. Following Encounter Theory, caribou exposed to helicopters are expected to reduce their home range size (blue dots) to avoid helicopter flight paths (gray outlines), to reduce the probability of encountering helicopters. Under GUD Theory, caribou exposed to helicopters are expected to increase their home-range sizes as a function of not being able to exploit all of the resources (e.g. lichen) within foraging patches.

implications through a reduced amount of functionally available resources. Home-range contractions (Encounter Theory) as a result of heli-skiing activities would result in smaller home ranges that may not provide sufficient resources, while home-range expansions (GUD) would result in more movement, with proportionally less time spent foraging.

Materials and methods

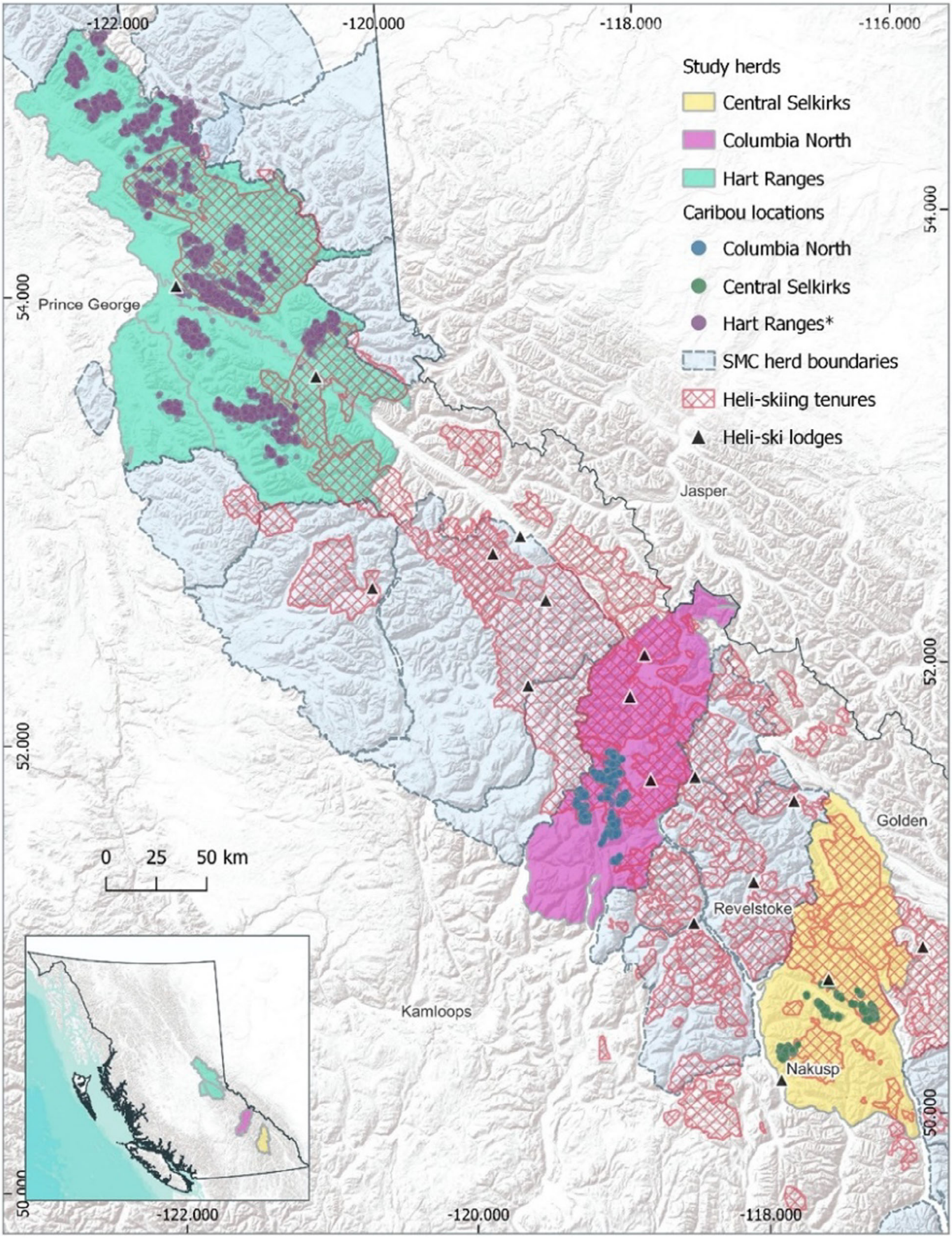
Study area

The study area encompassed moist to wet interior mountains of southern BC (Fig. 2). There are 13 extant sub-populations of southern mountain caribou – southern group (ECCC, 2014) comprised of *c*.1200 animals (BC Caribou Recovery Program, 2021). The Hart Ranges, North Caribou and Narrow Lake sub-populations (hereafter referred to collectively as Hart Ranges) occupy the mountains east of Prince George, BC, extending from near the Pine Pass in the north to Wells Gray Park in the south. The Columbia North sub-population occupies the mountains north of Revelstoke, BC. The animals in this sub-population are found throughout the Monashee, Selkirk and Rocky Mountains. The Central Selkirks herd boundary includes the mountains east of Nakusp, BC, to the Rocky Mountain trench, near Donald, BC. However, the animals in this sub-population are largely constrained to the southern portion of their range.

Quantifying habitat and anthropogenic disturbance

Our primary aim was to explore how patterns of caribou movement and habitat use differed during late-winters of the anthropause period (2020/2021) compared to years of normal heli-ski operations (two 'prior' years [2018/2019, 2019/2020], and one 'after' year [2021/2022]). We examined how changes in home-range size and movement rates differed due to the temporal effect of period but also how those home ranges may have changed with respect to spatial overlap with heli-ski tenures. For this, we required information on the characteristics of the environment these animals occupied. To this end, landscape attributes, vegetation and human disturbance were represented by raster layers. We acquired elevation data (meters above sea level) from federal repositories resampled to a 35-m resolution and projected as NAD83 BC Albers using the `R` packages `rgdal` (ver. 1.5-32; Bivand *et al.,* 2022) and `raster` (ver. 1.5-34; Hijmans *et al.,* 2022). We derived terrain variables (i.e. slope [degrees], aspect [degrees] and roughness [unitless]) from this layer using the `terrain` function in the `raster` package. Forest stand age was derived from the Vegetation Resources Inventory dataset (VRI), available from the provincial government (BC Ministry of Forests, 2020). Lastly, we generated a heli-ski tenure raster from the provincial tenure dataset (Crown Lands Registry, 2014, downloaded on February 8, 2021), which includes all approved commercial use of public lands. We subset this polygon layer to only hold heli-ski tenures, which was then rasterized with values of 1 representing areas within a tenure and 0 for those areas outside tenures.

We summarized weather data (snowfall, temperature, seasonal precipitation rates) from weather stations within the herd boundaries for each period to assess for risk of potential confounding effects on our results (data downloaded from https://aqrt.nrs.gov.bc.ca/). Weather station data were sparse, and metrics were not consistently collected among stations. For these reasons, we did not include them in the home-range analysis but examined them separately. The methods and figures are included in Section 4 of the Appendix.


-122.000
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54.000
52.000
50.000
Study herds
Central Selkirks
Columbia North
Hart Ranges
Caribou locations
Columbia North
Central Selkirks
Hart Ranges*
SMC herd boundaries
Heli-skiing tenures
Heli-ski lodges
Prince George
Jasper
Golden
Revelstoke
Kamloops
Nakusp
0 25 50 km

Figure 2 Southern mountain caribou (SMC) herd boundaries overlaid with heli-ski tenures and heli-ski lodge locations. Heli-ski tenures are polygons within which heli-skiing is permitted to operate and is specific to each commercial operation. Animals from herds neighboring the Hart Ranges (Narrow Lakes and North Cariboo) are included as Hart Ranges animals. Collar locations used in the study are shown as points colored to represent the herd to which they belong.

Collaring and monitoring

This study used data collected by the Government of BC from female caribou fitted with GPS collars to monitor population status and trends (Table 1). Individuals were monitored for various periods between 2018 and 2022. Caribou from the Hart Ranges and Central Selkirks were collared and released at the capture location; some animals from the Columbia North herd, examined in this study ($n = 12$), were sedated and transferred to a maternity pen where they were collared and housed until *c.* 5 weeks post-calving (Serrouya *et al.,* 2021). In this context, we note that maternity penning has been shown to affect home-range location and seasonal elevation occupancy, but no substantial impacts on caribou ranging behavior were detected (Ford *et al.,* 2022).

Caribou were fitted with GPS-enabled collars programmed to obtain locations every 13 hours. Each collar also transmitted a VHF signal for a period of time each day to facilitate recovery or mortality investigations. The make and/or models of collars deployed among herds and among years varied (see Serrouya *et al.,* 2021). For the Hart Ranges, Lotek Iridium and ATS Iridium collars were deployed on animals in 2018 and 2019, and Vectronic Iridium collars were deployed in 2020 and 2021 (M. Klaczek, pers. comm). The Columbia North and Central Selkirk animals were fitted with Vectronic Globalstar collars since 2018. Collars were deployed using recommendations from the provincial wildlife veterinarian and followed animal-care guidelines.

Data pre-processing

We subset the GPS data to the annual periods (winters of 2018/2019, 2019/2020, 2020/2021 or 2021/2022) and the season of interest. Due to the variability among herds, both annually and seasonally, the start and end dates for late-winter range residency were estimated for each herd and for each period separately (see Appendix S-1). We assessed each subset for location and speed outliers using the function `outlie` in the `ctmm` package in R (ver 1.1.0, Fleming *et al.,* 2022). Locations were considered outliers if they had a large distance from the median location and if the minimum speed required to explain the displacement was greater than the maximum expected movement distance for woodland caribou during late-winter of 5 km/day (±0.415) (Ferguson & Elkie, 2006). Any location that required a movement speed greater than 10 km/day from its last fix was therefore considered an outlier. In addition, we considered location measurement error in all of our analyses using the Dilution of Precision (DOP) values, which quantify the accuracy of each positional fix. As DOP values are unitless, we estimated a User Equivalent Range Error (UERE) from DOP values at mortality locations where the collar was known to be stationary. This conversion allowed the DOP values to represent estimates of measurement error in meters (Fleming *et al.,* 2021). We used these values as absolute error estimates for each fix when quantifying home ranges and movement metrics, thereby allowing the inclusion of 271 locations that had high DOP values or would otherwise have been considered potential outliers. Using the threshold of movement speed $> = 10$ km/day, we removed 2725 (Columbia North: 474, Central Selkirks: 212, Hart Ranges: 2039) locations as outliers. Constraining caribou locations to late-winter range for each herd, for each period, and removing outliers and mortality locations resulted in a dataset comprising 15 958 points from 120 individuals (Columbia North: 23, Central Selkirks: 12, Hart Ranges: 85; see Table S-1.1).

Table 1 The number of active collars throughout the study period for each herd

	Number of collars monitored annually				
Herd	2018/ 2019	2019/ 2020	2020/ 2021	2021/ 2022	Total individuals
Hart Ranges	43	40	47	24	85
Columbia North	12	12	9	13	23
Central Selkirks	6	10	7	4	12

Because many animals were monitored for more than one period, the total number of individuals monitored does not equal the sum of the total number of animals across each of the periods. Animals from herds neighboring the Hart Ranges herd (Narrow Lakes and North Cariboo) are included as Hart Ranges animals.

Late-winter home-range analysis

We first estimated 95% home-range areas for each individual separately for each period (2018/2019, 2019/2020, 2020/2021 and 2021/2022) using autocorrelated kernel density estimation (AKDE; Fleming *et al.,* 2015) via the `ctmm` R package. Because AKDE corrects for differences in autocorrelation (Noonan *et al.,* 2019), sampling (Fleming *et al.,* 2018) and measurement error (Fleming *et al.,* 2021), it allows for reliable comparisons across years, populations and devices. Each winter period is defined.

We fit a generalized linear mixed-effects model (glmm) with a Gamma distribution and log link to examine how heli-skiing, environmental factors and the anthropause influenced caribou home-range size. Covariates were examined for collinearity prior to fitting a global model to the data using the `corrplot` function from the `corrplot` package (Wei & Simko, 2021). Variables were considered correlated if the `corrplot` function returned a value > 0.70 or < -0.70 (Dormann *et al.,* 2013). The final global model was fit to the data using the R package `lme4` (ver. 1.1-28 (Bates *et al.,* 2022)) and was of the form:

$$\mathrm{HRper\tilde{i}od} + \text{tenure overlap} + \text{elevation} + \text{slope} \\ + \text{forest age} + (1|\text{herd}/\text{ID})$$

where ‘HR’ represents home-range area in km^2, ‘period’ is a categorical variable representing each of the winter periods (2018/2019, 2019/2020, 2020/2021 and 2021/2022), ‘tenure overlap’ represents the proportion of each home range that fell within a heli-ski tenure, ‘elevation’ is the mean-centered and scaled elevation, slope is the mean, mean-centered and scaled slope of each caribou’s home range, and ‘age’ is the mean-centered and scaled age of forested stands within each home range. The term ‘1 | herd / ID’ defines the random intercept structure of the model, which controls for the hierarchical data structure (individuals nested within herds). In this case, we were controlling for differences in baseline behavior between individual caribou, as well as variability between the three different subpopulations. We then evaluated candidate models, considering those parameters which have been shown to influence resource selection and space use (Apps *et al.,* 2001). We identified the best-fit model based on small-sample-size corrected Akaike’s Information Criterion (AIC$_c$) values while considering ecological variables that also contribute to home-range size.

We assessed movement within home ranges by estimating the mean rate of movement of each animal (or rate of diffusion, in km^2/day). Diffusion rates were estimated using the methods implemented in the `ctmm` package and are proportional to the area over which an animal can be expected to range on an average day. Diffusion was modeled as a function of the same habitat and human disturbance variables as for home range analysis using a glmm with a Gamma distribution and a log link, defining the global model:

$$\mathrm{Diffusionper\tilde{i}od} + \text{tenure overlap} + \text{elevation} + \text{slope} \\ + \text{forest age}(1|\text{herd}/\text{ID}).$$

Here again, we used AIC$_c$-based model selection to identify the best-fit model.

Modeling resource selection

We modeled resource selection to examine how individuals selected for or against specific habitat features within their home ranges and how that differed among periods. Resource selection was assessed using integrated resource selection functions (iRSF) implemented in the `rsf.fit` function from the `ctmm` package, which is functionally equivalent to an inhomogeneous Poisson point-process model. Separate iRSFs were fitted to the late-winter location data for each individual caribou for each period. Locations within each 95% home-range estimate were used as the known locations, while the `rsf.fit` function, generated randomly distributed non-detections (i.e. the quadrature points). The `rsf.fit` function does not require a pre-defined number of pseudo-absences; rather it specifies a target standard error, here 0.01, and generates an increasingly large sample of points (on the order of thousands to tens of thousands) until this threshold is reached (Alston *et al.,* 2022). Furthermore, the ‘available’ area (i.e. the sampling window) is jointly estimated with the selection coefficients and was therefore not specified.

For this analysis, we considered the same explanatory variables as per our previous models, namely, terrain attributes (elevation, slope), productivity (forest age) and human disturbance (heli-skiing tenures). Elevation and slope were mean-centered and scaled prior to analysis. No landscape disturbance variables were included in these analyses, as their effects are consistent among years, and likely attenuated by the deep snow of the late-winter period and high elevations of these home ranges. Population-level patterns in resource selection were then obtained by averaging the individual coefficients and their associated uncertainty using the meta-regression models implemented in the R package `metafor` (Viechtbauer, 2022, ver. 3.8-1).

Results

Heli-skiing reduced caribou home-range sizes

Our analyses revealed that late-winter caribou home range and movement during the anthropause (in 2020/2021) differed significantly from years of normal heli-ski operations. Modeling home-range size as a function of time period, landscape and tenure overlap, and controlling for individual and herd-specific differences in behavior, we found that home-range sizes tended to be significantly smaller in the years of normal heli-skiing operations (Fig. 3a,b). The selected model included elevation, slope, forest age and period but excluded the spatial effect of tenure overlap. The full model was the second best fit (ΔAIC 2.22; see Table S-1.3), and the null model scored the lowest using small-sample-size corrected AIC values. The next best-fitting model that did not include the effect of the anthropause period resulted in a ΔAIC of 13.4.

Compared to the anthropause, we found that among all periods the negative relationship between home-range size and heli-ski operations was significant (2019/2020 $P = 0.002$ $\beta = -0.56$, CI: -0.91, -0.20, 2018/2019 $P \leq 0.001$, $\beta = -0.79$, CI: -1.20, -0.37, 2021/2022 $P = 0.002$, $\beta = -0.60$, CI: -0.99, -0.21). The mean home range size during the anthropause (2020/2021–169 km^2) was between 80 and 120% greater than in any of the other periods (2018/2019–77 km^2, 2019/2020–97 km^2, 2021/2022–93 km^2).

The best-fit model also indicated that home range decreased with increasing slope ($P = 0.002$, $\beta = -0.87$, CI: -1.42, -0.32, Fig. 3c), elevation ($P < 0.001$, $\beta = -1.50$, CI: -2.07, -0.94, Fig. 3d) and forest age ($P = 0.02$, $\beta = -0.52$, CI: -0.96, -0.08, Fig. 3e). The spatial effect of heli-ski tenure (tenure overlap) on SMC late-winter home-range size was non-significant, and the magnitude of the difference

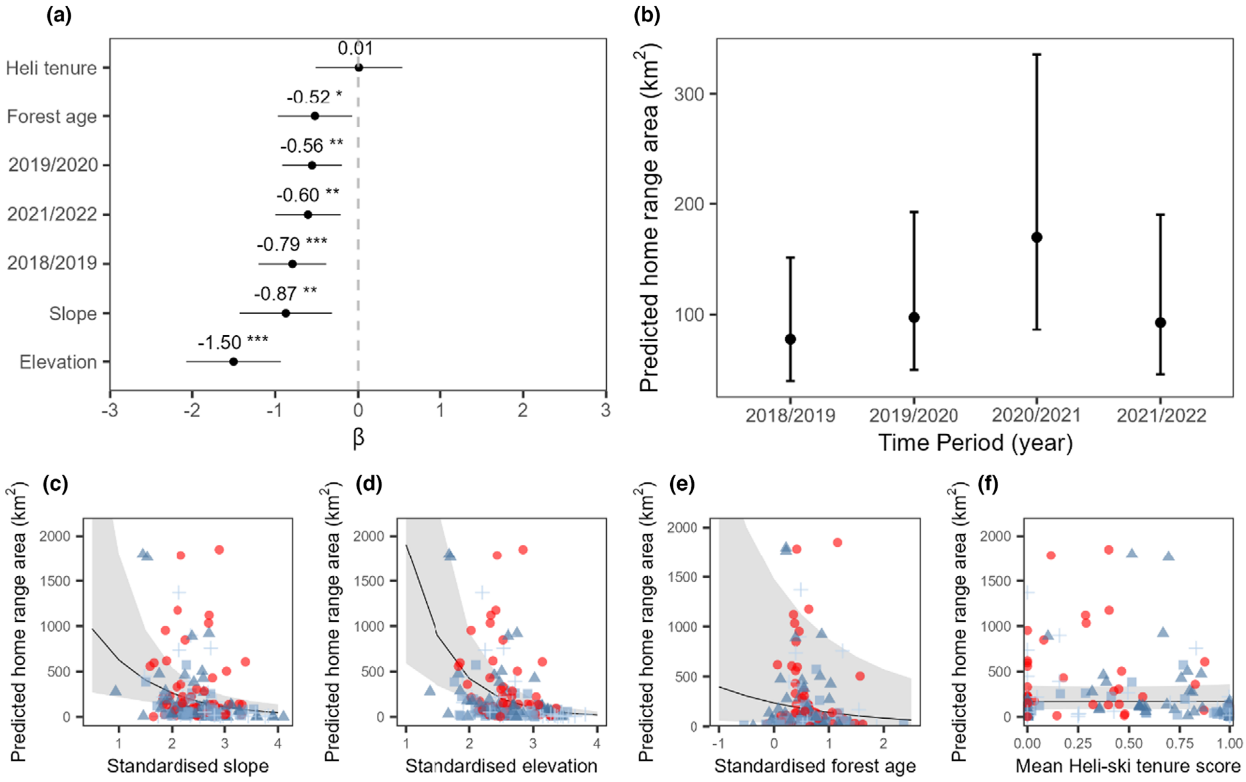

Figure 3 Results of the generalized mixed linear effects model examining home-range area as a function of period, habitat variables and heli-ski tenure overlap. The anthropause period (2021) is used as the reference year, against which the other periods are compared so it does not appear in panel a. Panel a) shows the parameter estimates (β) ±95% confidence intervals (CIs). Panel b shows the home-range predictions ±95% CIs. Panels c through f show the regression line and estimates for each parameter. Shape and color of empirical data represent each period (blue square = 2018/2019, blue triangle = 2019/2020, red circle = anthropause, blue cross = 2021/2022).

was near 0 ($P = 0.97$, $\beta = 0.008$, CI: -0.51, 0.53, Fig. 3f). Notably, an examination of the weather conditions among years showed an expected degree of inter-annual variability, but the 2020/2021 anthropause period was neither an outlier with regard to total snowfall (Fig. S-1.4), temperature (Fig. S-1.5), nor seasonal precipitation rates (Fig. S-1.6).

Heli-skiing reduced caribou movement rates

When examining movement rates within home ranges among periods, we found patterns that broadly mirrored the trends in home-range areas. Caribou diffusion rates varied among years, and modeling these effects, we found significant differences in diffusion rates between years (Fig. 4b). Model selection identified the top model as that which included only the effects of the anthropause-induced reductions in heli-skiing and slope as covariates underpinning caribou diffusion rates (see Table S-1.4). The full model ranked 7th using small-sample-sized AIC values, with a ΔAIC of 3.58. The next best-performing model that did not include the anthropause effect was ranked 8th, with a ΔAIC of 10.78 (Table S-1.4), indicating very little support for models that exclude this effect.

Compared to the anthropause, caribou tended to move less in 2019/2020 ($P = 0.001$, $\beta = -0.42$, CI: -0.17, -0.67) and 2021/2022 ($P = 0.028$, $\beta = -0.31$, CI: -0.67, -0.17) but not 2018/2019 ($P = 0.836$, $\beta = 0.028$, CI: -0.24, 0.30). Increasing slope reduced diffusion rates ($P < 0.001$, $\beta = -0.72$, CI: -1.06, -0.37, Fig. 4c), but elevation ($P = 0.60$, $\beta = -0.09$, CI: -0.44, 0.25, Fig. 4d), forest age ($P = 0.21$, $\beta = -0.20$, CI: -0.51, 0.11, Fig. 4e) and tenure overlap ($P = 0.24$, $\beta = 0.22$, CI: -0.14, 0.59, Fig. 4f) did not. The magnitude of change in movement rates was smaller than for changes in home ranges, with SMC diffusing across 11.9 km^2/day during 2020/2021, as compared to more movement in 2018/2019 (12.2 km^2/day) and less movement in 2019/2020 (7.8 km^2/day) and 2021/2022 (8.7 km^2/day).

Heli-skiing had little effect on caribou resource selection

Patterns in late-winter resource selection were consistent across years, with caribou selecting higher elevations, older forests and lower angle slopes in greater proportion to their availability, with no apparent differences in selection among periods, based on overlapping 95% confidence intervals (Fig. 5). Caribou also showed no selection for or against

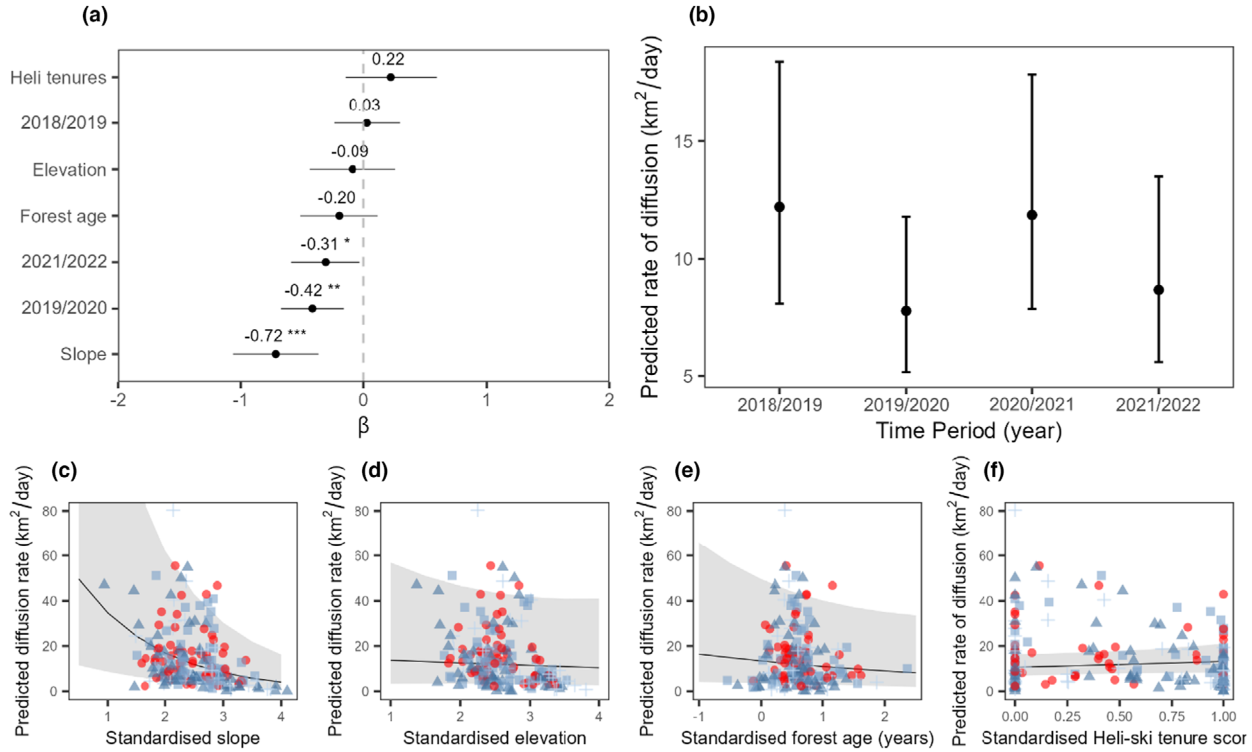

Figure 4 Results of the generalized mixed linear effects model examining rate of diffusion as a function of period, habitat variables and heli-ski tenure overlap. Panel a shows the parameter estimates (β) ±95% confidence intervals (CIs), panel b shows the diffusion predictions ±95% CIs. Panels c-f show the model predictions ±95% CIs, in black and gray respectively, overlaid on the empirical data. Shape and color of empirical data represent each period (blue square = 2018/2019, blue triangle = 2019/2020, red circle = anthropause, blue cross = 2021/2022).

heli-ski tenures once established on their high-elevation, late-winter range.

Discussion

In this study, we leveraged the unique conditions created by the COVID-19-mediated anthropause to examine the relationship between human recreation (in this case heli-skiing) and caribou movement ecology. Our analyses revealed that caribou home ranges were significantly larger during the late-winter period while COVID-19 restrictions were in place and heli-skiing was reduced (2020/2021), as compared to the 2 years preceding the anthropause period when heli-skiing was operating normally (2018/2019 and 2019/2020). Furthermore, in the year following the anthropause (2021/2022), heli-skiing resumed, and caribou home ranges were again reduced in size. These results lend support to the Encounter Theory hypothesis (Martinez-Garcia *et al.*, 2020) that caribou are restricting their movements within late-winter range to avoid encounters with activities associated with heli-skiing.

The effects of heli-skiing on caribou space use

As prey species move through landscapes, theory predicts that they attempt to optimize the energetic returns for the time invested in foraging (Charnov, 1976), while also minimizing the risk of predation (Hernández & Laundré, 2005; Noonan *et al.*, 2023). This behavioral trade-off has been refined over evolutionary timescales, and, for caribou, is manifested in a life-history strategy that depends on spatial separation from their natural predators (James, 1999; Wittmer, McLellan, & Hovey, 2006). Consequently, caribou tend to occupy low-productivity landscapes where predator densities and the risk of predation are reduced (Johnson *et al.*, 2002), but energetic costs can be high (Fancy & White, 1987). Our results indicate that partial refugia afforded by low-productivity areas are being further constrained by back-country recreation, likely not only limited to heli-skiing (Freeman 2007, Seip, Johnson, & Watts, 2007). Given our findings that caribou ranged more widely in the absence of heli-skiing, it is possible that the smaller home ranges to which they are restricted during years of normal heli-ski operations are also affecting resource availability and carrying capacities. The impacts of this constraint on caribou fitness are currently unknown, but smaller restricted home ranges have been associated with lower survival of adult female caribou (MacNearney *et al.*, 2016; Williams *et al.*, 2021). Furthermore, the energetic demands of a deep snow environment compounded by a low nutrition winter diet (Rominger, Robbins, & Evans, 1996), with avoidance or flight responses to disturbance (Webster, 1997; Freeman, 2007; MacNearney *et al.*, 2016; Lesmerises *et al.*, 2018), suggest the

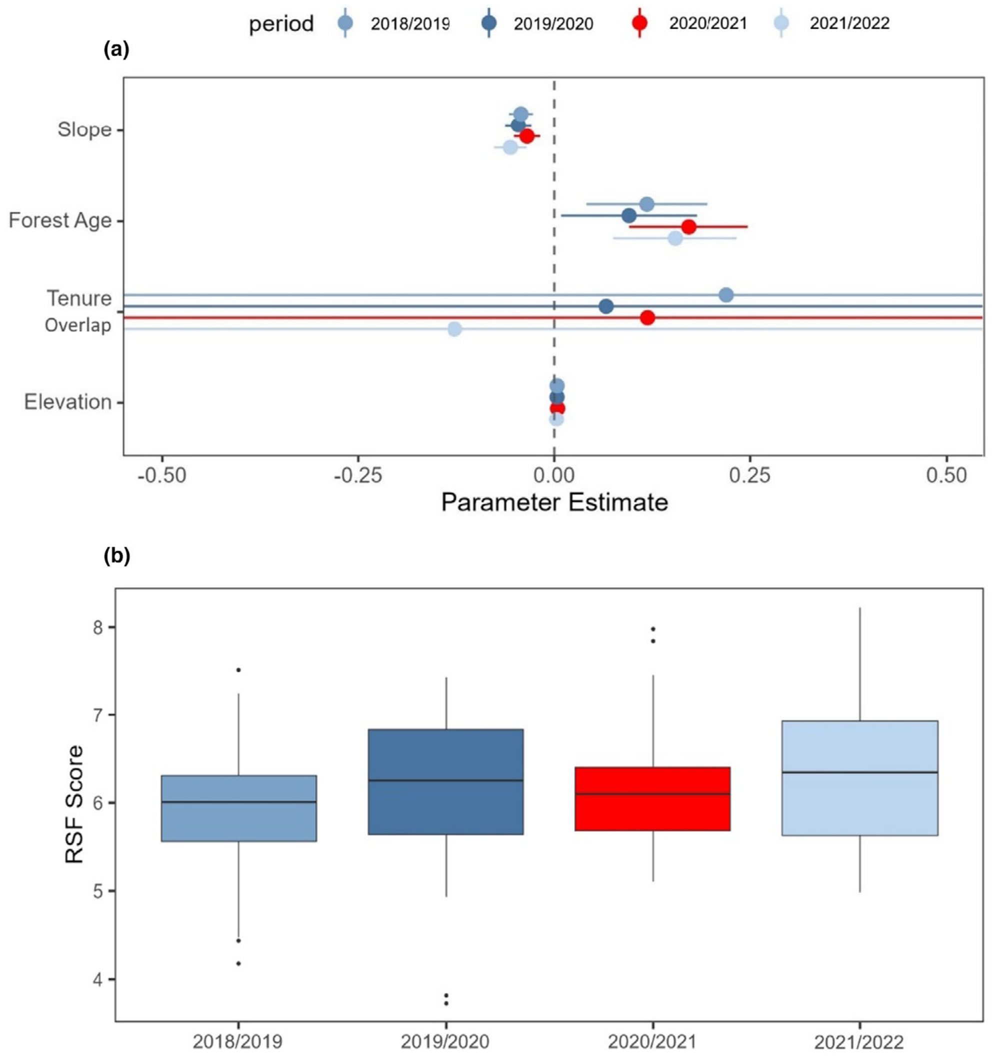

Figure 5 Estimates for each parameter used to fit an integrated resource selection function (iRSF) to caribou home range size (panel a). Each estimate has an associated confidence interval, but most intervals are very small, with the exception of heli-ski tenure overlap. Heli-ski tenure overlap confidence intervals extend beyond the figure limits and or display purposes, are truncated at the margins. Boxplots of average resource selection function score for occurrence distributions among periods (panel b). The year of the anthropause (2021) is shown in red.

potential for caribou to experience resource deficits when their ranges are artificially contracted. This potential restriction of resources could cause reductions in body condition or survival. Indeed, measurements of body condition conducted during capture of caribou from the Columbia North sub-population for the Revelstoke maternal penning project revealed that 56% of the captured caribou had <6% body fat, a level that has implications for survival depending on the progression of spring in a given year (Serrouya *et al.,* 2021). Notably, while heli-ski lodges exist at very low densities on the landscape, the Columbia North caribou occur within the highest density of heli-ski lodges of the sub-populations considered in this study (see Fig. 2). Restrictions in movements may also have direct demographic consequences, for example the ecological trap described for some SMC that previously migrated annually to low-elevation winter ranges and now restrict their movements to higher elevation (Williams *et al.,* 2021). Evaluating these potential demographic effects represents an important next step in considering the impact of human recreation on this vulnerable species.

Patterns of late-winter resource selection for slope, forest age and elevation did not differ among periods. The late-winter habitat use by SMC is generally characterized by high-elevation, old-growth forests which support high levels of the arboreal lichen upon which they feed (Stevenson & Hatler, 1985; Terry, McLellan, & Watts, 2000; Apps *et al.,* 2001). These habitats also emerged as important across all years in our study, irrespective of heli-ski activity. Caribou used tenures differently across years but showed no selection for or against heli-ski tenure among all periods, and there was substantial variation in this selection. The stable patterns of habitat selection across years indicate that the resources used by caribou during the anthropause were of the same quality as those used during years of normal heli-skiing. This pattern in selection suggests that home range expansion was associated with increased access to the key resources needed to meet fitness demands (Ochiai *et al.,* 2010; Bjørneraas *et al.,* 2012; Viana *et al.,* 2018).

We also found no evidence for a spatial relationship between heli-ski tenure overlap and home-range size. Notably though, heli-skiing does not occur uniformly across tenures, both spatially and temporally, and our binary classification of within versus outside of a tenure is less informative than the finer-scale, actual use by helicopters and skiers within those tenures would be. The lack of available information on the spatial distribution of heli-ski activity, due to reluctance by heli-ski operators to share these data, resulted in insufficient resolution to detect changes in the spatial effect of tenures of caribou. In other words, although we found evidence that heli-skiing may be impacting caribou movement ecology through our temporal analyses, we could not determine the spatial scale over which this effect may be occurring. Despite this, similar activities have demonstrated effects on caribou space use and behavior (Harrington & Veitch, 1992; Nellemann *et al.,* 2000; Reimers, Eftestøl, & Colman, 2003; Whittington & Mercer, 2004). Acquiring finer-scale movement data, along with data on heli-ski run use (as per Huebel, 2012) may provide insight into the mechanisms behind any anthropogenically driven resource selection, and inform ways to support efforts to mitigate impacts on this endangered species. Notably, caribou to exhibit similar responses to other forms of mechanized and non-mechanized back-country recreation (Nellemann *et al.,* 2000; Reimers *et al.,* 2003; Lesmerises *et al.,* 2018). Future work examining the finer-scale movements of both recreationalists and SMC is clearly needed to understand whether the effects seen elsewhere (Reimers *et al.,* 2003; Whittington & Mercer, 2004; Lesmerises *et al.,* 2018) are also acting on SMC.

Conservation implications

Southern mountain caribou are federally listed as threatened under the Species at Risk Act (SC, 2002, c.29) and have been declining across their range for most of the last century (Spalding, 2000). Management actions to maintain populations (Lamb *et al.,* 2022), preserve (Nagy-Reis *et al.,* 2021) or restore (Dickie *et al.,* 2017 [boreal caribou]) habitat, or manage trophic webs (Serrouya *et al.,* 2017, 2019) have had positive effects. However, the recent extirpations of caribou from the entire continental US, much of southern BC, and within Banff and Jasper National Park (Hebblewhite, White, & Musiani, 2010; Johnson, Ehlers, & Seip, 2015), indicate that current efforts are still proving insufficient to reverse the continued decline of this iconic and culturally important species. While loss or alteration of caribou habitat presents an ongoing threat to this eco-type, our findings suggest that back-country recreation is further reducing the functional value of otherwise high-quality habitat, which could diminish the benefit of these other conservation efforts (Wittmer *et al.,* 2007).

A review of management objectives (Boutin & Merrill, 2016) recognizes the potential effects of mechanized backcountry recreation on SMC but does not directly propose management initiatives to mitigate those effects. Between 2014 and 2017, heli-skiing in BC operated under a memorandum of understanding (MoU) between operators and the province (MFLNRORD and Helicat Canada, 2014). This MoU specified that within the confines of what is considered operationally safe, helicopters must maintain a 500-m separation distance from caribou observed during any flight. Furthermore, if caribou were detected, heli-skiers were to avoid those areas for 48 hours. The MoU expired in 2017, however, and has not been renewed since, so we were unable to directly evaluate its effectiveness. However, we assume here that heli-ski operators have continued to fulfill the requirements of this MoU to some extent in anticipation of revised wildlife guidelines with similar constraints. Under this assumption, our findings support the conclusion that the 500-m distance contained in the MoU may not be sufficient to mitigate the negative effects of heli-skiing on caribou. Under current operations, caribou appear confined to smaller areas than they might otherwise occupy, and we, therefore, suggest that protocols for mitigating any disturbance to caribou by heli-skiing should be revisited. In the absence of known, currently implemented mitigations, the precautionary approach for this endangered species would be restrict back-country recreation in areas of high-quality caribou habitat.

Conclusion

Southern mountain caribou are susceptible to multiple stressors. While many causes of their declines are well documented (Wittmer, Sinclair, & McLellan, 2005; Festa-Bianchet *et al.,* 2011; Nagy-Reis *et al.,* 2021), less is known about the transitory, indirect effects of human presence on this species. Our results demonstrate how caribou contract their late-winter home ranges in response to heli-skiing, occupying smaller areas than they might otherwise. They also echo global studies reporting responses of wildlife to the pandemic-induced anthropause, from increased wildlife sightings (Zellmer *et al.,* 2020), to changes in behaviors (Behera *et al.,* 2022). While we could not quantify a mechanistic link between reduced home-range sizes and caribou declines, small home ranges do make the population more susceptible to extirpation via stochastic events such as avalanches (Flaa & McLellan, 2000), extreme weather or years of locally poor food availability. These findings demonstrate the need to better manage back-country recreation in southern mountain caribou late-winter habitat in order to support ongoing recovery efforts.

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Author contributions

Ryan Gill (RG), Robert Serrouya (RS) and Michael Noonan (MJN) conceived of the study, RG and MJN conducted the analyses and wrote the first manuscript draft. All co-authors assisted with writing the final version of the manuscript.

Competing interests

Authors declare that they have no competing interests.

Data availability statement

The R scripts used to carry out this study, as well as the movement metrics derived from the location data, are openly available on GitHub at https://github.com/rygill/caribou_movement_ecology. Due to the sensitive nature of the GPS location data used in this study, they are not openly available, but access may be granted through application to the BC provincial Knowledge Management Branch.

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Supporting information

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

Appendix S1 Supporting analyses and information for the results presented in 'Movement ecology of endangered caribou during a COVID-19 mediated pause in winter recreation'.