RESEARCH ARTICLE

Habitat loss on seasonal migratory range imperils an endangered ungulate

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Abstract

1. Endangered species policies and their associated recovery documents and management actions do not always sufficiently address the importance of migratory behaviour and seasonal ranges for imperilled populations.

2. Using a telemetry location dataset spanning 1981–2018, we tested for changes in prevalence of migratory tactics (resident, migrant) over time, switching between tactics, shifts in seasonal space use including migration corridors, and survival consequences of migrant and resident tactics for 237 adult female endangered woodland mountain caribou in one population in western Canada.

3. Over more than three decades, the proportion of individuals displaying annual migration to the low elevation forested winter range declined from nearly 100%–38%. Correspondingly, there was a strong switch away from being migrant to being year-round residents at high elevation.

4. These behavioural changes corresponded to abandonment of low elevation winter ranges in association with increasing levels of anthropogenic land uses, including forestry and oil and gas developments. Furthermore, there were no identifiable migration corridors to target for migratory route protection.

5. These shifts translated to lower survival rates, particularly for caribou demonstrating resident tactics, consistent with recent declines of the caribou population. That migrants switched to residency in their largely undisturbed summer range, despite lower survival, indicates maladaptive habitat selection consistent with recent patterns of mountain caribou extirpations.

6. Globally, endangered species policies and their associated recovery plans and management actions often do not explicitly consider the challenge of protecting migratory species. Effective conservation of migratory species requires protecting critical

habitats needed for the entire life history of the species, including all seasonal ranges and migratory habitat.

KEYWORDS

Ecological trap, habitat loss, migration, *Rangier tarandus caribou*, survival, woodland caribou

1 | INTRODUCTION

Migration is a crucial ecological phenomenon that contributes to maintaining biodiversity, supports populations of many species, and connects ecosystems across spatial scales (Bauer & Hoye, 2014; Dingle, 1996; Milner-Gulland, Fryxell, & Sinclair, 2011). However, across the globe, species that migrate are disproportionately vulnerable to extinction, threatening the persistence of this behaviour and its ecological functions (Berger, 2004; Bolger, Newmark, Morrison, & Doak, 2008). There are notable examples of government policies and laws to accommodate migratory species, such as the North American Migratory Bird Convention and associated legislation. Yet, for many migratory species, important migration areas and habitats are not conserved or adequately managed. This can occur due to a lack of information on migratory behaviour and its demographic benefits, and due to challenges in implementing conservation strategies across jurisdictional boundaries (Bolger et al., 2008; Milner-Gulland et al., 2011; Pierce, Bleich, Wehausen, & Bowyer, 1999).

Migratory terrestrial species could benefit from approaches that identify and conserve seasonal ranges and migration corridors (Berger, 2004; Bolger et al., 2008; Seidler, Green, & Beckmann, 2018). For example, 20 years ago researchers in Wyoming identified a 160-km pronghorn (*Antilocapra americana*) migration route extending from Grand Teton National Park into unprotected lands threatened by energy and housing development (Sawyer & Lindzey, 2000). Berger and Cain (2014) highlighted the conservation difficulties associated with protecting this population's well defined, but narrow, migratory route and seasonal ranges, which together, span multiple land ownership and management types. Identification of this migration route and emphasis of its importance has led to numerous protections (Kauffman et al., 2018), yet the migration route and seasonal ranges are still not yet protected in entirety. Summer range was protected because of its location within a national park, and the migratory route itself benefited from a suite of conservation measures; yet habitat degradation on winter range continued (Middleton et al., 2020; Sawyer, Beckmann, Seidler, & Berger, 2019). This case study highlights the need to consider different threats and solutions on the entire seasonal migratory cycle for such species.

Other terrestrial mammal migrations have fewer protective measures than the pronghorn example, and future conservation will be unsuccessful unless key conditions are met. First, conservation of all seasonal ranges needs to be a core element of a migratory conservation strategy (Johnstone et al., 2020; Kauffman et al., 2018; Peters et al., 2019). In the pronghorn case, one seasonal range and the migration corridor benefitted from various protections, although erosion of the winter range continued, eventually resulting in altered pronghorn behaviour and possible demographic consequences (Sawyer et al., 2019). For other species, protections focus on one or more seasonal ranges, but the land used during migration itself is overlooked (Runge et al., 2015). Second, conservation of static migration corridors and stopovers will only be effective if animals consistently use defined migration corridors and stopovers. Again in the pronghorn example, individuals in this population used a narrow corridor with high fidelity (Middleton et al., 2020), but this is not the case for other species and populations. Studies show that some terrestrial mammals demonstrate variation in migratory tactics (e.g. timing of migration and route an individual uses) within populations and among years (Berg, Hebblewhite, St. Clair, & Merrill, 2019). For ungulates in particular, flexibility in migratory behaviour frequently results in uncertainty in the extent to which migration corridors are predictable; individuals within a population use different routes, and the route any individual uses may vary over time (Bolger et al., 2008; Cagnacci et al., 2016). Thus, while terrestrial mammal migratory populations are globally threatened, usually by anthropogenic land use (Berger, 2004; Dobson et al., 2010; Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009), the inherent variability of migratory behaviour can often make meeting these key conditions challenging.

Caribou (*Rangifer tarandus*) populations demonstrate some of the most pronounced migratory behaviours among ungulates (Joly et al., 2019), and the species is threatened and declining across North America (Festa-Bianchet, Ray, Boutin, Côté, & Gunn, 2011; Hervieux et al., 2013; C. J. Johnson, Ehlers, & Seip, 2015; Wittmer, McLellan, Serrouya, & Apps, 2007). Yet, within and across caribou populations, there is wide variability (Gurarie et al., 2019). Migratory behaviour varies between barren-ground caribou, where individuals migrate 1,000's of kilometres; mountain woodland caribou, which migrate between alpine habitats and low elevation forests; and sedentary boreal woodland caribou (Joly et al., 2019). Boreal and mountain caribou are increasingly threatened by anthropogenic land use change (e.g. C. J. Johnson et al., 2015; Palm, Jacob, Fluker, Nesbitt, & Hebblewhite, 2020; Wittmer et al., 2007), and the majority of woodland caribou populations are declining (Festa-Bianchet et al., 2011) with many notable recent extirpations. The causes of these declines are anthropogenic, resulting from direct and indirect habitat loss, increased efficiency of predators, and altered food-webs, which negatively affect caribou through apparent competition (Holt, 1977; Serrouya et al., 2019; Wittmer et al., 2007). Conservation of woodland caribou is one of North America's most pressing management issues, affecting boreal biodiversity conservation and carbon sequestration through the role of caribou as an umbrella species for both (Bichet, Dupuch, Hébert, Le
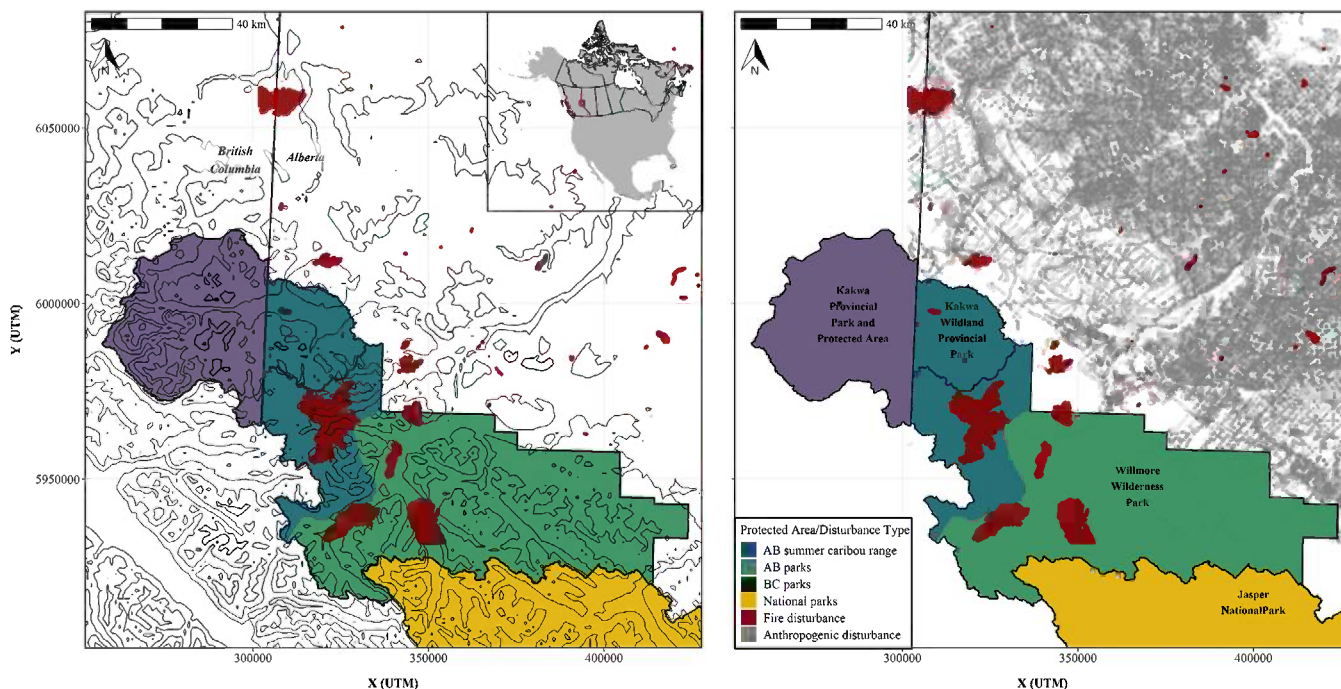
FIGURE 1 Study area in western Alberta/eastern British Columbia showing (left panel) elevation contour and (right panel) showing protected areas, fire disturbance and anthropogenic disturbance (buffered by 500 m)

Borgne, & Fortin, 2016; Bradshaw, Warkentin, & Sodhi, 2009; Yona, Cashore, & Schmitz, 2019). Their conservation is complex in consideration of the large economic benefits available from the exploitation of natural resources in and adjacent to woodland caribou ranges (Hebblewhite, 2017).

Woodland caribou conservation and recovery is mandated nationally in Canada through the federal *Species At Risk Act* (SARA; Government of Canada). Like many endangered species policies globally, associated recovery strategies contain the central elements of identification and conservation of critical habitat (defined as the habitat necessary for the survival or recovery of a listed species) for woodland caribou. For the Southern Mountain woodland caribou, critical habitat is identified as a specified minimum level of undisturbed habitat measured at landscape levels across low elevation winter ranges, high elevation winter and/or summer range, biophysical habitat attributes, and a concept of matrix range that includes low use, possible migration ranges, and specific predator-prey conditions (Environment Canada, 2014).

Almost all mountain woodland caribou were historically migratory, using mountainous high elevation areas during the summer, and lower elevation forested foothills during the winter (McDevitt et al., 2009). Anthropogenic-caused habitat loss, particularly clustered in low elevation areas, has reduced caribou distribution, altered resource selection, and reduced overall survival (e.g. Decesare et al., 2012; MacNearney et al., 2016). Anthropogenic disturbance occurs as both polygonal (e.g. cut blocks, fires) and linear (e.g. seismic lines, roads) features and impact caribou in varying ways. Removal of large sections of mature and old forest directly removes (direct habitat loss) forage critical for overwinter survival (Decesare et al., 2012; Wittmer et al.,

2007). Moreover, early seral forage promoted by cutblocks enhances forage availability for moose and deer, leading to increases in primary prey abundance and subsequently, predator population growth (Seip, 1992; Serrouya, McLellan, Boutin, Seip, & Nielsen, 2011). Simultaneously, linear disturbances increase predator efficiency at searching for, encountering, and killing caribou (Spangenberg et al., 2019; Whittington et al., 2011). In response, caribou attempt to avoid anthropogenic disturbances, leading to indirect habitat loss, and yet are still often unsuccessful at predator avoidance. As a result, woodland caribou populations experience lower adult and juvenile survival (Decesare et al., 2014), leading to population declines across North America (C. A. Johnson et al., 2020; Serrouya et al., 2019). For mountain woodland caribou, lower elevation ranges are frequently subjected to higher human disturbance, and avoidance of disturbance at low elevation winter range may lead to residency in lower quality, higher elevation summer ranges year-round (Edmonds, 1988). Such high elevation ranges are inherently lower quality (Decesare et al., 2014) because available forage is often covered by unfavourable snow conditions, increased wind and colder temperatures, and risk of fatal avalanches in mountainous regions (Hebblewhite, White, & Musiani, 2010). Yet, few studies have explicitly tested how differential anthropogenic development of seasonal ranges of migratory caribou affects behaviour and demography.

Here, we used a long-term dataset spanning more than three decades, 1981 – 2018, to understand consequences of increasing anthropogenic disturbance on migratory behaviours and adult female survival rates within a declining migratory mountain woodland caribou population in Alberta and British Columbia, Canada (Figure 1). First, we tested whether there were changes in migratory propensity for

the population and whether individual caribou changed their migratory behaviour. Second, we tested for changes in the seasonal spatial distribution of caribou over three roughly decadal time periods and examined whether increasing land use change from natural resource development over time in these three periods were correlated with changes in seasonal distributions. We focused primarily on the winter range area as disturbance due to anthropogenic development is less of a concern in the largely protected summer range. Next, we tested whether caribou migrations adhered to discrete identifiable migration corridors that could be used in conservation and recovery planning (*sensu* Berger & Cain, 2014). Finally, we tested whether any identifiable changes in migratory behaviour and space use had impacts on adult female caribou survival.

2 | METHODS AND MATERIALS

2.1 | Study area

The Redrock-Prairie Creek (RRPC) caribou are part of the Central Group of Southern Mountain caribou that were assessed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2014) but which are currently recognized as threatened under SARA (Environment Canada, 2014; see Ray, 2015). They reside in and adjacent to the Rocky Mountains in Alberta and British Columbia (Figure 1). Their range is comprised of low elevation boreal foothills forests containing terrestrial and arboreal lichens, a crucial winter forage, and higher elevation (up to > 3,000 m) alpine areas where caribou typically forage on windswept ridges for terrestrial lichens in winter (Environment Canada, 2014). Much of the alpine and sub-alpine areas used by this population are protected within provincial parks, while the forested foothills are subject to industrial land use, particularly forestry and oil and gas developments, which negatively affect caribou (e.g. Decesare et al., 2012, 2014; Smith, Ficht, Hobson, Sorensen, & Hervieux, 2000). While fire has been shown to have negative effects on caribou behaviour, habitat, and demography through the boreal forest (e.g. Johnson et al. 2020), it was rare in our study area < 2%; see Results). Therefore, we focus on anthropogenic disturbance. For more study area details, see Decesare et al. (2014).

Southern Mountain, Central Group woodland caribou occur along the eastern slopes of the Rocky Mountains, where they annually migrate between forested and alpine areas. Like most other populations of Central group caribou, the RRPC is a partially migratory population, with resident and migratory tactics employed by individuals (e.g., Berg et al., 2019). In the RRPC population, individuals displaying migrant and resident tactics are sympatric on high elevation mountain summer range and allopatric during winter, when migrant individuals move to lower elevation forested foothills and resident individuals remain at higher elevation. Movement to low elevation exposes individuals to higher winter forage biomass and quality (particularly of lichens, a key winter forage, Thomas, Edmonds and Brown 1996), but higher anthropogenic landscape disturbance (Decesare et al., 2014). High elevation resident individuals have reduced access to high-quality for-

age (Thomas, Edmonds, & Brown, 1996) and are exposed to the more extreme and hazardous conditions (e.g., avalanches) found in mountainous environments in winter (Hebblewhite et al. 2010; MacNearney et al., 2016; Alberta Environment and Parks, unpublished data).

2.2 | Caribou data and survival monitoring

We monitored adult female caribou in the RRPC population from 1981 to 2018, a 37-year period. Caribou were captured via helicopter net-gun and fitted with very high-frequency (VHF; 1981–2018) radiocollars to enable aircraft-based relocations (median relocation interval = 15 days) or Global Positioning System (GPS; 1998–2018, median relocation interval = 120 min) radiocollars. Caribou capture and handling methods followed Government of Alberta Wildlife Caribou Committee Class Protocol #8 and were approved by University of Montana IACUC (AUP 059-09MHWB-122209). Captures occurred in fall or winter in both winter (lower elevation forested foothills) and summer (high elevation mountainous) ranges. VHF and GPS collars were outfitted with a mortality sensor that was monitored via aircraft, or remotely, respectively. Our study design for estimating survival followed Decesare, Hebblewhite, Lukacs, and Hervieux (2016).

2.3 | Classification of migratory tactics

VHF and GPS locations were used to assess the occurrence and timing of migration to and from winter (January–March) and summer (June–August) ranges and to classify individuals as employing either 'migrant' (moving between high elevation summer range and low elevation winter range) or 'resident' (remaining in high elevation range throughout the year) tactics. Migratory tactic was assessed over the entire migration year (January to December) for each year an animal was monitored.

We classified migratory tactic using net-squared displacement (NSD) models in the 'migrateR' package in the program R (Bunnefeld et al., 2011; R Core Team, 2020; Spitz, Hebblewhite, & Stephenson, 2017) using a single location/day for individuals that had >20 locations/year to ensure model convergence using NSD. Other individuals' movement trajectories were not suitable for NSD models because of too few locations (e.g. VHF data) or lack of a complete annual cycle (e.g. mortalities, collar failures, etc.). To assess tactic for these latter individuals, we developed decision rules based on successfully NSD classified individuals who showed clear migration movements (Eggeman, Hebblewhite, Bohm, Whittington, & Merrill, 2016; see the Supporting Information). In cases where migratory tactic could not be determined, it was assigned as unknown.

2.4 | Migration tactic trends

We fit Bayesian logistic regression models to estimate the probability of an individual using a migrant tactic as a function of time and to assess

the probability of an individual switching migratory tactic from the previous year as a function of time and the animal's tactic during the current year (*sensu* Eggeman et al., 2016). We included a random effect for individual to account for non-independence of repeated records from the same individual in both models. We fit models using the program JAGS (Plummer, 2003) and the R package 'jagsUI' (Kellner, 2019). For each model, we ran three chains of 10,000 model iterations each and discarded the first 2000 iterations (considered the burn-in period when parameter estimates vary widely; see the Supporting Information for model code). We visually assessed trace plots and posterior distribution plots using the R package 'mcmcplots' (McKay Curtis, 2018) and used the Brooks–Gelman–Rubin statistic to assess model convergence ($\hat{R}$; Gelman et al., 2013).

2.5 | Space-use across seasons and time

We estimated space use during seasonal periods (winter and summer, defined above) and how space use changed over time. First, we estimated the space use of each individual caribou year during the summer and winter (hereafter referred to as an individual-season-year) using Brownian bridge movement models (BBMMs; Horne, Garton, Krone, & Lewis, 2007; Sawyer, Kauffman, Nielson, & Horne, 2009). We implemented these models using the 'BBMM' package (Nielson, Sawyer, & McDonald, 2013) in -program R using a 20-m location error for locations obtained from GPS collars and a 500-m location error for locations obtained from VHF collars. BBMMs produced a utilization distribution (UD) for each individual-season-year where the cell value represented the estimated relative time spent in that cell (670 m × 579 m resolution) between consecutive locations of the individual. We grouped the UDs into three time periods: early-historical (1981–1998), mid-historical (1999–2008), and current (2009–2018). We grouped according to these time periods for several reasons. First, data were collected via VHF collar only through 1998 and the switch to GPS collars, beginning in 1999, provided a natural break point for the earlier portion of the study. Second, these three periods serve as a proxy for variation anthropogenic disturbance intensity; 2008 was the end of a period of high economic activity (during which much disturbance occurred) and was the mid-point of the later portion of our study (after the transition to GPS collars began). For each time period, we combined all seasonal UDs for a cumulative measure of space use across individuals and calculated the 95% volume area for each season, estimating a boundary around the area of 95% of locations for each time period and season (hereafter 95% contour). Bauduin, McIntire, St-Laurent, and Cumming (2016) showed that relatively sparse movement data, such as those collected through VHF telemetry, were successfully employed within individual-based movement models to identify landscape use. Thus, we felt BBMMs generated with data from individuals with VHF collars were comparable to those generated with data from individuals with GPS collars.

Finally, we assessed the extent to which winter range area was impacted by fire and anthropogenic activities (energy and forestry)

across the three time periods of the study using available spatial data. Publicly available data for well sites, mines, pipelines seismic lines, transmission lines, roads, and cut blocks (Alberta Biodiversity Monitoring Institute and Alberta Human Footprint Monitoring Program, 2019) were combined with previously compiled date-time stamped seismic line and road data from previous studies (Decesare et al., 2014). Attribute data were identified for each feature wherever possible to assign a year and/or time period of the initiation of the feature. Each feature was also buffered by 500 m following previous studies that demonstrated indirect habitat loss affected demography of caribou (Johnson et al., 2020). We calculated the total area of impact by each category during each time period, individually and cumulatively, within the early-historical winter range boundary. Additional details on spatial data processing steps can be found in the Supporting Information.

2.6 | Spatial analysis of seasonal migration corridors

We estimated spring and fall migration corridors using locations only from migrant caribou individual-season-years that had an NSD model successfully converge and had more than two observations during the migratory movement (unique individuals $n = 77$, total migration events $n = 155$). We used only locations that occurred within the NSD-estimated start and end date to delineate migratory movements and estimate UDs. We followed the approach of Sawyer et al. (2019) where individual-season-year migration UDs were combined across years and seasons per individual, so that each individual had a single UD surface showing the probability of migratory movement for that individual across the study area (all cells scaled to sum to one). We overlaid all processed migratory UDs to obtain a cumulative probability surface of use during spring and fall migrations over the course of the study period and over all individuals to determine if highly used migration corridors existed. We log-transformed the total and used a threshold of the top 90% of the probability surface to aid in visualization.

2.7 | Survival consequences of migration

We estimated Kaplan–Meier survival for known migration-tactic caribou using the R 'survival' package (Therneau, 2020; Therneau & Grambsch, 2000). Individuals were assigned a fate of alive, dead, or censored for each year that they were monitored following capture. An individual that was not detected for a period greater than 200 days was right-censored and removed from the at-risk pool of caribou after its last known alive location. Previous analyses demonstrated minimal bias in survival estimates with this sampling design so long as fate was known, which functioning radiocollars ensured (Decesare et al., 2016). We tested for effects of migration tactic and time period on survival, corresponding with the time period of differing anthropogenic disturbance intensity (Table 1). We selected the best survival model using

TABLE 1 Impact of fire and anthropogenic disturbance in the Redrock-Prairie Creek population estimated adult female mountain caribou (*Rangifer tarandus caribou*) range, Alberta and British Columbia, Canada, from 1981 to 2018

Time period	Total hectares (and percent) of early-historical winter range impacted by fire during specified time period and cumulative through specified time period	Total hectares (and percent) of early-historical winter range impacted by anthropogenic disturbance during specified time period and cumulative through specified time period
Early-historical (1981–1998)	213 (0.09)	115,881 (50.56)
Mid-historical (1999–2008)	278 (0.12) *491 (0.21)*	110,716 (48.31) *150,927 (65.85)*
Current (2009–2018)	397 (0.17) *889 (0.39)*	26,207 (11.43) *161,319 (70.39)*

*If multiple fires or anthropogenic disturbances occurred in the same location during a given time period, the area of impact was only counted once for the total.

Akaike's Information Criterion (AIC; Burnham & Anderson, 2002) and performed a Cox-proportional hazards test of the significance of the factors influencing survival (Therneau & Grambsch, 2000). Finally, we tested the proportional-hazards assumption of the Cox model using Schoenfeld residuals (Grambsch & Therneau, 1994).

3 | RESULTS

3.1 | Monitoring movement

We monitored 237 unique individuals, obtaining 511,462 locations for 914 individual-years of caribou movement data. Caribou monitored by VHF radiocollars were located, on average, 5.72 times per year (range 1–36 locations). GPS radiocollar use began in 1998; individuals monitored by GPS were located 1653 times per year on average (range 3–6981 locations). In total, locations obtained from GPS monitors accounted for most of the dataset (99.3%, $n = 507,661$).

3.2 | Classification of migration tactic and trends

We classified 638 individual-years (70% of the individual-years) to migrant or resident tactic (GPS $n = 205$, VHF $n = 433$). Of these classified individual-years, 172 had successfully converging NSD models, while the rest of the individual-years were assigned a migration tactic based on decision rules. Migrants accounted for 79.8% of the classified individual-years ($n = 509$). For migrants classified using NSD models, median spring migration start date was May 11 (SD = 30.9) and median spring migration end date was June 4 (SD = 39.7 days). Median fall migration start date was October 7 (SD = 33.5 days), and median fall migration end date was November 15 (SD = 106.3 days). Fall migration generally took longer than spring migration; median fall migration length was 36 days (SD = 120.1 days), while median spring migration length was 20 days (SD = 42.1 days).

The probability of using a migrant tactic decreased significantly with time ($n = 638$, $\beta = -2.90$, SD = 0.488; Figure 2a); the probability at the first year of the study (i.e. 1981) was nearly 1 and decreased to 0.38 by the last year (i.e. 2018). The probability of an individual switching
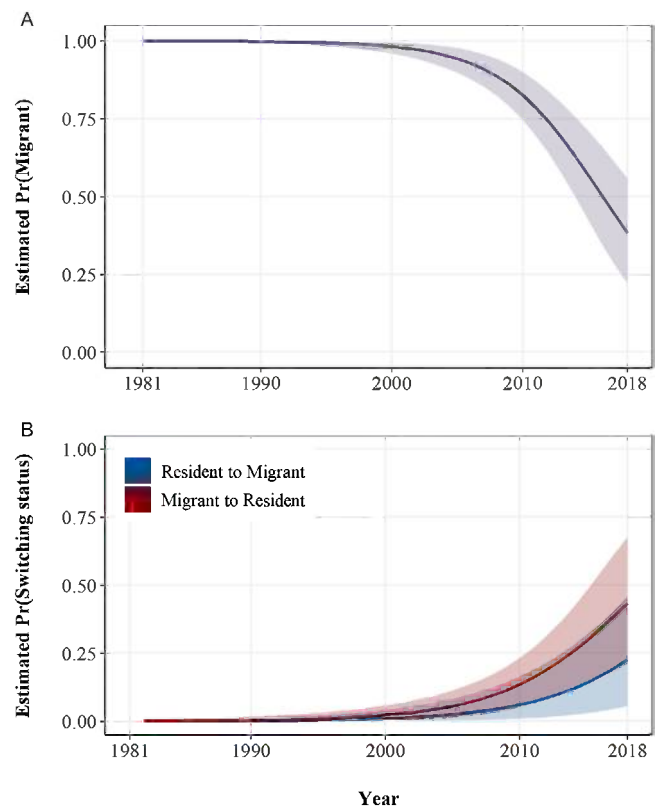
FIGURE 2 Proportion of radiocollared adult female mountain caribou (*Rangifer tarandus caribou*) migrating each year (a) and the proportion of the population switching migratory tactics each year (b) of individuals with known migratory status in the Redrock-Prairie Creek population, Alberta and British Columbia, Canada, from 1981 to 2018. Dark line is mean probability parameter estimate; shaded region is 95% credible interval, which indicates the interval of posterior distribution that contains the parameter value with probability = 0.95

migratory tactics increased over time (Figure 2b). Year had a significant impact on the probability of switching migration tactics ($n = 392$, $\beta = 2.02$, SD = 0.539). A small portion of the posterior distribution for the effect of migratory tactic in year 1 (i.e. starting tactic) overlapped 0; however, 96% of the posterior distribution had the same sign as the parameter estimate mean, suggesting that being a migrant in year
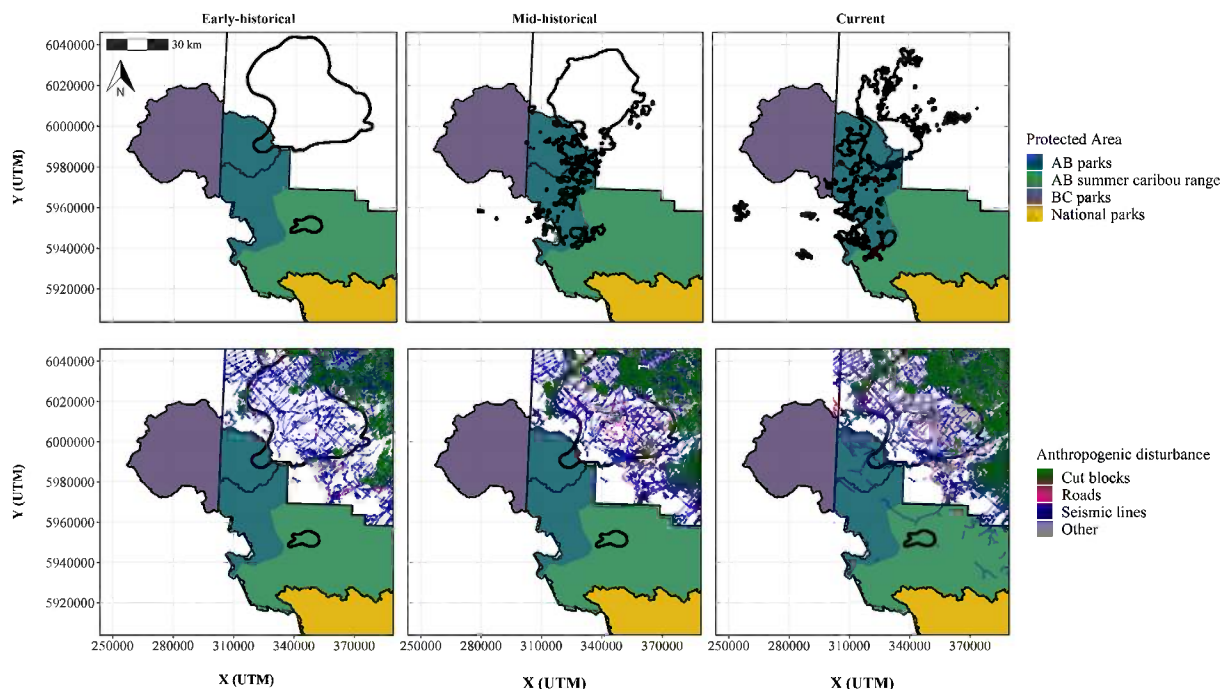
FIGURE 3 Seasonally used winter ranges for Redrock–Prairie Creek radiocollared adult female mountain caribou (*Rangifer tarandus caribou*) derived from cumulative Brownian bridge movement models across three time periods of the study (early-historical 1981–1998, mid-historical 1999–2008, and current 2009–2018; top row) in Alberta and British Columbia, Canada. Polygons represent the 95% contour of combined Brownian bridge movement model outputs for each individual-season-year obtained for winter. Cumulative anthropogenic disturbance across three time periods with early-historical winter range in background compared to winter range boundaries (bottom row)

1 did have a positive influence on the probability of switching migration tactic in the subsequent year ($\beta = 1.011$, SD = 0.617). Diagnostic assessment of both Bayesian logistic regression models indicated convergence ($\hat{R} < 1.1$ for all parameters).

3.3 | Space-use across seasons

We estimated space use for 374 individual winter ranges obtained from 202 individuals; the number of season-year estimates from a single individual ranged from one to five, with the majority being one, two and three season-years from a single individual ($n = 87$, $n = 126$ and $n = 144$, respectively). Few individuals provided four or five season-year estimates ($n = 12$ and $n = 5$, respectively). We estimated space use for 167 individual summer ranges obtained from 114 individuals; the number of season-year estimates from a single individual varied from one ($n = 65$) to three ($n = 12$). Brownian motion variance was similar between VHF and GPS data used to estimate winter space use (mean $\sigma_m^2 = 2842$ and 4466, median $\sigma_m^2 = 615$ and 1838 for VHF and GPS, respectively) and summer space use (mean $\sigma_m^2 = 4544$ and 4861, median $\sigma_m^2 = 2244$ and 2466 for VHF and GPS, respectively).

Estimated winter ranges showed change over the study, in terms of both location and size (Figures 3 and S1). In the early-historical period ($n = 103$), winter space use across individuals was concentrated in the northeastern portion of the study area (i.e. focused within the lower elevation foothills). This period only had VHF monitored individuals

and their locations resulted in a 95% contour encompassing 229,188 ha (Figure 3). The mid-historical period ($n = 133$) 95% contour covered 176,071 ha and demonstrated a southwestward shift. The estimated winter range from the current period ($n = 138$) had a 95% contour that encompassed 115,456 ha. The current period winter range showed that the southwestern shift continued, and a portion of the formerly occupied winter seasonal range was no longer occupied (Figure 3). Only 21% of the total area of the early-historical period winter range, and 38% of the total area of the mid-historical winter range, fell within the boundary of the winter range estimated from the current period.

The summer range during the early-historical period included 28 VHF monitored individual ranges; the 95% contour of the estimated range was 551,995 ha and covered much of the study area (Figure S1, right panel). The area covered by the mid-historical and current time periods was smaller (127,740 and 106,906 ha, respectively). Only 17% of the early-historical range fell within the boundary of the current summer range. -Nearly half (49%) of the mid historical summer range fell within the boundary of the current summer range.

The area delineated by the early-historical winter range boundary impacted by fire was small across the entire study period (Figure 1; Table 1); the total area during a single time period ranged from 213 ha during the early-historical period to 397 ha by the current period, and the cumulative total percentage of the winter range impacted was only 0.39%. Anthropogenic activities impacted a substantially larger area of winter range across all three time periods (Figures 3 and S2; Table 1). Up to the time period from 1981 to 1998, over 50% of
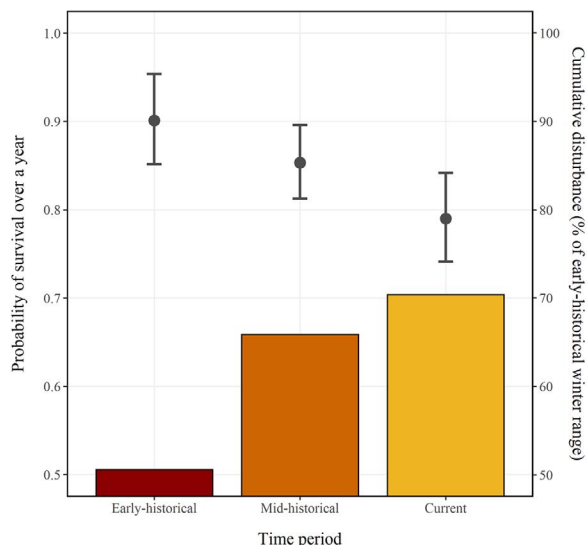
FIGURE 4 Cumulative fire and anthropogenic disturbance in the Redrock-Prairie Creek radiocollared adult female mountain caribou (*Rangifer tarandus caribou*) population in Alberta and British Columbia, Canada, as a percent of the early-historical winter range that is disturbed across three time periods (bars) and estimated probability of survival over a year timespan across the same three time periods (points). Note there was little fire disturbance in our study area (< 2% maximum in current time period)

FIGURE 5 90% cumulative UD for migration movements across spring and fall for individuals that were classified as migrants and had a NSD model that converged and produced parameters for of Redrock-Prairie Creek adult female caribou in Alberta and British Columbia, Canada, from 1981 to 2018. Value of relative use is log-transformed and rescaled from 0 to 1
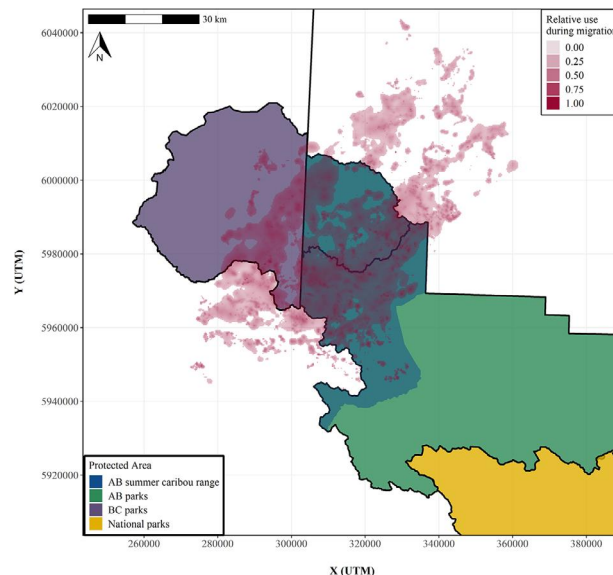
the early-historical winter range (115,881 ha in total) was impacted by anthropogenic development (Figures 4 and S2; Table 1). During the mid-historical period, anthropogenic activities impacted over 110,000 ha, leading to a cumulative total of 150,927 ha disturbed (66%) within the early-historical winter range boundary (Table 1). During the current time period, 26,207 additional ha were impacted by anthropogenic disturbance, resulting in 70% of the early-historical winter range being impacted cumulatively over the study period (Figures 4 and S2; Table 1).

3.4 | Seasonal migration

Migration routes varied greatly across individuals and covered large portions of the winter and summer ranges, as well as intervening areas. The 90% contour of the cumulative probability of all migratory UDs covered 280,266 ha and 53% of the migration area occurred within the interface of summer and winter ranges (Figure 5). These results indicate no discretely identifiable migration corridors were used by migrating individuals, instead pointing to widespread overlap between migration corridors and seasonal caribou ranges.

3.5 | Survival

We recorded fates for 231 known-migration tactic individuals, over 562 individual-years of data. The dataset included 81 mortality events from the 231 individuals. Schoenfeld residuals suggested hazards were

not proportional over time for migration tactic, especially during winter (day 0 [start of January] until day 110 [mid-March]). Thus, we included only models that included time strata, split at day 110, with the migratory tactic covariate. The model including migration tactic stratified by time was the most supported model in our candidate set (Table 2).

Migration had a strong influence on survival. High elevation residents experienced significantly reduced survival compared to migrants (reference level of the migration tactic covariate to which other covariate levels are compared) during winter (for residents during winter: $\beta = 1.77$, Hazards Ratio (HR) value = 5.85, p-value < 0.001, global p-value < 0.001; Figure 5). At day 365, migrant survival probability was 0.862 (SE = 0.017) while resident survival probability was 0.760 (SE = 0.044; Figure 6). However, migration did not influence survival over the rest of the year (reference level for this covariate was migrant during the summer season; for resident during the summer season: $\beta = 0.099$, HR value = 1.104, p-value = 0.0768).

Time period also had an influence on survival. The model including both migration tactic, and time period was the second most-supported model with an AIC < 1 higher than the most supported model (Figure S3; Table 2). For the three time periods, only the current time period was significantly different at the 90% confidence level compared to the reference (reference level of this covariate was the early historical time period; for current time period, Cox Proportional Hazards (PH) $\beta = 0.600$, value = 1.822, p-value = 0.094, global p-value < 0.001). At day 365, the probability of survival during the early-historical period was 0.907 (SE = 0.027), while the probability of survival during the current period at day 365 was 0.810 (SE = 0.028), indicating declining survival over time (Figure S3).

TABLE 2 Candidate model set, AIC values and parameter estimates for Cox-proportional hazards survival analysis of adult female mountain caribou (*Rangifer tarandus caribou*) with known migratory status in the Redrock-Prairie Creek population, Alberta and British Columbia, Canada, from 1981 to 2017

Model	AIC	Covariate	Cox-proportional hazards		
			β	$\exp(\beta)$	SE
Migration tactic: Season	987.99	Resident: Winter	1.766**	5.845	0.428
		Resident: Summer	0.099	1.104	0.334
Migration tactic: Season + time period	988.86	Resident: Winter	1.625**	5.077	0.441
		Resident: Summer	−0.053	0.949	0.881
		Mid-historical	0.480	1.616	0.353
		Current	0.600*	1.822	0.358
Time period	1367.24	Mid-historical	0.424	1.528	0.318
		Current	0.829**	2.290	0.310

** indicates significance at 5% confidence level; * indicates significance at 10% confidence level.
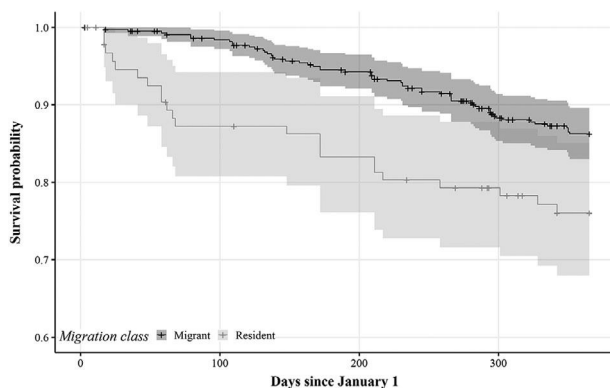
FIGURE 6 Annual Kaplan–Meier survival plots for adult female mountain caribou (*Rangifer tarandus caribou*) in Alberta and British Columbia, Canada, from 1981 to 2017 across migration status in the Redrock-Prairie Creek population

4 | DISCUSSION

Our results provide another example of disappearing migratory behaviour in the world's large ungulates associated with rapid land use change (Berger, 2004; Harris et al., 2009; Wilcove & Wikelski, 2008). We tested for changes in adult female seasonal range use, migration and survival over time in an endangered woodland caribou population. We found that the probability of individuals migrating decreased over time and that the probability of an individual switching between tactics increased over time, especially for individuals switching from a migratory to a resident tactic. Thus, both individual behavioural decisions and demographic consequences drove a decrease in migratory prevalence at the population level. At the beginning of our study, caribou in the RRPC population were predominantly migrants. By 2018, the probability of being a migrant decreased to 0.38. While many studies have assessed migratory trends at the population level (e.g. Berg et al., 2019; Berger, 2004; Spitz, Hebblewhite, & Stephenson, 2020), few explore the relationship between individual migratory tactic and probability of survival, as we have done here. Annual survival differed dramat-

ically between migrant (0.862) and resident adult females (0.760). Corresponding with the increasing proportion of residents through time and the lower survival rates observed in residents, the RRPC caribou population rapidly declined from 1998 to 2012, approximately by 10–14% per year (Hervieux et al., 2013). Consistent with previous studies (e.g. Decesare et al., 2012; MacNearney et al., 2016; Smith et al., 2000), the decline of migration and abandonment of historical winter range that we have documented occurred in concert with rapid anthropogenic habitat loss on the low elevation winter range.

Similar patterns of lost migratory behaviour coupled with population decline driven by land use change on one seasonal range have been seen elsewhere for migratory caribou populations in western Canada and the United States (Hervieux et al., 2013; Johnson et al., 2015). Timber harvesting, oil and gas development and associated road and pipeline infrastructure increase landscape-level habitat disturbance and remove essential biophysical elements of caribou habitat, including mature and old forest stands containing lichens, a crucial winter forage for woodland caribou (Shepherd, 2006; Thomas et al., 1996). Changes to forest age-class structure can negatively affect caribou through apparent competition (Holt, 1977; Serrouya et al., 2019; Wittmer et al., 2007) and expanding road and seismic exploration line networks facilitate increased predator efficiency (DeMars & Boutin, 2017; Whittington et al., 2011), thereby expanding the potential for direct and indirect effects of predators on caribou fitness (reviewed in C. A. Johnson et al., 2020).

Caribou respond to land use alterations through shifts in space use, resource selection and migratory tactics that ultimately lead to indirect habitat loss. Previous studies have often categorized changing migratory behaviour as either due to changes in behaviour or demography. Our results show they are inextricably linked. As a result of direct and indirect habitat loss, and commensurate increases in mortality, reduction in RRPC caribou survival drove population declines (Hervieux, Hebblewhite, Stepnisky, Bacon, & Boutin, 2014). Our results indicate that survival is poorest for caribou employing the high elevation residency tactic, despite that area being largely undisturbed and protected. High elevation dwelling resident mountain

caribou are exposed to lower forage availability (Thomas et al., 1996), harsher weather conditions, and additional mortality from avalanches (Alberta Environment and Parks, unpublished data). Indeed, another nearby high elevation resident caribou population without the ability to migrate to lower elevation range outside a national park (Banff) was extirpated in 2009 by an avalanche (Hebblewhite et al., 2010). The increased mortality risk for high elevation resident caribou, in combination with the growing tendency for animals to switch to a resident tactic, suggest that RRPC caribou are displaying maladaptive selection and therefore falling into an ecological trap (Robertson & Hutto, 2006). Similar studies in the region have comparably showed caribou are, if not 'trapped' into making poor choices, at least ill-adapted to avoid predation risk at landscape scales (Decesare et al., 2014), consistent with our results.

Detection of non-linear thresholds in ecological responses are important to guide conservation and restoration activities for endangered species (C. J. Johnson, 2013). The non-linear changes in both migratory behaviour and survival rates over time suggest the presence of a threshold in anthropogenic disturbance, which is conceptually consistent with recent national meta-analyses (Environment Canada, 2011; C. A. Johnson et al., 2020). For example, based on dozens of mostly sedentary, boreal populations across Canada, adult female survival must be ~ 0.85 with average recruitment rates to sustain viable population growth rate, $\lambda, > 1$ (Environment Canada, 2011; C. A. Johnson et al., 2020). Johnson et al. (2020) showed that when > 35% of an *entire caribou range* was within 500 m of disturbance, populations decline, with growth rate, $\lambda, < 1$ (Environment Canada, 2011). In our long-term study, adult female survival declined below 0.85 sometime during the mid-historical period between 1999 – 2008, corresponding with an increase in anthropogenic disturbance on *just the winter range*. This resulted in loss of migratory behaviour from nearly all individuals migrating to ~ 0.80 of individuals by 2008, and an accelerating rate thereafter to less than 0.30 by 2018. Thus, demographic responses to habitat loss on just one seasonal range (rates of disturbance on high elevation ranges were close to 0%) were indicated by losses of migration early enough that loss of migratory behaviour could offer a useful indicator of population trends for migratory species. This also indicates that seasonal range-specific disturbance thresholds may be different from range-specific targets for resident boreal populations (*sensu* Johnstone et al., 2020). These non-linear trends were also supported by behavioural switching of migratory strategies in response to winter range disturbance (Figure 2).

Many large herbivores can display variable space-use behaviours over time in response to environmental variation. For example, Morrison and Bolger (2014) showed tropical savannah-dwelling wildebeest (*Connochaetes taurinus*) demonstrate partial fidelity between wet season ranges across years in response to variation in rainfall. In our current study, the probability of an individual switching tactics from year to year increased and the trend was towards more switching from low elevation migration to high elevation residency. This asymmetry in switching behaviour between different tactics was similarly reported

for elk by Eggeman et al. (2016), who found migrants more likely to switch than residents because of predation risk refugia on the resident range. The strong directional trend in switching that we documented suggests that weather variation did not drive the loss of this behaviour, as in wildebeest. Instead, we conclude that cumulative land use change on the low elevation seasonal range was responsible for loss of the migratory tactic as individuals sought refuge from increased risk and access to forage (MacNearney et al., 2016). While seasonal range abandonment of this nature has been reported across species and taxa (Dinkins et al., 2017), our study is unique in linking such changes to population performance.

Some migratory species show rigid migratory behaviour with little to no individual plasticity in migratory routes and high consistency across individuals in routes enabling fixed spatial conservation strategies (e.g. mule deer, *Odocoileus hemionus;* Sawyer et al., 2019). For such species, identifying and conserving migratory corridors may help conserve migratory behaviour when anthropogenic disturbance threatens the actual migratory route. However, this not the case for the mountain woodland caribou we studied, which showed a high degree of spatial variation in movement paths between seasonal ranges (Figure 4). Unlike other species, such as mule deer (Sawyer, Merkle, Middleton, Dwinnell, & Monteith, 2019), we did not find evidence for consistently used stopover sites and the area used during migration overlapped with large portions of summer and winter ranges. For the RRPC caribou population, it seems impossible to define areas that are strictly migratory habitat; any narrowly defined routes would not be biologically effective in protecting migration behaviour of this caribou population. This emphasizes the need to broadly integrate seasonal migratory habitat requirements (summer, winter, migratory) into critical habitat delineation.

Land use can differentially impact critical habitat at different times of the year. Habitat disturbance might be concentrated in one seasonal-use area but may be low or non-existent in areas used during other seasons (Dinkins et al., 2017). If disturbance is measured collectively across all seasonally used areas, it may appear that the overall impact level is low. A recovery plan for an endangered species might then assume that the population should be resilient, while in reality, a high level of disturbance in one essential seasonal habitat area could threaten population viability. Our results demonstrate this challenge. During the early years of our study, caribou made wide-ranging use of low elevation areas during winter (Edmonds, 1988). However, especially in the last decade, the traditional winter range was avoided as anthropogenic disturbances increased (MacNearney et al., 2016), and more individuals switched to become year-around residents at high elevation. While provincial and national parks have considerably protected high elevation summer range in our study area, winter range continues to be subjected to forestry and oil and gas development, with associated impacts to this seasonally critical habitat. Similarly across British Columbia, there is disproportionate protection of low-timber value, high elevation habitats, with the same patterns of ongoing land use of high economic value, low elevation caribou winter ranges (Palm et al., 2020). Accordingly, most caribou populations throughout the

Southern Mountain distribution have very low population viability (Wittmer, Ahrens, & McLellan, 2010). Failure to protect all seasonally critical habitats may render protection of other seasonal habitats ineffective for species conservation.

The unique genetics and associated migratory behaviour of these mountain caribou has led to their identification as their own Designatable Unit 8 by COSWEIC, signifying the value of protecting this distinctive population (COSEWIC, 2014). Yet, the very behaviour contributing to the identification of Designatable Unit 8 is being lost due to habitat change on low elevation winter range. As we show here, however, the shift in migratory behaviour to adopt a high elevation resident tactic resulted in decreased survival. Thus, while the change in tactic from migratory to resident behaviour is becoming increasingly common, coincidental with and likely as a consequence of growing anthropogenic disturbance, the lower survival represents an insidious ecological trap (Decesare et al., 2014; Robertson & Hutto, 2006). Reduced use and abandonment of low elevation winter range, and increased winter occurrence in high elevation areas, is a repeating pattern for central group woodland caribou (ASRD and ACA, 2010), ultimately leading to the loss of caribou populations (e.g. Johnson et al., 2015). To ensure effective protection of endangered migratory species, there is an urgent need for conservation and recovery of habitats to support their year-round migratory requirements.

5 | CONCLUSIONS

In our study, habitat change and degradation was concentrated on the low elevation winter seasonal range, resulting in declining survival and population size of the entire population over more than 30 years. It is important, therefore, that effective critical habitat targets be established, and actioned, to enable conservation, restoration and/or protection of each seasonal migratory range for caribou (e.g. Dinkins et al., 2017). For example, critical habitat disturbance thresholds and definitions that apply to the entire caribou range will fail if development is concentrated disproportionately on one seasonal range; and the loss of one migratory component of partially migratory populations may threaten the viability of the entire population, and thus, hinder recovery. Enhanced restoration of degraded seasonal ranges could also, over time, mitigate the current conservation challenge of habitat degradation (e.g. Ray, 2015; Spangenberg et al., 2019). Avoiding further extirpation of migratory caribou will only be possible if the full suite of landscape and habitat requirements for this species are affectively conserved in all seasonal ranges. This approach will be necessary for many other migratory species.

AUTHORS' CONTRIBUTIONS

M.H., D.H., R.S., T.H., M.R. and S.W. conceived and designed the study. D.H., M.R., R.S. collected data. S.W. and M.H. conducted analyses. All co-authors contributed to interpretation and writing.

DATA AVAILABILITY STATEMENT

Processed datasets used in probability of migration, switching, and survival analyses are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cc2fqz652 (Williams et al., 2021). Spatial location data itself (X,Y locations) are prevented from being shared due to their status as threatened /endangered species in Alberta/Canada and legal restrictions on sharing raw location data, and associated third-party data-sharing agreements.

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SUPPORTING INFORMATION

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

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